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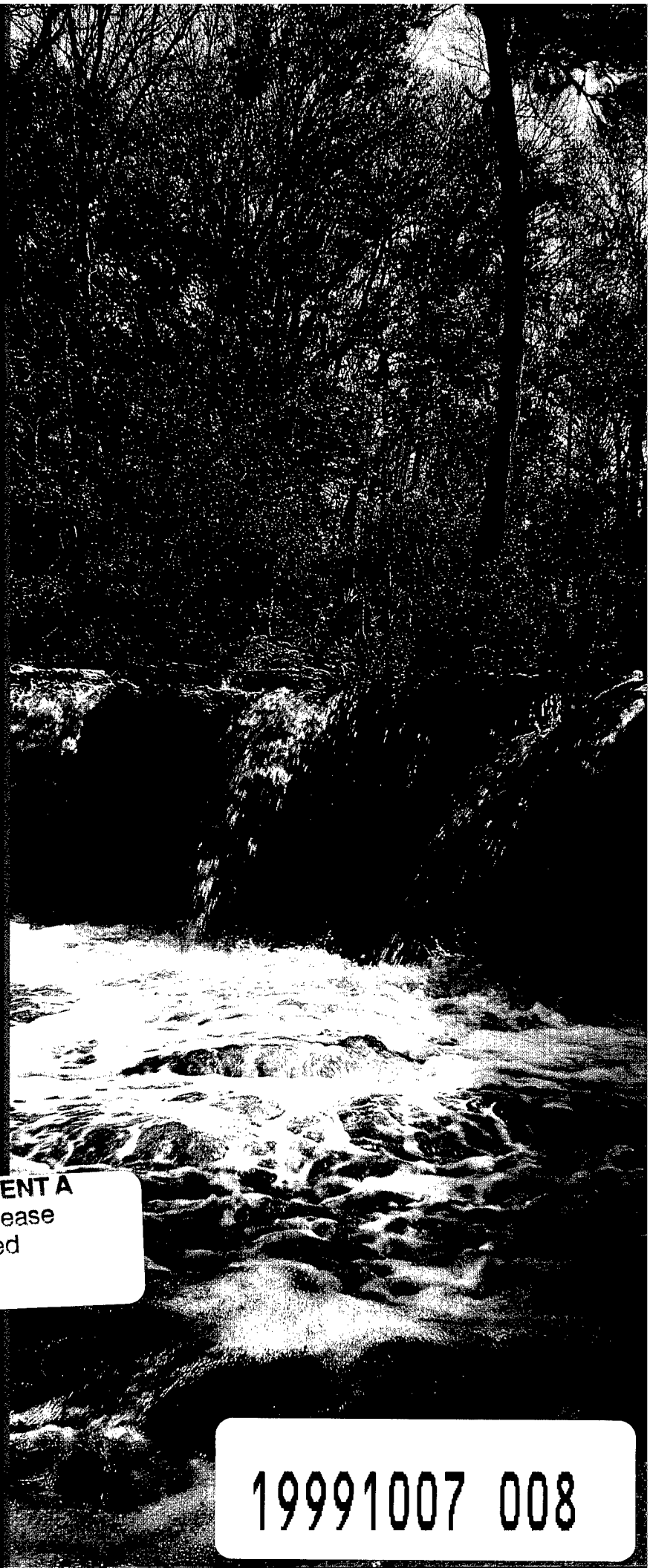
Status and Trends of the Nation's Biological Resources

Volume 1



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Status and Trends of the Nation's Biological Resources

Volume 1

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U.S. Geological Survey's National Wetlands Research Center provided editorial support and project administration.
The Bureau of Land Management's National Applied Resource Sciences Center provided graphic design and production.

U.S. Department of the Interior
U.S. Geological Survey
1998

Library of Congress Cataloging-in-Publication Data

Status and trends of the nation's biological resources / project director, Michael J. Mac; science editor, Paul A. Opler; technical editor, Catherine E. Puckett Haecker; graphics editor, Peter D. Doran. 2v. (xi, 964 p.): ill.; 28 cm. Includes bibliographical references and index.
ISBN 016053285X

1. Biological diversity—United States. 2. Biological diversity conservation—United States. 3. Species diversity—United States. 4. Indicators (Biology)—United States. I. Mac, Michael J. II. Opler, Paul A. III. Haecker, Catherine E. Puckett. IV. Doran, Peter D. V. Geological Survey (U.S.)
QH104.S74 1998
333.95'11'0973—dc21

This publication may be cited as follows:

Mac, M. J., P. A. Opler, C. E. Puckett Haecker, and P. D. Doran. 1998. Status and trends of the nation's biological resources. 2 vols. U.S. Department of the Interior, U.S. Geological Survey, Reston, Va.

The volumes may be cited individually as follows:

Mac, M. J., P. A. Opler, C. E. Puckett Haecker, and P. D. Doran. 1998. Status and trends of the nation's biological resources. Vol. 1. U.S. Department of the Interior, U.S. Geological Survey, Reston, Va. 1-436 pp.

Mac, M. J., P. A. Opler, C. E. Puckett Haecker, and P. D. Doran. 1998. Status and trends of the nation's biological resources. Vol. 2. U.S. Department of the Interior, U.S. Geological Survey, Reston, Va. 437-964 pp.

Foreword

Sound decisions about the use and conservation of natural resources require high-quality, independent scientific information accessible to all who need it. Provision of such information, particularly on the status and trends of the nation's biological resources, is central to the mission of the U.S. Geological Survey's (USGS) Biological Resources Division, formerly the National Biological Service (NBS). This report, *The Status and Trends of the Nation's Biological Resources*, is a major contribution to meeting the nation's need for better information about our nation's living resources.

This two-volume book provides the first large-scale assessment of the health of the nation's plants, animals, and ecosystems and is intended for use by managers, scientists, policy makers, and the general public. It synthesizes existing and new information about birds, mammals, fishes, plants, and other species and summarizes what is known about the status and trends of major U.S. ecosystems. The findings reported here offer valuable insight into both successes and failures in resource management and point the way to better management of biological resources in the future.

The manner in which this report was produced typifies the partnership approach that the Biological Resources Division (BRD) will use to fulfill its mission of providing sound information about biological resources to decision-makers and the public. Information in this report came from state and federal agencies, universities, and nongovernmental organizations; the varied authorship of the articles and chapters in the report reflects this diversity as well. We must and will continue to build on the long history of collaborative efforts in the collection, cataloguing, and interpretation of information about our nation's living resources. The future calls for more coordination and integration, not less.

This report is the second major publication of the BRD's comprehensive inventory and monitoring program and the first in a continuing series of scientific publications that will compile and present status and trends information for use by resource managers and the public. The first publication, *Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems*, was published by the fledgling NBS (LaRoe et al. 1995). With these publications, and with related scientific efforts such as the establishment of uniform standards for collecting biological information, the inventory and monitoring program is well on its way toward meeting its goal of providing scientifically sound, timely, and relevant information—a cornerstone of the USGS—about the health of the nation's biological legacy.

The merger of the National Biological Service with the USGS provides an important context for release of this report. The NBS was created to address the historical fragmentation and agency-specific focus of scientific activities in the Department of the Interior. Merging NBS with the USGS was an additional, critical step in providing unbiased, independent, integrated information about plants and animals, their habitats, and how they are affected by human and natural change. The merger allows integration of biological and physical science perspectives on important natural resource issues, thereby giving us more comprehensive information to support better decisions. With these capabilities, and an ability to communicate complex scientific information to decision-makers and the public, the USGS stands to play an even larger role in supporting natural resource management in the twenty-first century.

Americans value this nation's natural heritage and expect that those who are entrusted with its management will exercise care and make smart, informed decisions. This report and the Department of the Interior can help ensure that we meet that expectation, now and in the future.

Bruce Babbitt, Secretary, Department of the Interior

Acknowledgments

For their instrumental work in envisioning the organization of this landmark report, we thank H. R. Pulliam, former director of the National Biological Service, and others, including G. Frampton, R. O'Malley, M. Ruggerio, T. Sisk, and the late T. LaRoe. We also appreciate the many constructive suggestions and the guidance of G. Farris, co-editor of Our Living Resources: A Report to the Nation on the Distribution, Abundance, and Health of U.S. Plants, Animals, and Ecosystems.

We realize that this report would not have been possible without the dedication, graphic design, editorial work, management, guidance, and good instincts of the following people: T. Charron, G. Farris, M. C. Hagar, and B. Vairin of the USGS National Wetlands Research Center; N. Batik of Pleiades Publishing, and L. Stroh Huckaby of Fort Collins, CO.

Likewise, we gratefully acknowledge others who helped improve the report with information, support, or other work. R. Gregory, and staff including J. Cox, C. Lemos, M. Nichols, E. Rockwell, P. Vohs, and J. Zuboy, provided editing, review, and development of the report in its early stages. For their generous support and for improvement of this project in many areas, we also thank J. Buys, R. Davis, M. Hixon, D. McGrath, S. Price, and H. Turner of the USGS National Wetlands Research Center; L. Barkow, R. Dodd, and M. Kirby of the Bureau of Land Management; and J. Shoemaker, P. Smith, R. Stendell, L. Lucke, and M. Dodson of the USGS Midcontinent Ecological Science Center; D. Morris, formerly of the USGS National Wetlands Research Center; and C. Savitt and his staff at Island Press.

Many photographers, both inside and outside our agency, graciously contributed their original photographs for use in the report. Their names are given in the photo credits in the body of the report. In addition, we appreciate the many publishers, state agencies, universities, and private organizations that allowed us to reproduce figures at no cost to the government.

We also thank the peer reviewers of the chapters and highlight boxes in this report; we believe their insightful comments and reviews help make this report scientifically sound.

Volume 1 Contents

Foreword
Secretary of the Interior Bruce Babbitt v

Acknowledgments vi

Introduction
Peter H. Raven 3

Part 1—Factors Affecting Biological Resources

Natural Processes
Steward T. A. Pickett 11

The Impact of Hurricane Andrew on Louisiana's Coastal Landscape
Glenn Guntenspergen 20
Ecosystem Recovery Following a Catastrophic Disturbance: Lessons Learned from Mount St. Helens
Charles M. Crisafulli and *Charles P. Hawkins* 23

Land Use
Monica G. Turner, Stephen R. Carpenter, Eric J. Gustafson, Robert J. Naiman, and *Scott M. Pearson* 37

Effects of Fire Suppression on Ecosystems and Diversity
John D. Stuart 45

Water Use
Raymond Herrmann, Robert Stottlemyer, and *Laura Scherbarth* 63

Impounded River Systems
Clair Stalnaker and *Dale Crawford* (artist) 69

Climate Change
Stephen H. Schneider and *Terry L. Root* 89

Understanding Climate Change Effects on Glacier National Park's Natural Resources
Daniel B. Fagre 105

Nonindigenous Species
James D. Williams and *Gary K. Meffe* 117

American Chestnut Blight
James D. Williams and *Gary K. Meffe* 121
Eastern and Western Mosquitofishes
James D. Williams and *Gary K. Meffe* 124

Environmental Contaminants
Christopher J. Schmitt 131

A History of Aquatic Toxicology
Mary G. Henry 145
Endocrine-Disrupting Compounds in the Environment
Michael J. Mac 148

Harvest
Thomas D. Nudds 167

Part 2—Regional Trends of Biological Resources

Northeast

William F. Porter and *Jennifer A. Hill* 181

Birds and Landscape Changes in Northeastern Forests
Sam Droege 187

Northeastern Spruce–Fir Forests
Robert S. Seymour 191

American Woodcock
Daniel McAuley and *David A. Clugston* 193

American Black Duck
Jerry R. Longcore and *David A. Clugston* 198

Trends in the Chesapeake Bay Watershed Wetlands
Ralph W. Tiner 201

Status of Living Resources in Chesapeake Bay
Tawna Mertz 204

Coastal Maine: Island Habitats and Fauna
Catherine M. Johnson and *William B. Krohn* 207

Great Lakes

Thomas A. Edsall 219

Habitat Change in a Perched Dune System Along Lake Superior
Walter L. Loope and *A. Kathryn McEachern* 227

Sea Lamprey in the Great Lakes
Carlos Fetterolf 237

Southeast

Peter S. White, Stephanie P. Wilds, Gwendolyn A. Thunhorst, and contributing authors *(John M. Alderman, Matthew Barnett-Lawrence, J. Whitfield Gibbons, Thomas C. Gibson, David S. Lee, Michael R. Pelton, David Penrose,* and *James D. Williams)* 255

Texas Natural History: A Century of Change
David J. Schmidly 264

Environmental Change in South Texas
Duane C. Chapman, Diana M. Papoulias, and *Chris P. Onuf* 268

Caribbean Islands

James W. Wiley and *Francisco J. Vilella* 315

Coral Reefs of the U.S. Virgin Islands
Caroline S. Rogers 322

Reef Fishes of St. John, U.S. Virgin Islands
Virginia Haney Garrison 325

Sea Turtles of the Virgin Islands and Puerto Rico
Zandy-Marie Hillis-Starr, Ralf Boulon, and *Michael Evans* 334

Mississippi River

James G. Wiener, Calvin R. Fremling, Carl E. Korschgen, Kevin P. Kenow, Eileen M. Kirsch, Sara J. Rogers, Yao Yin, and *Jennifer S. Sauer* 351

Coastal Louisiana

James G. Gosselink, James M. Coleman, and *Robert E. Stewart, Jr.* 385

Volume 2 Contents

Grasslands

Fred B. Samson, Fritz L. Knopf, and *Wayne R. Ostlie* 437

Tall-Grass Prairie Butterflies and Birds
Ann B. Swengel and *Scott R. Swengel* 446

Amphibians of the Northern Grasslands
Diane L. Larson, Ned Euliss, Michael J. Lannoo, and *David M. Mushet* 450

Wetland Birds in the Northern Great Plains
Lawrence D. Igl and *Douglas H. Johnson* 454

Waterfowl in the Prairie Pothole Region
Jane E. Austin *456*

Duck Plague: Emergence of a New Cause of Waterfowl Mortality
Milton Friend 458

Population Trends for Prairie Pothole Carnivores
Raymond J. Greenwood and *Marsha A. Sovada* 461

Rocky Mountains

Thomas J. Stohlgren 473

Whitebark Pine
Katherine C. Kendall 483

Limber Pine
Katherine C. Kendall 486

Amphibians of Glacier National Park
Leo Marnell 490

Great Basin–Mojave Desert Region

Peter F. Brussard, David A. Charlet, and *David S. Dobkin,* and contributing authors *(Lianne C. Ball, Kathleen A. Bishop, Hugh B. Britten, Erica Fleishman, Scott A. Fleury, Tom Jenni, Tom B. Kennedy, Ron Marlow, Christine O. Mullen, Mary M. Peacock, Don Prusso, Michael Reed, Lynn Riley, Richard W. Rust, Janice L. Simpkin, Gary Vinyard,* and *Ulla G. Yandell)* 505

Human-Induced Changes in the Mojave and Colorado Desert Ecosystems: Recovery and Restoration Potential
Jeff Lovich 529

Southwest

Michael A. Bogan, Craig D. Allen, Esteban H. Muldavin, Steven P. Platania, James N. Stuart, Greg H. Farley, Patricia Mehlhop, and *Jayne Belnap* 543

A Ponderosa Pine Natural Area Reveals Its Secrets
Craig D. Allen 551

Soils and Cryptobiotic Crusts in Arid Lands
Jayne Belnap 558

Changing Landscapes of the Middle Rio Grande
Michael A. Bogan 562

Rare Aquatic Snails
Patricia Mehlhop 564

Perils Facing the Gila Trout
Steven P. Platania 568

Arizona Leopard Frogs: Balanced on the Brink?
Michael J. Sredl 573

Elk Reintroductions
Craig D. Allen 577

Endemic Mammals of the Henry Mountains, Utah
Michael A. Bogan 580
Southwestern Bats
Michael A. Bogan 581

California

Stephen D. Veirs, Jr., Paul A. Opler, and contributing authors *(David S. Gilmer, David M. Graber, Tim Graham, Laurie S. Huckaby, Mark R. Jennings, Kathryn McEachern, Peter B. Moyle,* and *Rosemary A. Stefani)* 593

Fire and Fuel in a Sierra Nevada Ecosystem
Jan W. van Wagtendonk 609
Torrey Pine
Stephen D. Veirs, Jr. 611
Emerging Diseases in Southern Sea Otters
Nancy J. Thomas, Lynn H. Creekmore, Rebecca A. Cole, and *Carol U. Meteyer* 613
California Abalone
Gary E. Davis 614
Channel Islands and California Desert Snail Fauna
Steven M. Chambers 618
Western Snowy Plovers and California Least Terns
Abby Powell 629

Pacific Northwest

Jeff P. Smith, Michael W. Collopy, and contributing authors (*R. Bruce Bury, Michael A. Castellano, Stephen P. Cross, David S. Dobkin, Joan Hagar, John D. Lattin, Judith Li, Karl J. Martin, William C. McComb, Jeffrey C. Miller, Randy Molina, J. Mark Perkins, David A. Pyke, Roger Rosentreter, Jane E. Smith, Edward G. Starkey,* and *Steven D. Tesch)* 645

Complex Interactions of Introduced Trout and Native Biota in High-Elevation Lakes
William J. Liss and *Gary L. Larson* 659
Spotted Frogs in the Western Pacific Northwest
Kelly R. McAllister 669
Northern Spotted Owl
Eric D. Forsman 672
Wintering Canada Geese in the Willamette Valley
Charles J. Henny and *Maura B. Naughton* 676
Sage Grouse in Oregon
John A. Crawford 680
Translocated Sea Otter Populations off the Oregon and Washington Coasts
Ronald J. Jameson 684
Roosevelt Elk and Forest Structure in Olympic National Park
Douglas B. Houston, Edward S. Schreiner, and *Andrea Woodward* 687

Alaska

David R. Klein, David F. Murray, Robert H. Armstrong, and *Betty A. Anderson* 707

Pacific Halibut in Glacier Bay National Park, Alaska
Philip N. Hooge and *Spencer J. Taggart* 712

Hawaii and the Pacific Islands

Lloyd L. Loope 747

The Effect of Introduced Euglandina Snails on Endemic Snails of Moorea, French Polynesia
Lloyd L. Loope 763

Marine Resources
Loh-Lee Low, Allen M. Shimada, Steven L. Swartz, and *Michael P. Sissenwine* 775

Northeast Region
John B. Pearce, Emory D. Anderson, Kenneth Sherman, John E. O'Reilly, Robert N. Reid, Frank W. Steimle, and *James H. W. Hain* 775

North Atlantic Right Whale
James H. W. Hain 791

Southeast Region
Thomas D. McIlwain 792

Linkages Between Coastal Wetlands and Fishery Resources
Thomas J. Minello and *Roger J. Zimmerman* 796
Bottlenose Dolphins
Robert A. Blaylock, Larry J. Hansen, and *Keith D. Mullin* 804

Alaska Region
Loh-Lee Low, Howard W. Braham, James C. Olsen, Patrick J. Gould, and *Allen M. Shimada* 806

The *Exxon Valdez* Oil Spill
William P. Hines 811
Northern Sea Lion
Howard W. Braham 814

Pacific Coast Region
Bruce B. McCain, Alec D. MacCall, Robert L. Emmett, and *Richard D. Brodeur* 814

Effect of El Niño on the Southern California Bight
Howard W. Braham 815

Western Pacific Oceanic Region
Bruce C. Mundy and *Alan R. Everson* 824

Genetic Diversity of Central Pacific Marine Mammals
Bruce C. Mundy 841

Hawaiian Monk Seal
Bruce C. Mundy 842

National Status and Trends
Loh-Lee Low, Howard W. Braham, James H. W. Hain, Stephen C. Jameson, Steven H. Jury, Mark E. Monaco, Allen M. Shimada, David L. Stein, and *Steven L. Swartz* 844

National Issues and Threats
Loh-Lee Low, Bruce C. Mundy, Bruce B. McCain, Thomas D. McIlwain, Emory D. Anderson, and *Kenneth Sherman* 847

Common and Scientific Names Appendix 869

Glossary 895

Indexes 911

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Introduction

Introduction

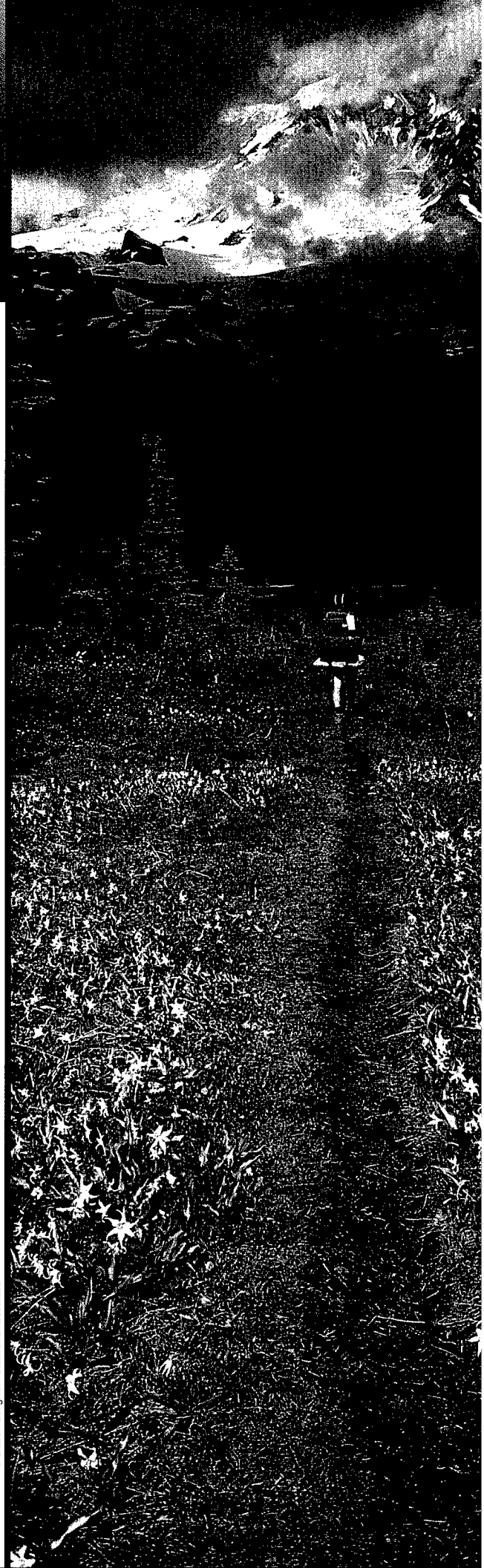
Biological resources are this nation's treasure. Their key attribute is that they are alive, and as living organisms they are, if properly maintained, renewable. They sustain Americans by contributing food, water, fuel, medicine, employment, recreation, and, especially, the splendor and wonder that inspire and nurture our spirits. Use of these resources, whether in consumptive ways such as logging, commercial fishing, hunting, and agriculture or in nonconsumptive activities such as hiking, birdwatching, sailing, and catch-and-release fishing, requires effective management that allows for all these uses and more while assuring that the uses are compatible with resource renewal. But effective management of complex life forms and systems demands scientific understanding.

Even a seemingly innocent hike in the woods has a range of potential effects, most likely minor, on the living resources in those woods. Simple footprints may lead to developing a path, or may even carry the beginnings of a colonizing species foreign to that place. The pathway, though, may halt nature's spread of a native plant, open a corridor for a migrant animal, or enable the first nonindigenous seed or insect to spawn a vast invasion unimpeded by natural controls. In such instances, native species could be in a sensitive stage of nesting or pollination, vulnerable to unanticipated disruption by the newcomer.

Most small, accidental incursions will fail because they occur in places and climates inhospitable to invading species, and most minor damage will have few effects because of the resilience of nature. But anyone familiar with nonindigenous species such as European starlings, kudzu, or zebra mussels knows that the competitive advantages of invaders can overpower their native hosts, particularly in stressed habitats. And we have all lamented the loss of species that could not bear the changes brought about in their habitats by such invaders. But if we understand components of the woods, including its plants and animals, the tolerance of its soils to disturbances such as compression, and what species use the woods for critical nesting habitat, we can effectively manage a resource so it can be enjoyed for generations. In short, our land and its water and the inhabitants of both can usually tolerate some change and survive, remaining vigorous and vibrant, as long as we understand what we are doing to them and how to protect the critical parts of the living, dynamic system they represent.

The use of natural resources is often significantly more intrusive than the passage of a lone hiker, however. Human needs may call for removal of acres of mature trees from a steep hillside that overlooks a stream in which salmon spawn. The logical construction path for a highway may take it directly through a large wetland that shorebirds use as wintering habitat. Our need for simple sustenance provides the impetus for continued removal of thousands of tons of marine life for seafood. In such cases, the scale of both potential effects and the scientific information needed to manage these activities so that a resource will continue to be renewable increases.

Widespread need for the scientific information vital for wise management of our biological resources was the force that influenced Bruce Babbitt, Secretary of the Interior, to establish the National Biological Service (NBS), now the Biological Resources Division of the U.S. Geological Survey (USGS). As one of his first assignments to NBS, Secretary Babbitt asked its scientists to produce a report that would



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provide the first comprehensive summary of the status and trends of our nation's biological resources. The report was to be scientifically accurate but written and presented so that it could inform the general public in straightforward, nontechnical ways. The goal was to synthesize existing information for scientists and resource managers, policy makers, and the general public. If this report, *Status and Trends of the Nation's Biological Resources*, accomplishes its intended purpose, it will be an important contribution to the understanding of the condition of biodiversity on a national scale (see box on Organization of the Report).

A tremendous amount of information on habitats and organisms from each region of the country can be found in these two volumes. The book's authors explore the major factors affecting biodiversity and biological resource health and how these factors affect our regional biological resources or our management of them. For example, the remaining individuals of a species can be so limited in number and by available habitat that a single natural process can dramatically reduce its population, such as the way Hurricane Hugo drastically reduced the numbers of endangered Puerto Rican parrots. An example of how our understanding of biological processes has led to effective resource management is that regulations prohibiting the use of certain contaminants have enabled eagles, ospreys, and pelicans to come back from the brink of extinction across the country. In the Northeast, changes in land use have allowed forests to return in many places, thereby increasing habitat for numerous woodland species. The unhealthy and declining status of so many aquatic organisms in the Southeast is the result of the high degree to which rivers in that region have been dammed, channelized, or negatively affected by activities in the watershed.

Similarly, improved transportation and industrial technologies have not only shrunk the worlds of trade, commerce, and tourism, but they have also removed geographic and economic barriers, sometimes with unintended biological effects. Many nuisance aquatic species, for example, have gained entry to the Great Lakes, causing, in some instances, devastating problems for native species such as fishes and mollusks. Also, atmospheric changes caused by certain industrial technologies have the potential to alter many populations whose ranges are limited by climate and habitat availability and hence cannot "escape" such atmospheric changes.

As you read this report, you will also find examples of resources that nearly collapsed under the cumulative pressure of several factors. For example, lake trout were eliminated from four of the five Great Lakes, surviving only in Lake Superior. These fish succumbed to the pressures of severe overharvest by commercial fishermen, as well as to predation by the sea lamprey, a parasitic nonindigenous species that entered the Great Lakes through the Welland Canal (see box on Sea Lamprey in the Great Lakes chapter). While these two forces were reducing stocks of adult lake trout, the trout's reproductive capacity was greatly compromised by chemical contaminants and degraded habitat. Such relationships among the forces that cause change and the biological resources themselves are themes repeated throughout the report.

This report synthesizes information about the status and trends of America's natural resources, and it represents the combined knowledge of hundreds of experts who served as authors or reviewers. Yet even with the extensive information presented in these chapters, the information available to describe the status and trends of many organisms is extremely limited. The paucity of scientifically credible population data that would enable strong statements to be made about the status and trends of many biological resources is of great concern. It is essential to realize that these data provide more than just information about the health of a particular population or resource. They also provide a basis for assessing the sustainability of biological resources and the effectiveness of current resource management policies and strategies.

Why is there not more known about the status and trends of our biological resources? The federal government spends about $600 million a year on environmental monitoring, but the vast majority of these funds are dedicated to measuring attributes of air, water, soil, and habitat trends. Substantial trend information is only found on birds, some game animals, and commercially exploited species. And much of the information concerning exploited species comes from the harvest activity itself and is not independently measured. Thus, the limited information itself sometimes reflects the biases and limitations of the practitioners. In contrast, the information derived from objective scientific monitoring is not judgmental—it has no preconceived outcomes.

Multiple reasons exist for this dearth of information on the status and trends of animals and plants. Scientifically sound population status and trend information can only be obtained through monitoring programs. Monitoring information is developed *by using repeated measurements at regular intervals over a long time* and *using the same standardized methods to make those measurements*. For monitoring populations, the repeated measure must indicate the relative abundance of target species.

Organization of the Report

This report attempts to achieve Secretary of the Interior Bruce Babbitt's vision of a comprehensive summary of the status and trends of our nation's biological resources. The report describes the major processes and factors affecting biological resources, and it treats regional status and trends. Authors of the chapters and boxes in this two-volume report were drawn from federal and state agencies, universities, and private organizations, reflecting the U.S. Geological Survey's national partnership approach to providing comprehensive, reliable information about our biological resources. Following scientific tradition, each chapter and box was peer-reviewed by anonymous scientific reviewers.

The first seven chapters in Volume 1 describe the *major factors affecting biodiversity and biological resource health.* The aim of these chapters is to promote an understanding of the reasons for the current conditions of resources and the biological and physical relationships among the different parts of ecosystems. The first chapter, an essay by ecologist Steward Pickett, describes in some detail the natural processes affecting our nation's ecosystems. Other chapters in this section cover subjects such as contaminants, land use, water use, nonindigenous species, climate change, and harvest. Yet other chapters—on disease, tourism, management practices, and even politics, for example—could have been usefully added. This report does not dismiss such factors; it offers chapters on those forces that were judged to represent the most significant ones affecting our biological resources.

The remainder of the chapters in Volume 1 and Volume 2 explore how these natural and human-induced factors have led to the *condition or status of regional biological resources*; the chapters also provide information on *biological resource trends.* These chapters are drawn from existing information. Authors were asked to "tell a story" about the regions they describe and to document findings with data. Other than this guideline and a basic outline for the scientists to follow, there were few rules or limitations. Thus, the style in the end product reflects the ideas, the insights, and the great variety of approaches these ecological experts used in each chapter. Their varied emphases also reflect the relative importance of changes occurring in the conditions of biological resources in different geographic areas. The professional insight of these scientists is critically important in the regional chapters because there are so few biological resources for which comprehensive, substantive, scientific status and trends data are available.

Volume 1 ends with a chapter on coastal Louisiana and Volume 2 begins with a chapter on grasslands. At the end of Volume 2, readers will find a glossary, an appendix of scientific and common names for organisms mentioned in the report, and an index to both volumes.

Monitoring must occur at regular intervals for a significant number of years because of the variable nature of animal and plant populations and their sensitivity to a variety of conditions. Short-term monitoring is of limited value because annual fluctuations in populations may reflect such variables as precipitation patterns, temperature regimes, predator populations, or natural cycles. Consequently, long-term trend analysis is essential to reliably separate this natural variability from changes in a population that may require investigation or special management strategies. The frequency and duration of monitoring that is needed to provide usable information on population trends depend on the species being monitored. What may be a significant number of years for monitoring insects that have a life span of a year or less may be a meaningless period for monitoring sea turtles or lake sturgeon, which are species that require decades to reach reproductive maturity. Likewise, some plant species survive hundreds or even thousands of years, which means that generations of human study may be required before we even approach an understanding of the life patterns of these strands in nature's fabric. As with sampling methods, meaningful time periods for monitoring require a thorough understanding of an organism's life history and ecology.

In monitoring, scientific methods must be used that have been technically validated as effective for whatever organism is being monitored and that have been standardized across the program. If methods are improved as technology changes, we must still demonstrate comparability to the old methodology. At present, this characteristic is somewhat limiting because relatively few established methods now exist for accurately monitoring populations. Each organism creates its own set of monitoring problems because of its unique behavior, habitat requirements, or identifying characteristics. In some cases, even taxonomic identification may be problematic, such as when a plant species can only be identified when its flower is present. Much of the national-scale environmental monitoring is conducted by using remote sensing, satellite imagery, or other mechanical systems that enable automated data collection. This type of monitoring, however, is suitable for only a few species of plants or animals because the information such monitoring provides is generally at a landscape level and does not reveal enough about local changes in biological diversity.

Two misguided perceptions perhaps have limited the amount and kind of biological monitoring now conducted. One perception is that such monitoring may lead to overregulation. In reality, however, status surveys and monitoring

have often allayed rather than heightened fears about wild animals and plants, particularly imperiled populations. Although most fears are in response to the possibility of perceived over-regulation, experience has shown, in fact, that the opposite is true: regulations tend to be tighter when the knowledge base is limited. For example, regulations that reduce human health risks often incorporate large margins of safety factors where uncertainties exist. For the most part, wild populations have a tendency to increase both in number and in range. In addition, increased scientific understanding of our biological resources can only lead to proactive management strategies that often prevent the need for further regulations.

A second unfortunate perception is that monitoring is less scientifically challenging than other scientific research, resource management, or any of the technical roles of the environmental scientist. Because of the repeated nature of monitoring activities, the field is viewed by some as being less creative or ingenious, thereby discouraging some scientists from pursuing monitoring in their professional careers.

The need for effective monitoring programs and the information they provide has never been greater. In *A Biological Survey for the Nation*, the National Research Council (1993) proposed a research agenda and identified a number of critical issues that NBS (now the Biological Research Division of USGS) would provide information to address. To achieve preservation of the "nation's biological heritage, . . . extensive information on the current status and trends in distribution and abundance of species" is needed, the report stated. Similarly, the President's Council on Sustainable Development (1996) recommended long-term scientific study to address the loss of biodiversity in this country. The Interagency Ecosystem Management Task Force (1995) recommended that agencies require a monitoring component as an integral part of all ecosystem efforts, that agencies develop common monitoring and evaluation standards, and that policy makers commit the adequate resources to conduct the long-term monitoring necessary for successful management. Such a program, though, must maintain its funding through periods of budget cutting and downsizing while competing with "new" and often more overtly "interesting" scientific ideas. Additionally, the critical need for longevity in a monitoring program mandates that it not rely on a single individual: a monitoring program must be designed to withstand the loss of individual scientists and changes in administrative management.

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Yet even with substantial new investments in monitoring plant and animal populations, we would still only have status and trend information for an extremely small percentage of our nation's species. Fortunately, not all species need to be monitored. Recently, the concept of ecosystem management has gained credibility and favor over a species-by-species management strategy. Because an ecosystem management strategy protects biodiversity of entire ecosystems instead of just select species and their microhabitats, this strategy should be promoted despite the limited number of tools now available for measuring ecosystem health. And although population monitoring information is species-specific, there is a relationship between trends in species—particularly indicator or keystone species—and healthy, functioning ecosystems. Thus, increased monitoring of plant and animal populations is essential to ecosystem management. Monitoring of habitat extent, ecosystem type, and habitat quality also needs to be expanded. Some of this information is available from existing programs; the real lack of information is in organism population trends.

Developing status and trend information on enough species to understand ecosystem dynamics and effectively manage our nation's natural resources is sufficient, but monitoring information must be improved so that it accounts adequately for at least keystone species and representative members of each community and habitat type. Even as this report goes to press, a significant proportion of the freshwater fauna of this country, particularly in the Southeast, is imperiled (The Nature Conservancy 1996), and Hawaii's unique assemblage of species is rapidly being lost: the Hawaiian Islands have lost more than 50% of their birds, perhaps 50% of their plants, 90% of their native land snails, and an unknown percentage of their terrestrial insects (see chapter on Pacific Islands; also see LaRoe et al. 1995).

To be effective stewards of our nation's complex life forms and systems, it is critical to advance our scientific understanding of our biological resources. This report assembles information from thousands of sources and presents the first national synthesis of our knowledge concerning the status and trends of these resources. Because the authors did not have all the scientific information they would have liked for an assessment of this nature, and given the breadth of this report, there will be some missing pieces. Overall, though, I believe this report provides a much-needed summary view of the nation's biodiversity and is an important contribution to our understanding of our biological resources on a national scale.

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Courtesy C. Puckett Haecker

Part 1
Factors Affecting Biological Resources

Natural Processes 11
Land Use 37
Water Use 63
Climate Change 89
Nonindigenous Species 117
Environmental Contaminants ... 131
Harvest 167

Natural Processes

Biological Diversity and Heterogeneity

We had decided to look at an unusual place—an enormous blowdown in the old-growth forest in the Tionesta Scenic Natural Area in western Pennsylvania. Chris Peterson (at that time a graduate student at Rutgers University) and I were visiting Tionesta Scenic Natural Area to see if he would like to conduct the research for his doctoral dissertation there (Fig. 1). I was enthusiastic because it was a rare opportunity to study an intense, natural disturbance in a virgin forest (Peterson and Pickett 1991).

But it might be a tough place to work. It was nearly a day's drive from New Brunswick, and the tornado, estimated to have packed winds in excess of 386 kilometers per hour, had made a jumble of the forest. Many of the largest trees were between 1 and 1.5 meters in diameter and had stood more than 30 meters tall—these were now scattered like pick-up sticks. We had to make our way over the interlocking mass of downed logs; this intermittent, elevated highway of logs was the easiest way to move through the blowdown because the massive crowns of the downed forest giants made a nearly impassible tangle on the surface. The ground surface itself was now punctuated by traps and barriers. Some of the trees were uprooted, and next to the roots were the deep pits from which those roots had been wrenched. If we were lucky, we could see the pits, rather than stepping through a seemingly solid mat of leaves and branches into the soggy hole they covered. Other trees were twisted and broken, and their splintered trunks pointed at the clear blue sky. These snags became our landmarks as we navigated across the 900-meters-wide blowdown (Fig. 2).

In spite of the difficulty of working in the blowdown at Tionesta Scenic Natural Area, Chris agreed that it was a fascinating place, and over the next 7 years we came to understand this stunning place (Peterson and Pickett 1995). The piles of woody debris and leaf litter we poked through during that first visit would prove to be barriers that protected some tree seedlings from hungry deer. The pits would become ringed with ferns and mosses, and many tree seedlings would die on the dry, clayey mounds. Small clusters of American beech sprouts would turn into dense, shady patches where competition would be intense. All of these insights taught us the lesson of Tionesta Scenic Natural Area: the severe tornado of 31 May 1985 set up a patchy template of physical and biological structure, called *environmental heterogeneity*. The heterogeneity interacted with the organisms to determine how the forest would regrow, and the template itself changed with time. That lesson may sound specific to the effects of a tornado in an old-growth forest in western Pennsylvania, but the lesson is general and applies to the entire biological heritage of the United States. The diversity of organisms and of the communities, ecosystems, and landscapes in which they participate is a response to the processes that generate heterogeneity (Wiens 1977; Chesson 1985; Kareiva 1990; Caswell and Cohen 1991; Naeem and Colwell 1991; Tilman 1994). Heterogeneity appears in many guises and is generated by a handful of important ecological processes that operate everywhere in one form or another.

Courtesy National Interagency Fire Center

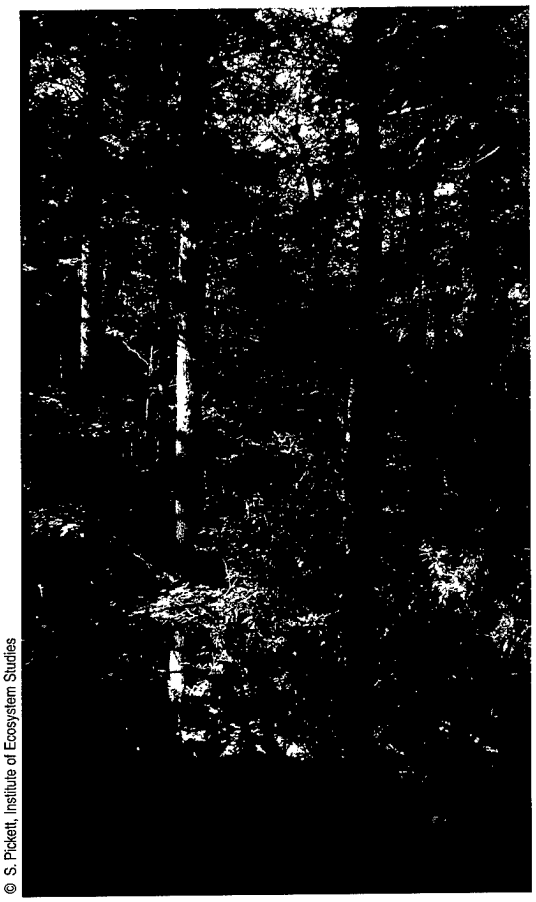

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Fig. 1. The intact old-growth forest at the Tionesta Scenic Natural Area, Pennsylvania. This forest, never cut, is dominated by sugar maple, American beech, eastern hemlock, and several birches.

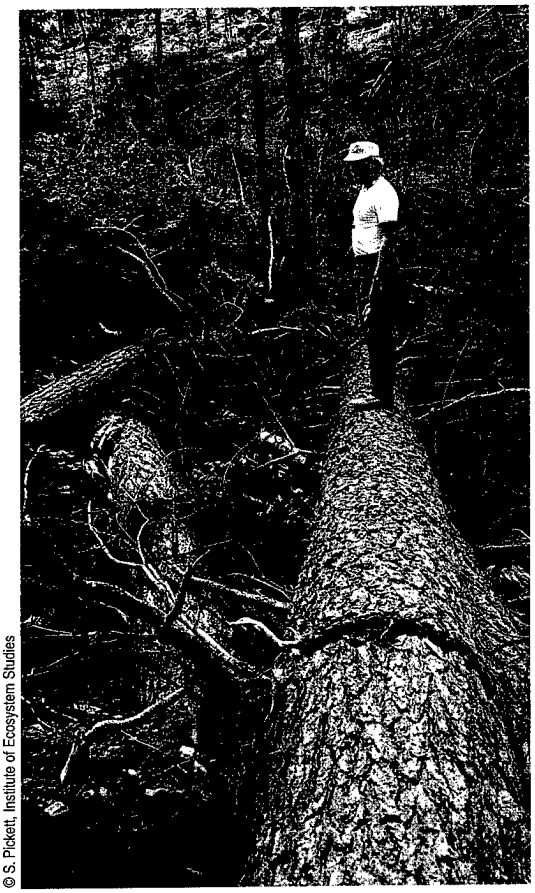

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Fig. 2. The tornado blowdown at Tionesta Scenic Natural Area one year after its creation. Chris Peterson, now assistant professor of botany at the University of Georgia, stands on the downed and broken trunk of an eastern hemlock.

How Do Organisms Respond to Heterogeneity?

Another excursion into a different forest points to the answer. Beneath the patchy oak canopy of the last remaining primary forest in the New Jersey uplands, a population of spicebushes shows one way organisms can respond to heterogeneity (Pickett and Kempf 1980; Kempf and Pickett 1981). Walking from one bush to another, I find myself first in shade then in a bright patch of sun. I sample the leaves and figure out how much woody structure supports those leaves. The different individual spicebushes show markedly different architectural patterns—one has upright branches, reaching high into sunflecks in the forest. The leaves spiral upward around the erect shoots. But in the shadier spots, the main shoots of the shrubs lean over horizontally, and the leaf bases are twisted so that the broad blades of the dark green leaves are spread out in a plane (Fig. 3). The leaves hardly overlap at all, so there is little self-shading within a single plant, an advantage where the light level is only 1%–5% of that available in the open field next to the forest. The striking difference between spicebushes in the shade and those in brighter patches in the same forest is an example of response to heterogeneity. Differences among organisms match the contrasting environments of different patches.

Several kinds of differences among organisms permit them to respond to natural heterogeneity. Perhaps the most fundamental difference is the genetic variety so common among even individuals of a single population of plants or animals (Futuyma 1986). The genetics of an organism affect its capacity to deal with its environment, and the structure and behavior of an organism depend to some degree on its genetics. The genetic reshuffling between generations, the accumulation of mutations over time, and the natural selection among genetically different individuals are basic mechanisms that generate and reinforce inheritable differences among organisms. Of course, genetic variation itself exists in a variety of forms, ranging from the number of alternative expressions of a single gene (alleles at a locus); to differences in the genetic constitution among individuals within a population; to the division of a population into different breeding subunits; to differences between separate populations; and ultimately to the differences among species.

A given genetic type of organism can exhibit different structure or behavior, depending on its environment. The spicebushes, for example, differed in their architecture of branching and leaf display most likely because of individual flexibility, or *plasticity*, rather than genetic

differences between individuals. Although no genetic data are available on spicebush branching, such long-lived individual shrubs are likely to experience years when the canopy above them is thin and other periods when they are in deep shade. Thus, individual flexibility is the key to survival in such situations. In experiments many other organisms have been shown to exhibit genetic differences that relate to differences in environment (for example, Antonovics et al. 1987).

Organisms can also differ from one another in physiology (Bazzaz 1983). For example, the woodland herbs like those that predominate in the intact forest at Tionesta Scenic Natural Area can use low levels of light to manufacture food (Fig. 4), but they cannot tolerate bright light. In fact, full sun for prolonged periods can damage their physiological machinery or can cause them to lose so much water that they may die. In the blowdown at Tionesta Scenic Natural Area, forest herbs that were not protected by the shade of moderate amounts of debris quickly gave way to herbs such as pilewort that need bright light and cannot grow in the closed forest. Contrast in physiological tolerances between organisms of stressed and unstressed environments is common. Tolerance to salt, heavy metals, soil acidity, flooding, drought, and the like are well-known adaptations (Bradshaw and McNeilly 1981).

The timing of events during an organism's life span is another important way it accommodates heterogeneity (Stearns 1976). Contrasts in the life history of organisms appear in the potential length of life, the rate of growth, the time required to reach reproductive maturity, the investment of resources in reproduction, the sizes and number of offspring, and the degree of parental care or provisioning for its offspring. For example, the pilewort in the Tionesta Scenic Natural Area blowdown grows rapidly, matures and reproduces within one year, and produces many small seeds. It is a classic opportunist species that can take advantage of an open site and its resources before slower-growing organisms having lower resource-use rates can take over. Pilewort was shaded out over several years in the blowdown by longer-lived woody plants, some of which may become a part of the future forest canopy.

The most general answer to the question of how do organisms respond to heterogeneity is that they have contrasting capacities to deal with environmental limitations and opportunities. A basic principle of ecology is that organisms have limited amounts of energy that they have accumulated from photosynthesis or from consuming other organisms. They must divide this stored energy among all the functions they must perform, including foraging, growth, reproduction, and defense (Cody 1966; Levins 1968; Tilman 1988). Each organism exhibits a specific way to divide energy among its vital functions, but all organisms face a limit to the amount of stored energy. Each species, or often a subpopulation within a species, represents a different way to solve the universal problem of a limit to the energy that organisms have accumulated. The amount of data required to calculate the stored energy budgets of organisms is immense, but the metaphor that translates this rigorous scientific study into everyday terms is *a jack of all trades is the master of none*. So one key to understanding the processes that govern biological diversity is to appreciate that different organisms vary in their capacities to deal with their environments. Evolution has yielded a diverse array of organisms that differ in their genetic, physiological, and structural means of solving the problem of limited stored energy. What then is the nature of the environmental variety to which this array of organisms responds?

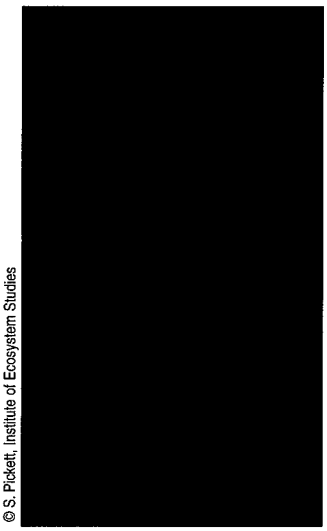

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Fig. 3. A branch of spicebush in the dense shade of a mixed oak forest. Although the leaves are attached to the twig in a spiral fashion, in the shade the leaves adjust to lie in a single plane on the horizontal branches.

Spatial Heterogeneity in the Environment

A walk along a desert hillside is an exercise in contrasts. The rock outcrops at the top of the hill are barren or support only a few shrubs in deep cracks. As I walk down a sunny south-facing slope, the environment changes. Soil appears at the horizontal joints between layers of rock or in potholes (Fig. 5). Deeper pockets of soil support many annuals after the winter rains begin in earnest. The arroyo or streambed at the base of the slope has deep, fine-textured soil and supports many plants; here there are signs of much animal activity. Amid the blooming annuals and the showy perennials in the arroyo, there is the debris of a recent flood. From the riot of wildflowers at the base of the slope, a glance up at the north-facing slope shows a greater number and size of shrubs and denser clumps of flowering herbs in the pockets of soil than on the south-facing slope. Even a small desert watershed shows great environmental heterogeneity (Inouye 1991; Shachak and Brand 1991; Fig. 6).

This desert walk has illustrated the nature of the environment. There are physical aspects, such as the soil and rock, the solar radiation, and the rainfall and flooding. There are also biological aspects (Polis 1993), such as the shrubs and herbs, the animals whose presence may only be hinted at by burrows or tracks during a midday walk, the organic matter accumulated beneath the shrubs, and the almost invisible crust on the soil surface, which is composed of bacteria, cyanobacteria (blue-green algae),

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Fig. 4. White trout lily. Even though this woodland herb of the eastern deciduous forest is active before the tree canopy leafs out, it has a photosynthetic capacity set to accommodate the 30% reduction in light that even the leafless forest canopy can generate compared with open adjacent sites.

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Fig. 5. An accumulation of soil in a pothole of a rocky desert outcrop. Runoff from the rocky area upslope of the soil pocket generates sufficient moisture to support a rich annual and perennial herbaceous community in desert areas with low precipitation. Canyonlands National Park, Utah.

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Fig. 6. A rich desert plant community in a stream valley. Such arroyo communities contrast with the relatively bare valley slopes. Canyonlands National Park, Utah.

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Fig. 7. Cryptobiotic crust in Canyonlands National Park. The apparently bare soil in this photograph is actually covered by a crust of microbes and nonvascular plants. Where the crust has been broken by the soil from the small pit, annual plants have established themselves. Soil crust is common in the deserts of the United States.

lichens, or drought-tolerant mosses (Vestal 1993; Fig. 7; also see box on Soils and Cryptobiotic Crusts in Southwest chapter.) These components of the environment are not uniform over space, even in a small desert watershed. For example, there is less solar radiation on a north-facing slope than on a south-facing one. Rainfall is converted to runoff on the bare, rocky areas, while runoff accumulates in the patches of soil just downslope of the rock outcrops; the arroyo experiences high, even catastrophic, water input compared with other sites in the area (Yair and Shachak 1987). Shade, another example of heterogeneity in the desert, is a rare commodity, found only in small patches beneath shrubs. Rodents burrow beneath only some of these shrubs, and ant mounds show a profusion of green around them. In other words, slowing down to look reveals a rich patchwork in both the physical and biological components of the environment (Polis 1993). Any environment shows such heterogeneity.

These features of the environment exhibit patterns through time as well. Over very long periods, even the rock and soil on the slope change, with periods of greater or lesser erosion and deposition. Some ant species move their nests periodically, and the seeds of annuals find more moisture and richer soil in the burrows that rodents abandon. In some extreme years, the deep soil of the arroyo may be eroded by particularly severe floods.

Environmental heterogeneity as illustrated in a desert watershed can be thought of in two complementary ways: as gradients and patches. Moving down from the crest of the divide to the arroyo takes you along an environmental gradient. Overall, soil depth tends to be greater at the base of the slope than at its top. The probability of runoff accumulation varies along the slope as well. On finer spatial scales, gradients may be observed in the soil moisture from the center to the edge of a pocket of soil in the rocky slope.

Gradients exist in all sorts of environments, not just deserts (Vannote et al. 1980; Austin 1985; Peterson and Pickett 1990; Gosz 1991; Keddy 1991). The climate changes up and down a mountainside, the salinity changes up and down a slope in a salt marsh, the air temperature changes from a field to the intact canopy of a forest, the amount of oxygen declines with depth into the water-saturated sediments beneath a stream, and bog community structure changes with moisture (Fig. 8). Some of these gradients are driven by the physical environment, but others are driven or modified by organisms or their activities. For example, the trees and understory plants along the forest edge modify the air temperature in the forest by altering solar radiation and wind input. Likewise, predators may modify the behavior of a prey organism so that, for example, the distribution and effect of deer are reduced, on average, from a forest edge to the center of a large open field.

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Fig. 8. Gradients of flooding frequency, water depth, and depth of the sphagnum moss mat control the composition and structure of vegetation in this Michigan bog. The gradient runs from the open water in the center of the bog through herbaceous, shrubby, and small tree woodlands. A forest grows in the mineral soil surrounding the lake in which the bog has grown on the expanding sphagnum mat.

Organisms are distributed differentially—or grow and survive differentially—along gradients. This pattern is especially clear when the distributions of related species are plotted in space (Austin and Smith 1989). Different species concentrate on contrasting portions of a gradient. Oaks in the eastern United States, for example, achieve dominance at different points along a moisture gradient. From moister to drier sites, ecologists expect to encounter swamp white oak, northern red oak, white oak, black oak, and chestnut oak (Fig. 9).

Animals also respond to gradients. For example, the peak densities of different rodent

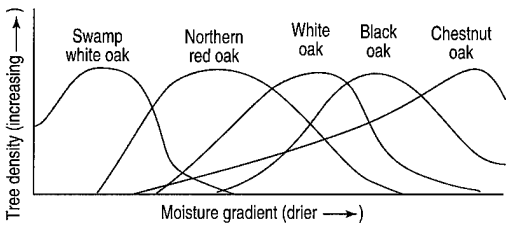

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Fig. 9. An idealized distribution of oak along a slope in the northeastern United States. Although there is considerable overlap in the distributions, the peaks indicate that the species responses differ with habitat conditions (Austin and Smith 1989).

species are displaced on habitat gradients in deserts (Rosensweig and Abramsky 1986), and vole populations respond to gradients of plant cover in fields (Adler and Wilson 1989). Another example of animal response is seen in differential distribution of birds along habitat gradients (Able and Noon 1976) or resource gradients (Fleming 1992). Such differential distribution of organisms on gradients demands that the unique assemblages that appear in each kind of habitat be recognized. A hillside apparently uniformly clothed in green may be in fact a subtle array of different species from top to bottom (Milchunas et al. 1989). A given species will not appear in equal abundance throughout the gradient. In fact, depending on the environmental extent of the gradient and the requirements of the species, it may appear on only a small part of the gradient.

As important and informative as gradients are, there is another important way to view environmental heterogeneity—patches. A patch, in contrast to a gradient, has distinct boundaries and can be readily delimited on a map. A pocket of wet soil in a forest, a rock outcrop on a hillside, and a buffalo wallow are all examples of patches. When one hikes in the Pinelands of southern New Jersey, the view is usually of an open forest dominated by pitch pine with perhaps some bear oaks and an understory of leathery-leaved plants, members of the heath family. In spots, however, a group of darker green, spirelike trees will appear through a break in the pine canopy. In only a few meters, the hot, dry air of the pines becomes cool and moist, and the sandy soil blanketed by brittle pine and oak litter is replaced by a spongy carpet of sphagnum. This quick transition is a patch boundary, and the newly encountered shady patch is an Atlantic white-cedar swamp (McCormick 1979; Fig. 10). In this type of patch the delicately serrated leaves of red maple share the light with Atlantic white-cedar; the aromatic leaves of sweetbay trees are dappled in shade beneath them; and on the edges of the stream snaking its way through the Atlantic white-cedars, the tubular leaves of common pitcher-plants and the sticky, glandular leaves of roundleaf sundews

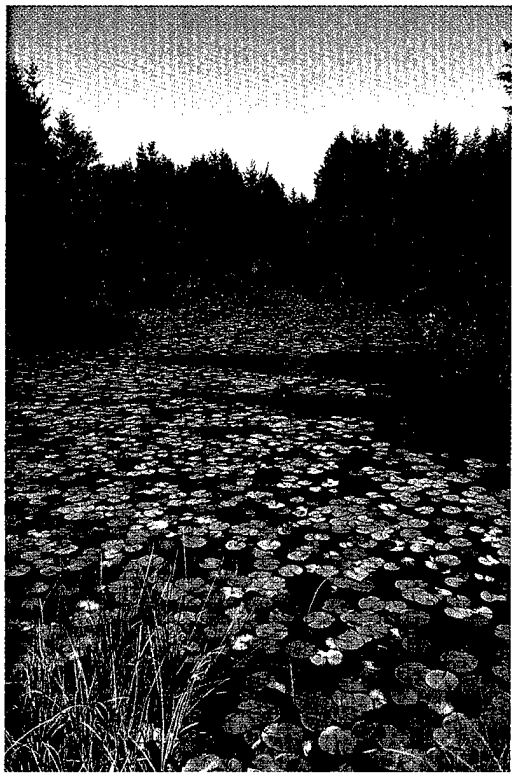

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Fig. 10. A stream running through an Atlantic white-cedar swamp in the New Jersey Pinelands. Atlantic white-cedar swamps are the wet end of the soil moisture gradient in the Pinelands.

await their insect prey (Fig. 11). This quick transition from dry pine forest to moist Atlantic white-cedar swamp illustrates the alternative to gradients as a way to visualize environmental heterogeneity: rapid transitions between contrasting structures or compositions appear on the landscape as patchiness. In the example of the Atlantic white-cedar swamp, a slight slope has brought the water table to the surface, changing the dominant feature of the environment.

Patches can also be formed by biological activity. Tall goldenrod, a clonal plant that spreads by means of branching roots, can create a large clump over a few years from a single stem. Other famous patch-forming clonal plants include aspen (Fig. 12) and sumac (for example, smooth sumac). Animals can form patches too,

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Fig. 11. A roundleaf sundew plant. This species is found in open sections of gradients in Atlantic white-cedar swamps and bogs. Hairs on the spatula-shaped leaves exude a sticky substance that traps insects, which the plant then digests. Nitrogen from such insect prey is a critical supplement to the low amounts of nitrogen available in bogs and many swamps.

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Fig. 12. A patch of quaking aspen in the Rocky Mountains. Aspen clones can form large, dense patches.

by burrowing, trampling, eating, and other concentrated activities (Brown and Heske 1990; Jones et al. 1994; Fig. 13). Animal-generated patchiness appears as beaver dams, coral reefs, mussel beds on rocky ocean shores, prairie dog towns, and others. Of course, animals respond to patchiness as well as create it, and such responses are key regulators of animal populations (Wiens 1984; Ostfeld 1992).

Settled landscapes are patchy at a scale obvious to even casual observers—the old farm woodlot now surrounded by suburbs, the wetland at the edge of town, the clear-cut on the hillside, or the island isolated by the creation of a reservoir (Fig. 14). So patchiness results from the way that human society, as well as organisms, uses landscapes (Forman 1987).

In part, whether you choose to view a single phenomenon as a patch or as a part of a gradient depends on the spatial scale of the data (Allen and Hoekstra 1991). Both viewpoints are valuable and both highlight the fundamental link between environmental heterogeneity and biological diversity. Biological diversity is a response to environmental heterogeneity (Huston 1994). Heterogeneity presents the opportunity for organisms to use different resources, to be limited by different stresses, to respond to different signals, and to interact with differing combinations of other organisms, including those that facilitate and those that limit survival, growth, behavior, and reproduction (Kolasa and Pickett 1991).

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Fig. 13. Patchiness created by animal activity. The mound is an abandoned ant mound surrounded by a ring of enriched vegetation. The photograph is from the Negev Desert, Israel. Similar effects of ants or of burrowing animals such as woodrats and pocket gophers are found commonly in the United States.

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Fig. 14. A low-elevation aerial photograph of abandoned agricultural lands on the grounds of the Institute of Ecosystem Studies in Dutchess County, New York, reveals how human modification of landscapes also results in patchiness. The lines of trees and shrubs indicate stone walls erected as long ago as two centuries to delineate fields and pastures and to accumulate rocks that frost heaved out of the soil of the fields over winter.

The relation between heterogeneity and biological diversity may indicate a fixed and immutable match between organism and environment, but there is great dynamism in the relation. The dynamics of change in the environment, in the organisms, and in the relation between them is another dimension of heterogeneity that helps govern biological diversity.

Dynamics of Communities and Biological Diversity

In 1958, Murray Buell, Helen Buell, and John Small (all of Rutgers University) set up long-term permanent study plots in old fields that had just been abandoned after 200 years of row crop agriculture (Myster and Pickett 1994; Fig. 15). Ecologists had known for a long time that communities and ecosystems change through time, but most of the studies had been based on comparing similar sites of different ages (Pickett 1989).

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Fig. 15. A farm field in Somerset County, New Jersey. The farm of which this field was a part was used continuously from the early 1700's but was abandoned in 1983. Shown here in 1984, the field has since been added to the holdings of the Hutcheson Memorial Forest Center to help buffer the old-growth forest at the center from encroaching suburban development.

The basic fact of succession was not in doubt when the Buells and Small started their study. Indeed, succession is one of the most widely observed and well-accepted phenomena in the natural world (Miles 1979; West et al. 1981; Glenn-Lewin et al. 1992). Many ecologists had observed reasonably directional changes in a wide variety of communities through time (Barbour and Billings 1988). There was general agreement about the cumulative changes in species composition and community structure on sites capable of maintaining generally moderate soil moisture. In the eastern United States, bare soil was immediately invaded by an assemblage of opportunistic annuals and remnant crop weeds. The site then became dominated by

biennials such as asters, short-lived clonal perennials such as goldenrods, shrubs such as sumac, short-lived sun-loving trees such as eastern redcedar (Fig. 16), a red maple woodland and, later (presumably), the mixed oak forests such as those that had blanketed central New Jersey before Europeans cleared the land for agriculture. These trends were clear enough to provide a general understanding of the patterns of succession, and indeed, most of the dynamics of communities throughout the world had been described as a result of comparing sites of different ages to discover the trends through time. For example, the Mediterranean shrublands of the West Coast of the United States change structurally and compositionally following fire, with a conspicuous burst of annuals immediately after the fire. Coniferous forests in Yellowstone National Park after fire yield carpets of brightly flowering fireweed, grasses, and later quaking aspens and, again, the conifers. Hurricanes in New England periodically return the forests to earlier successional stages so that pines precede eastern hemlock and shade-tolerant hardwoods. Floodplain forests are occasionally opened by severe floods to reshuffle the community and allow the emergence of grape vines, poison ivy, and herbs in the understory (Fig. 17). Sand dunes are stabilized by American beachgrass (Fig. 18), which gives way to little bluestem and then to a variety of shrubs and trees such as American holly and beach plum. Even in deserts, small areas opened up by the deaths of shrubs can undergo a cycle of species composition. Ecologists, however, needed to check the assumption that substituting a comparison of spatially distinct, different-aged sites for a study of the changes in a particular site over a long period was valid. In addition they needed to know the details of change from year to year. The only way to satisfy both these requirements was to lay down permanently marked plots and to patiently study them year after year (Pickett 1989; Fig. 19).

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Fig. 16. A 10-year-old-field at the Hutcheson Memorial Forest Center. The herbaceous vegetation is dominated by asters and goldenrods. The evergreen trees in the field are eastern redcedar, and the broadleaved tree is a flowering dogwood. The wedge of dense, darker-colored vegetation in the upper left of the photograph is part of an adjacent older field, with the crowns of the oaks of the old-growth forest showing slightly above the successional trees.

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Fig. 17. A meander of the Big Muddy River, Illinois. Looking down from Pine Hills this southern Illinois river channel is bounded by a dark green flood plain forest of the sort that would periodically have experienced major disturbance from infrequent floods. The annual floods would not open the stand and therefore would not be counted as a disturbance to the entire forest.

The permanent plots established by the Buells and Small have confirmed a generally expected succession trend. There have been significant surprises, however: some species that were expected to be abundant hardly made an appearance. For example, little bluestem is present only as scattered individuals in some fields, not as the uniform cover that turns a warm reddish bronze in fall (Fig. 20). Yet some species expected to appear only later in the succession were present, though not obvious, earlier in the process (Pickett 1982). Some oaks, such as black oak, appeared within the first two decades. Herbaceous species that were common early often persisted for very long periods after they declined from prominence in the fields. This was true for even some early dominants such as the annual, common ragweed. These observations have documented that local trends and community structure are probabilistic or chancy. There is some degree of chance in exactly what species appear and become common at a particular spot. Overall, the species in a succession will divide time (as though it represented other environmental resources) and conditions, just as they divide resources and differentially respond to environmental constraints on spatial gradients (Pickett 1976).

The phenomenon of succession, which occurs in virtually every type of known

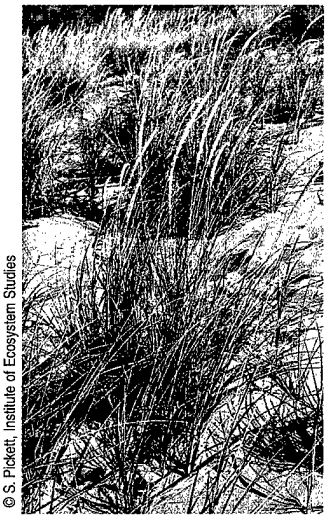
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Fig. 18. American beachgrass colonizing the sand dunes of the southern shore of Lake Michigan. This grass species is usually the first perennial plant to establish on the dunes and thus plays a crucial role in stabilizing the dunes. American beachgrass spreads underground to send up nearby shoots.

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Fig. 19. A sampling frame laid down on permanent plot markers. The plot is one of 480 used in the study of old-field succession started in 1958 at the Hutcheson Memorial Forest Center. The photograph was taken in a 33-year-old field that would have looked like the field in Fig. 15 when it was abandoned.

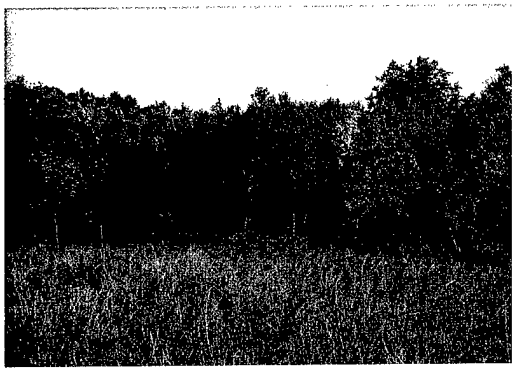
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Fig. 20. Little bluestem in a successional field at the Institute of Ecosystem Studies. This early fall photograph shows the grass beginning to take on the color that gives it its name.

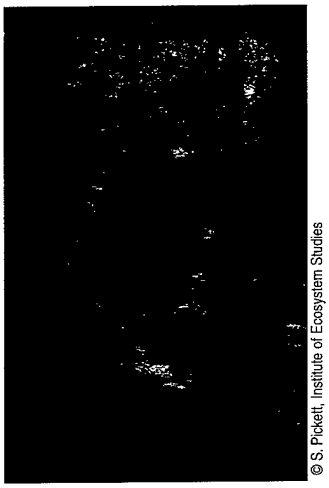
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Fig. 21. A view of the intact forest at Tionesta Scenic Natural Area.

ecosystem, suggests a caution in how we look at the natural world. People seem to have a tendency to view the natural world as static (Johnson 1995). We go to the woods and are impressed by the seeming permanence and stability implied by the massive trees and often by the very quiet and stillness of the air (Fig. 21). We sit at the edge of a waving meadow and remember that every summer we have seen the blossoms of the black-eyed susans and the purple coneflowers nodding in the warm breeze. Or we walk along the rocky seashore and peer into tide pools encrusted with layers of mussels whose armor is tried and tested by the slow-moving sea star. It was like this last year or when we were some idyllic younger age or for as long as we can remember.

We are tricked into viewing nature as static because so many important natural changes are slow and are not obvious in our personal experience over several decades or at the spatial scales we normally examine. It is also based on our ability to avert our view from the surprising to the familiar. Long-term studies of communities and ecosystems and precise measurement of the status of those ecological systems do not permit us these comforting biases, however. When we are forced to look long and precisely, the apparent permanence of the scene is revealed as illusion (Weatherhead 1986). The persistent scene is painted by many processes, some of which are rapidly changing, while others are slow or only periodic in appearance. Sometimes the length of time we must look has to be extended by analyzing pollen; by carefully digging, as an archaeologist would, for clues buried in the forest floor; by skimming the deeds in Dutch colonial land records; by finding a species residing in a location where conditions for its establishment are now absent; by hoping that a study we start in our middle age will be extended by a younger generation. These techniques have revealed the ubiquitous dynamism of ecological systems (Likens 1989).

Interaction among organisms is also a key to understanding biological diversity (MacArthur 1972; Begon et al. 1990; Huston 1994). Such interactions are sometimes cryptic or invisible without rigorous observation or experiments. As we snoop through a meadow with noses close to the fragrant thatch, the tunnels that voles have sculpted in the grass appear. These rodents, kin to lemmings, do not burrow belowground but rather make roofed runways beneath the grass and litter of meadows and grassy old fields. These green subways conceal the voles from predators. Voles eat the vegetation that they encounter in their runways, sometimes sampling newly emerging woody seedlings, whose stems they clip. A new seedling, too young to have set buds, cannot resprout after being damaged, and so the nipped seedlings die. In fields with moderate to high levels of vole density, the percentage of seedlings killed can be immense (Ostfeld and Canham 1993). Therefore, large vole populations can act as a brake on succession of old fields from dominance by herbaceous species to dominance by woody species; it is an important interaction influencing succession but one that is not obvious.

Not all interactions are detrimental to one or both species. Many interactions in nature are in fact mutually beneficial (Boucher et al. 1984). In many ecosystems where conifers and oaks are important, the roots harbor fungi that do several things (St. John and Coleman 1983; Read 1991). The combination of root and fungus produces a new structure, a joint fungus-root (or *mycorrhiza*, from the Greek). The tree provides carbon-based nutrition, derived from photosynthesis, while the fungus transports mineral nutrients and, in some cases, water to the tree. In particular, mycorrhizae are especially effective in searching out nutrients that do not move very much in the soil and transporting them to the plant root (St. John et al. 1983). Phosphorus is the best example of such an immobile nutrient. The fungi that participate in the complex do two things to supply immobile nutrients to plants. First, they metabolically extract the nutrients from the soil very effectively, and second, the tissues of the fungi extend far out into the soil in the form of microscopic threads. This second feature is hinted at when mycorrhizal roots are dug out of the soil. Often small aggregations of soil particles cling to the roots as a result of the net of fungal threads that hold on to them.

The mutual benefits of plants and mycorrhizal fungi are widespread. In fact, most plants are mycorrhizal, although not all have the same form of fungus; grasses, orchids, heath shrubs, oaks, and pines only begin the long list of plant groups that are mycorrhizal.

Mutualism is the general class of interaction represented by the reciprocal benefit of fungus and plant in mycorrhizae. Mutualisms are major contributors to biological diversity not only

because of the obvious benefits that each partner reaps but also because the partners often become specialized to interact. Such specializations can drive diversification among organisms.

Another example of mutualism appears in pollination. Stretched out on my stomach in a grassy field, concentrating on counting herbs for a study of succession, I am interrupted by the loud buzzing of a bumble bee. The bee lands on the flag of a legume flower and deftly opens the two petals that are normally closed over the nectar and reproductive parts of the flower. Only a large insect capable of fine motor control and some learning and that possesses sufficient strength to operate the tricky door to the flower can transfer pollen from flower to flower. Less effective pollinators, such as beetles and flies, that might happily consume the nectar, simply cannot get at it. This mutualism is an example of the kind in which only a certain kind of insect can participate, and the structure of the flower is the key to the restriction (Real 1983; Fig. 22). As with the mycorrhizae, the mutualism is not obvious. The interactions in mutualisms are processes that appear only on close inspection or by using special tools for observation or experiment.

Other interactions take place in the natural world, but not all are as finely targeted as the mutualisms just discussed. In fact, many organisms are involved in some of the most important and widespread processes. An example of a widespread interaction is the phenomenon of decomposition. The decomposition of plant matter—such as the conversion of leaf litter or downed wood—is a key process that depends on organisms most people rarely see (Fig. 23). In a city park woodland, for example, earthworms are especially active in breaking down fallen leaves into smaller bits and mixing them deep into the soil where microbes rapidly turn them into organic matter—that resists further decay—and mineral nitrogen. The litter layer in these city parks is much thinner and more patchy than the litter layer in country forests only a short drive away. Fungi, which are sensitive to pollution and perhaps to the direct disruption of the litter layer in the city, are more active in the country (McDonnell et al. 1993; Pouyat et al. 1994).

What does this difference between the decomposition processes in the city parks and the country forests mean? It is too early to know, but there may be effects on water quality, tree seedling survival, and other organisms that depend on fungi for food. Inconspicuous or hidden processes involving the physical environment and chains of interacting organisms, however, are crucial to the functioning of the world around us. This wisdom has been captured in the concept of the ecosystem (Likens 1992). Organisms exchange nutrients and energy with the physical environment and interact with one another by exchanging nutrients, by transferring energy processed and stored in their tissues, by altering one another's behavior and structure, and by generating by-products and structures that become habitat for other organisms. The interactions are patchy in space and involve soil, air, and water, influencing the flows and quality of these physical components of the world. All these factors are tied together in an ecosystem—a web of processes, fluxes, and interactions. Defining an ecosystem as an interacting community and the physical environment with which it exchanges energy and matter—although correct—needs to be embellished with the reality of actual interactions seen in bumble bees and legumes, earthworms and leaves, bacteria and nitrogen, and rain and soil. The definition of an ecosystem is one of the liveliest in biology, and the interactions in ecosystems are a key to biological diversity (Schulze and Mooney 1993).

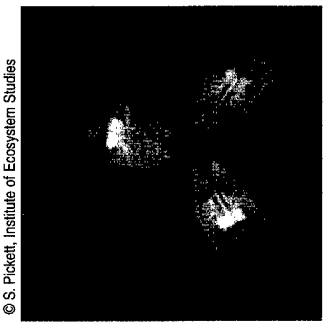

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Fig. 22. A dwarf crested iris. The view is directly downward and shows the conspicuous markings that help orient large bumble bees to the flower, which has a structure that they must manipulate in a particular way to retrieve the flower's nectar reward. Red River Gorge, Kentucky.

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Fig. 23. Fruiting bodies of wood-rotting fungus. These mushrooms emerged from an old downed log at Tionesta Scenic Natural Area. Note that one of the mushrooms has been partially eaten, undoubtedly by the mollusk that left the mucus trail on the log just above the damaged mushroom. Recycling of nutrients can sometimes be directly from dead organic matter through fungi to animals.

Disturbance and Episodic Events

The controls on biological diversity discussed previously are not all obvious, but they generally are continuous. Even ecologists have missed or undervalued some key processes, however, because these processes do not act all the time. Periodic natural disturbances and episodic events became widely recognized ingredients in the recipe for biological diversity only in the past two decades (White 1979). Understanding their effect has required that ecologists look at systems over long periods and give up the assumption that the controls on system structure and organism growth and behavior have acted uniformly through time (Pickett and White 1985).

The Impact of Hurricane Andrew on Louisiana's Coastal Landscape

Hurricanes have long affected the Atlantic and gulf coasts of North America. Return times (how frequently a hurricane strikes an area) can average from 5 to 20 years along the northern gulf coast, depending on location. Hurricanes are widely viewed as destructive agents responsible for the loss of human lives and economic disruptions, but their impact on natural ecosystems is poorly known. On 26 August 1992, Hurricane Andrew made landfall along the south-central Louisiana coast with sustained winds of 54 meters per second (about 120 mph) and a storm surge of 1–2 meters, making it one of the more powerful storms to hit the gulf coast in recent memory (Fig. 1).

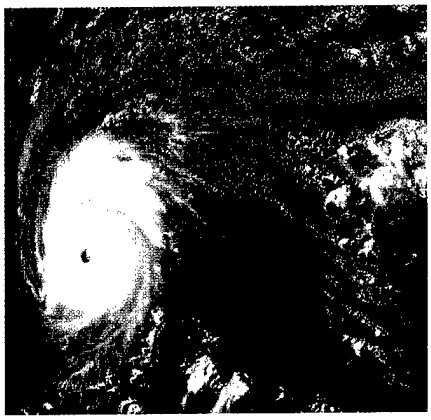

Fig. 1. Satellite imagery of Hurricane Andrew over the Gulf of Mexico.

Coastal Wetlands

Louisiana's coastal marsh ecosystems contain 40% of the coastal wetlands found in the United States and are the result of geomorphic processes linked with the formation and degradation of deltas associated with the Mississippi River (see chapter on Coastal Louisiana). Plant species are distributed along dominant gradients of salinity and elevation, which result in broad zones of saltwater, brackish, and freshwater marsh paralleling the coast. Previous investigations in these coastal marshes have shown intrusion of saltwater, flooding, herbivory, and disturbance as dominant variables controlling plant species richness.

Storms such as Hurricane Andrew are part of the evolution of coastal systems. Hurricanes help form and alter the shapes of coastlines and play a role in maintaining plant species diversity. Fresh and brackish marshes along the Louisiana coast appear structured, in part, by the infrequent and intense salt-intrusion events associated with hurricane storm surges. Coastal wetlands in Louisiana are also increasingly at risk from various natural and human influences. Louisiana leads the nation in wetland loss, averaging some 65.6 square kilometers lost each year. Since the 1930's, the state has lost an estimated 3,950 square kilometers of coastal wetlands; this represents 80% of the nation's total coastal wetland loss. Subsidence, sea-level rise, human activities, and erosion caused by storms have all been implicated in these high rates of loss. A storm such as Andrew can result in a year's worth of loss in a single day.

Physical damage to coastal wetlands was evident following the passage of Hurricane Andrew. Sediment overwash, ripped and torn marsh, erosion of pond and lake margins, wrack (large amounts of plant debris) deposition, and lateral compression of marshes were common. Substantial sediment deposition was associated with the passage of the storm resulting, in some cases, in the burial of the prestorm surface and smothering vegetation. Extensive areas of marsh were pushed against firm barriers (for example, levees and firmly grounded marsh), resulting in a ridge and trough pattern with ridges 60–200 centimeters higher in elevation than the surrounding marsh surface. Areas of wrack completely buried the vegetation. Freshwater marsh species exposed to water half as saline as seawater (10–15 parts per thousand) were "burned," and the aboveground portions of these plants were killed. In scoured areas, unconsolidated or weakly rooted marsh was eroded.

No sites were without some impact. Sites that received some sediment but not enough to bury the dominant vegetation were least impacted. Hurricane Andrew created a heterogeneous landscape with different disturbance patches juxtaposed in complex configurations. These disturbance patches represented habitats for uncommon and less widely distributed plant species to invade. The relative abundances of species in the different disturbance patches also changed. Differences in vertical elevation (height above the water surface), the amount of organic material, and the amount of new sediment surface created complex gradients of soil moisture, salinity, and nutrient availability.

Marsh Vegetation

Vegetation loss and initial recovery differed in areas with different types of storm damage. At sites where prestorm data were available, one was able to see how Hurricane Andrew caused changes in the composition of the vegetation. In 1991, before the hurricane, 20 species of angiosperms were present at these sites, which were dominated by salt meadow cordgrass and American bulrush. The dominant species were distributed broadly throughout the marsh, with salt meadow cordgrass generally more abundant than American bulrush. Permanent plots sampled in 1991 before the hurricane differed in plant species composition from the same plots sampled in 1992 after the hurricane, and were different still when sampled again in 1993. Total plant cover decreased sharply in all damage categories except compressed marsh sites. The surface of the compressed marsh was elevated, creating drier and nonflooded habitat. Plant cover increased significantly there. There was, however, a shift in species composition from a community dominated by perennial grasses to one dominated by forbs (Fig. 2). Areas smothered by thick sediment deposits were quickly recolonized by short-stature wetland species, such as small spikerush, but later developed a dense plant cover as taller species became established. Plants were very slow to colonize wrack-covered areas because the wrack had to decay or be removed before plants could grow through the debris. Significant numbers of species did not become established until late in 1993. By October 1993, most damage types showed comparable levels of total plant cover except for the wrack sites. Scour areas were generally devoid of vegetation and represent permanent marsh loss. Areas where the aboveground parts of plants suffered from salt burn and died back simply regrew within weeks after the storm.

Individual plant species responded differently to Hurricane Andrew. Coverage of the dominant species showed quite different responses to each disturbance type (Fig. 3). The compressed sites were dominated by salt meadow cordgrass and creeping waterprimrose with only modest amounts of American bulrush. In contrast, wrack areas showed a slow recolonization by salt meadow cordgrass and creeping waterprimrose. Areas of thick sediment showed a strong

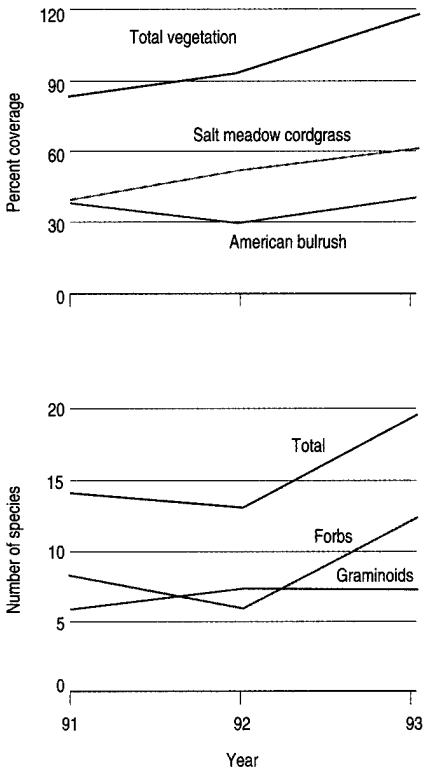

Fig. 2. Data from transects established before Hurricane Andrew at Otter Bayou, Louisiana; these transects were later located in areas of compressed marsh. Data points from 1992 are from after the hurricane. The upper figure presents data for the total percent coverage of vegetation as well as data for salt meadow cordgrass and American bulrush. The lower figure presents data on the total number of species, the number of graminoids (grasses, sedges, and rushes), and the number of species of forbs (other herbaceous species).

recolonization by salt meadow cordgrass, American bulrush, salt marsh camphor-weed, and small spikerush. Least-impacted sites were characterized by nearly equal amounts of salt meadow cordgrass and American bulrush, with lesser amounts of salt marsh camphor-weed and creeping waterprimrose. Compressed marsh also provided habitat for terrestrial weeds uncommon in the coastal wetlands, and because the soils were not waterlogged, these sites may ultimately provide habitat for woody shrubs and trees more commonly found on the tops of levees.

Perhaps as important as the habitat heterogeneity created by the storm is the effect on sediment supply to coastal wetlands. Hurricanes represent an important mechanism by which coastal wetlands cut off from normal riverine sediment supplies may receive significant amounts of sediment that might partially offset the effects of coastal subsidence and marsh deterioration. Along much of the Louisiana coast, sediment accretion rates are often insufficient to maintain the elevation of the marsh surface relative to sea level. Although Andrew deposited sediment along large areas of the coast, these accumulations varied. Areas closer to the path of the storm and near a ready supply of sediments accumulated more sediment than areas distant from the track of the storm or from a sediment supply. The thickest sediments ranged from 10 to 16 centimeters and were deposited in marsh areas corresponding to the northeast quadrant of the storm track as it passed near the sediment-rich Atchafalaya River and delta. As the storm passed the delta, the accompanying storm surge mixed these sediments into the water column and deposited them onto the marsh surface. The hurricane-deposited sediments corresponded to a 100%–200% increase over prestorm deposition rates.

Barrier Islands

Andrew's impact was not confined to coastal wetlands. Barrier islands are the outermost land exposed to hurricanes and often lose significant areas of beach and marsh to erosion. Storm waves associated with tropical storms continuously alter the shape and profile of these islands. On some islands, up to 68 meters of beach were lost to erosion and significant overwashing and deposition of sand on back barrier wetlands occurred. Recent photo interpretation has documented that between 1990 and 1992 (after Hurricane Andrew passed near them), the Isle Dernieres barrier chain lost 30% of its land area. This is particularly devastating because over the past 130 years, nearly 78% of the land area in the Isle Dernieres chain had already been lost. Overwash and sand movement also damaged many island plant communities. Because plants on barrier islands are generally adapted to sand movement and salt spray, it is not surprising that despite burial by sand and exposure to saltwater, the vegetation on these islands is recovering. Changes in elevation caused by the movement and accumulation of sand, however, resulted in varying environmental conditions and a redistribution of plant species on the landscape.

Hardwood Forests

Hurricane Andrew diminished in strength after making landfall. The storm, though, passed through the Atchafalaya basin with sufficient force that more than 450 square kilometers of forested wetland were put at risk. This area contains 35% of the remaining bottomland hardwood forest and swamp forest of the Lower Mississippi floodplain. The impact of Hurricane Andrew on this forested landscape varied greatly with forest type, canopy structure, topography, and location relative to the storm's path. Most of the initial loss of tree density and canopy was restricted to bottomland hardwood forest. Stands lost between 10% and 60% of their basal area (the cross sectional-area of their trunks). Willow trees were particularly susceptible to damaging winds and in certain sites more than 85% of them were toppled. Surprisingly, baldcypress and tupelo trees were largely unaffected except for the loss of an occasional branch. The recovery of the forest will depend on the previous forest cover, the type of damage, the specific environmental conditions created, and availability of seeds and seedlings. Understory trees and saplings were unaffected by the hurricane despite the loss of canopy trees. These survivors will grow rapidly because of the removal of the

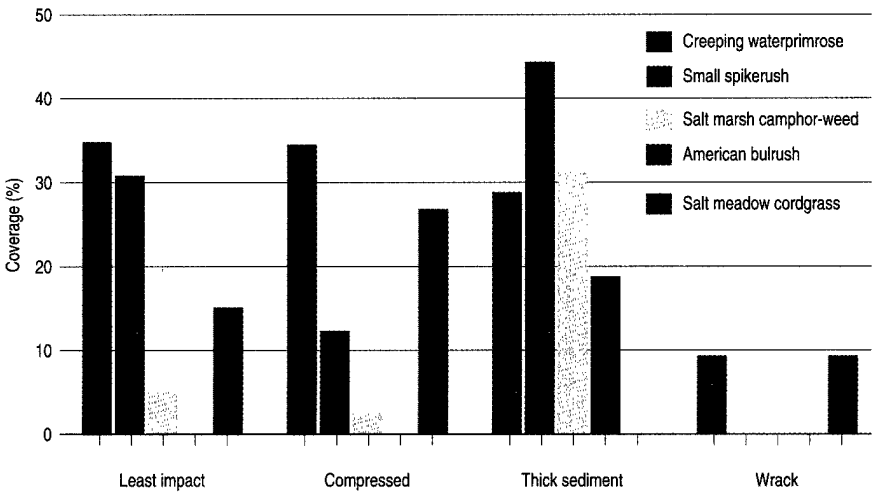

Fig. 3. Data from plots established after Hurricane Andrew struck coastal Louisiana. Species cover in 3 x 3 meter plots varied according to the type of damage sustained. See text for an explanation of categories.

canopy, which shaded them and suppressed their growth. In other cases, seeds and new tree seedlings will become established and form the new forest.

Hurricanes are a major factor affecting coastal ecosystems along the northern Gulf of Mexico. Not only are they responsible for habitat loss, but their frequent landfalls also create a mosaic of different disturbed areas resulting in a heterogeneous landscape. The plant communities that develop in the different patches are dynamic and respond to changing environmental conditions resulting from disturbance. Louisiana's coastal ecosystems are increasingly at risk from human activities. Most climate models predict a period of increased hurricane activity and a tendency toward stronger storms as we approach the new century. Continued research and monitoring are needed to determine the extent to which these ecosystems will become more vulnerable to disturbance from hurricanes.

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When I walk in an old-growth forest on a calm day, absorbed in the soft murmur of the wind in the leaves of the canopy 30 meters above and the quiet chatter of a flock of small birds, it can be a soothing experience for me. It is easy to believe that these oaks and eastern hemlocks, which have stood here for hundreds of years, are virtually eternal and the forest changeless. Suddenly, though, I freeze at the sound of an immense rumble and crash somewhere else in the forest. The reverberation is substantial enough to be felt as much as heard. It is a rare sound in the forest, and worth investigating. It was caused by the fall of a huge, old, hollow oak. The delicately lobed leaves that were exposed to the bright sun just moments before and now lie in partial shade suggest a story. Looking around the forest, I am reminded of the other, older light gaps in which seedlings of birches and red maples reach upward, spring flowers proliferate, and insects swarm. Some of the gaps appeared after violent thunderstorms or the high winds of a hurricane or after an early heavy, wet snow storm that came while the broad-crowned deciduous trees still held their leaves. These events have left downed logs scattered about the old forest floor (Fig. 24). Some of these logs end in the partially filled pits and eroded mounds where the roots were wrenched from the soil (Goodlett 1969; Fig. 25).

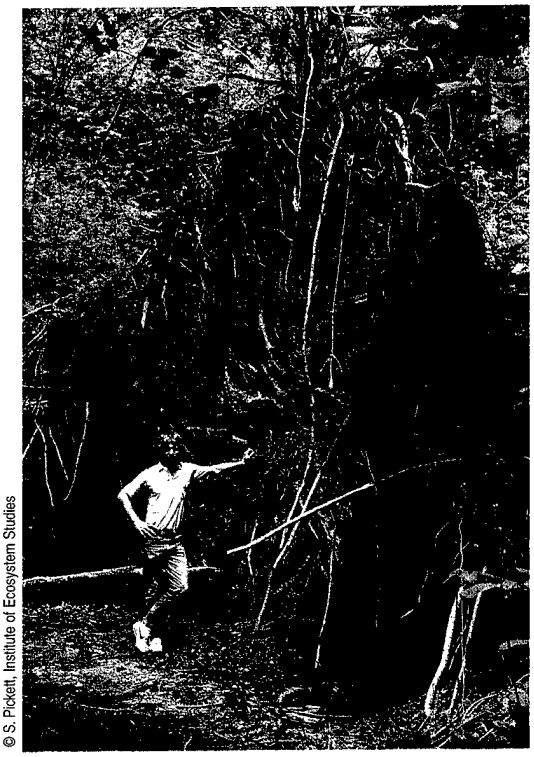

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Fig. 25. Wetlands and restoration ecologist Mark Gallagher stands by an upturned root mat of a downed magnolia in a forest on the inner Coastal Plain of New Jersey.

The old forest shows the work of natural disturbance. A disturbance to a community such as a forest is a sudden event, usually driven or started by some outside force that disrupts the community structure and alters the resource levels and environmental conditions at particular spots in the community (White and Pickett 1985). A fire, for example, disrupts the structure of a prairie by burning off the aboveground parts of the grasses, consuming the litter, and perhaps killing any invading trees and shrubs (Collins and Wallace 1990). Light, temperature, and nutrients are all changed by the event, and organisms respond to the changes. The surviving grasses begin to grow earlier in the next season, taking up nutrients deposited in the ash. Grazers may preferentially visit the new growth in the burned patch. Some relatively sedentary insect populations decrease for a time after the fire.

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Fig. 24. A large canopy gap in an old-growth forest in the Great Smoky Mountains National Park. The large, broad-crowned American beech was snapped off by severe winds, suddenly exposing a large area on the forest floor to a highly altered environment.

USGS
science for a changing world

The Status and Trends of our Nation's Biological Resources

EXECUTIVE SUMMARY

The Status and Trends of Our Nation's Biological Resources is a report that synthesizes current information on status and trends of biological resources with a historical perspective of ecosystems across the country to assess how the nation's resources are changing. The report was produced by the U.S. Geological Survey's Biological Resources Division with contributions from nearly 200 experts from federal government, academic, and nongovernmental communities, including a section on Marine Resources written by the National Marine Fisheries Service. The 1,000-page, peer-reviewed, full-color, two-volume report is written in non-technical language to be usable by policy makers and interested citizens as well as natural resource professionals.

The report is organized into two parts. Part One details seven major factors affecting biological resources nationwide: Natural Processes, Land Use, Water Use, Climate Change, Nonindigenous Species, Environmental Contaminants, and Harvest. Part Two describes the status and trends of biological resources in different regions of the country, the ecosystems in that region, and how these resources have been affected by the factors described in Part One. The regions covered are the Northeast, Great Lakes, Southeast, Caribbean Islands, Mississippi River, Coastal Louisiana, Grasslands, Rocky Mountains, Great Basin-Mojave Desert, Southwest, California, Pacific Northwest, Alaska, Hawaii and the Pacific Islands, and Marine Resources.

Part 1: Factors Affecting Biological Resources

Of the seven factors detailed in the report, six are human-induced and one, natural processes, covers natural events such as fire, hurricanes, and even precipitation extremes that induce changes in physical habitat. These natural processes, when not extremely severe or highly regular in their occurrence, can promote biodiversity by varying physical habitat. Hurricanes can provide some benefits to ecosystems by distributing sediment to coastal wetlands. Similarly, biological populations can respond surprisingly fast in areas devastated by volcanos (Fig. 1).

Land use, water use, and nonindigenous species are the three factors that have had the greatest broad-scale effects

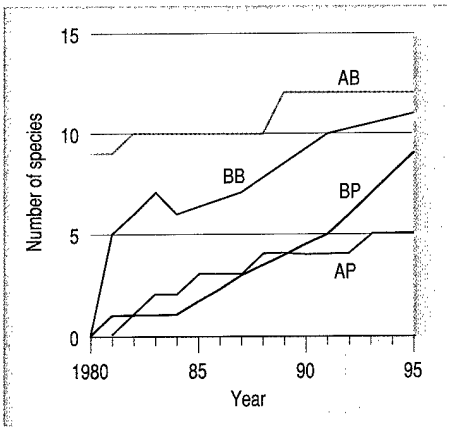

Fig. 1. Changes in number of bird and amphibian species in the blowdown and pyroclastic flow zones following the eruption of Mount St. Helens. AB = amphibians in the blowdown zone, BB = birds in the blowdown zone, BP = birds in the pyroclastic flow zone, and AP = amphibians in the pyroclastic flow zone.

on biological resources. Urbanization, conversion of lands to agriculture, draining of wetlands, and the fragmentation of forests are some of the land-use changes repeatedly cited in Part Two as major forces negatively affecting the health of biological resources. Changes in our nation's waterways to accommodate navigation, irrigation, hydroelectric power generation, and municipal use have drastically altered the biological integrity of aquatic environments. Consequently, aquatic organisms now dominate lists of imperiled species. Changes in land and water use have altered habitats so that they are more favorable for the establishment of nonindigenous species, which are posing increasing threats because of our more global economy and increased international travel. The invading spe-

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cies become established in habitats that have no natural competitors or predators, and thus, these species can thrive to the extent that they may significantly harm the habitat (Fig. 2).

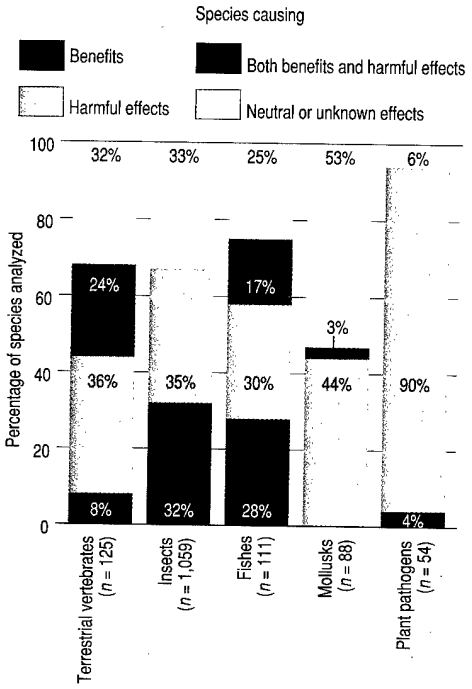

Fig. 2. Percentage of nonindigenous species that cause beneficial, harmful, both beneficial and harmful, and neutral or unknown effects (Office of Technology Assessment 1993).

The impacts on biological resources due to environmental contaminants and climate change are often not as obvious as the effects of a dammed river or a drained wetland, but potential effects can be severe. Birds, for example, accumulate selenium from used irrigation water, which decreases their reproductive success, and acid drainage from abandoned mines reduces the diversity of thousands of miles of freshwater streams. Climate change also has the potential to alter the geographic ranges of species and to possibly change habitats significantly enough to cause species endangerment.

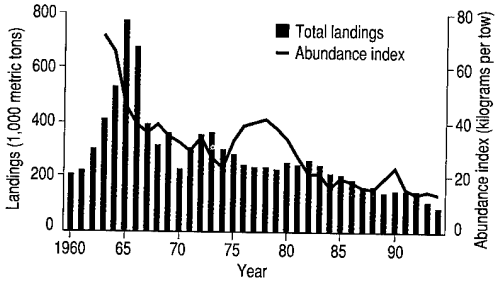

Fig. 3. Landings and abundance index of principal Northeast flounders and groundfishes, 1960—1994 (from National Oceanic and Atmospheric Administration 1996).

The effects of harvest, both economically and biologically, are most apparent in the depletion of marine resources (Fig. 3). Harvest also affects genetic diversity when population size is reduced, but the relation between diminished genetic diversity and the ability of a population to sustain harvest is not well understood. Consideration of harvest effects must go beyond focusing on the single harvested population and toward considering all related members of the community.

This report articulates the status and trends of individual species and particular habitats, which, if lost, can threaten the ecosystem functions on which humans depend. In the face of environmental change, biodivesity may provide the stability that buffers ecosystems against the collapse of ecological function.

Part 2: Regional Trends of Biological Resources

Northeast: This region is the most heavily populated and hence has been negatively impacted by urbanization and fragmentation of remaining forests. Over the last century the region has become increasingly forested because of declines in agriculture. Consequently, populations of some woodland bird species have grown. The forests, however, are somewhat changed from the native forests not only in their size, but also in their composition; elm and beech have declined, and chestnut trees have disappeared-all due to nonindigenous diseases. As these forests have matured, there are fewer early successional forests, which has negatively affected birds that inhabit scrub habitats, such as the woodcock. (Fig. 4). Alterations of aquatic habitats in the Northeast have resulted in the listing of 13 species of freshwater mussels as endangered. In addition, nonindigenous species

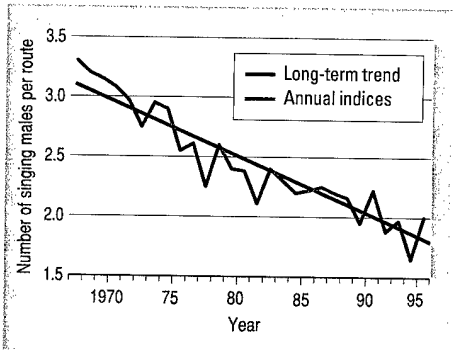

Fig. 4. Long-term trend and annual indices of the number of woodcock heard on the woodcock singing-ground survey in the eastern region, 1968—1995 (Bruggink and Kendall 1995)

have also impacted aquatic habitats; purple loosestrife, for example, has degraded habitats in many wetlands, the zebra mussel is established in the Finger Lakes, and sea lamprey and several nuisance plants have invaded Lake Champlain. A number of valuable resources have severely declined in the Northeast because of the combination of harvest, lost or degraded habitat, and disease; these resources include the black duck (Fig. 5), blue crab, oysters, and submerged aquatic vegetation in the Chesapeake Bay. Conversely, some populations have made successful comebacks, such as striped bass. Many species that adapt well to urbanized environments, such as Canada geese, white-tailed deer, and beavers, are even becoming nuisance species because of their dense numbers.

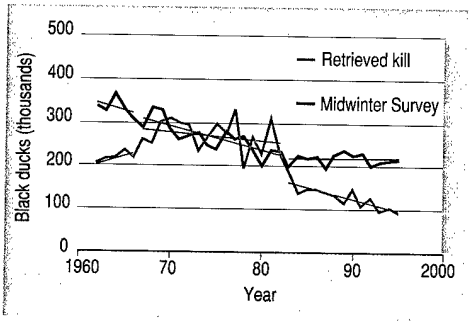

Fig. 5. Retrieved kill and Midwinter Survey counts of American black ducks for the Atlantic Flyway, 1962—1995. Three regression lines each, for black duck retrieved kill and the Midwinter Survey data, represent the periods 1962—1966, when hunting regulations were most liberal; 1967—1982; and 1983—1995, when hunting regu lations were most restrictive.

Great Lakes: The biological resources of the Great Lakes and their connecting waterways have been drastically affected by nonindigenous species and historical commercial fishing. Non-native species entered the Lakes because of the man-made connections to the ocean. At least 25 non-native fish species, as well as numerous other invasive aquatic organisms, have become established in the Great Lakes, resulting in a fishery that is highly managed by stocking nonindigenous salmonids. While commercial fishing contributed to the demise of the native lake trout and whitefish fisheries, (Fig. 6) these two species are being restored. The Great Lakes have also suffered from environmental pollution; inputs of nutrients and toxic chemicals negatively affected a number of fish and wildlife species between the 1950's and 1970's. Clean-up efforts have been successful in reducing the levels of persistent toxic chemicals and have contributed to the restoration of bald eagles. Reduced nutrients in Lake Erie have also sparked the resurgence of burrowing mayfly populations, a critical food for vertebrates.

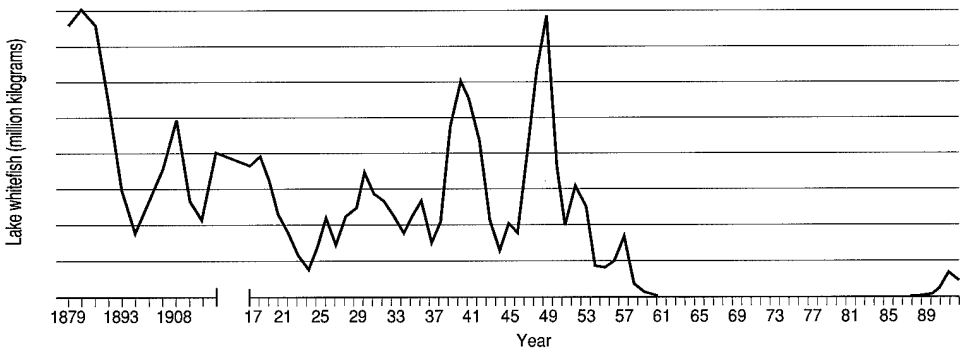

Fig. 6. Commercial catch of lake whitefish in U.S. waters of Lake Erie, 1879—1992 (Baldwin et al. 1979).

The coastal shore of the Great Lakes provides unique habitat in the dunes that are found in the upper lakes. Dune communities support more localized native species than any other part of the basin. Forests in the Great Lakes region have significantly changed. Much of the forest in the southern part of the region has been lost to agriculture and urban development, greatly affecting the native oak forest and savanna habitats. In the north, public ownership of lands has protected some forests, although the make-up of these forests has changed.

Southeast: Variation in climate, topography, and soil provide the Southeast with a rich diversity of habitats. The result is that a number of taxonomic groups reach continental high points of species richness. Amphibians, fishes, mollusks, aquatic insects, and crayfish have more species in the Southeast than anywhere else in North America. Because the Southeast has little public land and a fast-growing human population, this diversity is at significant risk due to land and water use. Nearly all major stream systems have been channelized or dammed, thus eliminating another important natural process—flooding—and adversely affecting stream habitat. As many as 144 major reservoirs have been built in this region, and the effects of these dams on the wealth of aquatic biodiversity are dramatic—19% of the freshwater fish species are threatened or endangered, and 73% of the freshwater mussels are at risk. Nonindigenous species have also had a great impact on aquatic habitats.

Although 55% of the land in the Southeast is forested, almost all is second-growth. Forests have been affected by nonindigenous species such as gypsy moths, wild pigs, and chestnut blight—an invasive disease that has decimated the American chestnut tree. Southeastern ecosystems have also been harmed by the absence of an important natural process, fire. Natural fires have been suppressed across the country, not only because of their potential danger, but also because they were viewed as being harmful to forest resources. Ecological research has shown that fire is important to the maintenance of many ecosystems and species in the Southeast and elsewhere. More than 50% of the rarest plants in the region depend on a natural frequency of fire.

Caribbean Islands: Island ecosystems are more vulnerable to change than continental systems, and land use and nonindigenous species have severely affected the Caribbean Islands. Forest habitats across much of the Caribbean were decimated by early settlement, but on some islands, most notably Puerto Rico and St. Johns, reforestation is occurring. These islands now have 38% and 75% forest cover, respectively. In Puerto Rico, 118 species of nonindigenous plants have become established, competing with native species and altering habitats. Almost two-thirds of Puerto Rico's endemic amphibians are declining, in part due to habitat destruction and introduced mammals such as the black rat. However, as in other locations around the world, some amphibian declines have been noted in areas with protected natural habitat, such as the Caribbean National Forest in Puerto Rico.

Puerto Rico and the Virgin Islands include significant marine resources that, similar to the marine resources of the mainland U.S.A., are increasingly stressed. Coral reefs of the Virgin Islands, for example, have declined because of diseases, hurricanes, sedimentation from coastal development, and destruction by boat anchors. Efforts to restore populations of threatened and endangered sea turtles that nest in the Vir-

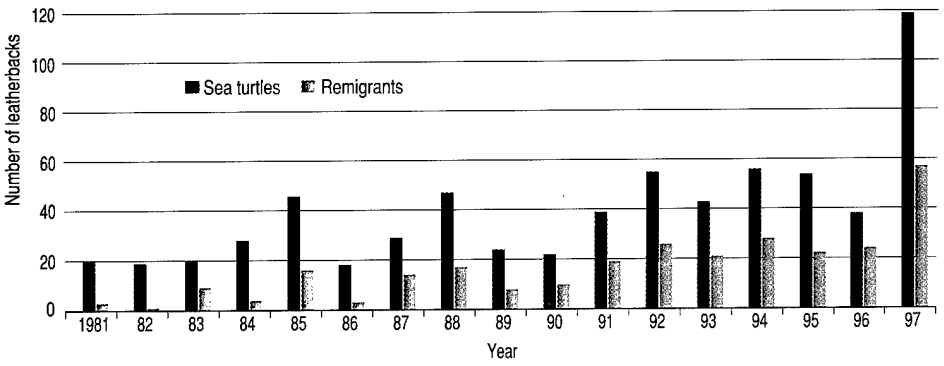

Fig. 7. The number of leatherback turtles and leatherback remigrants (that is, a nesting female who returns to nest at a particular site in subsequent nesting seasons) returning to nesting grounds at Sandy Point, St. Croix, U.S. Virgin Islands, 1981 to 1997 (modified from Boulon et al. 1994).

gin Islands have met with some success (Fig. 7), although commercial harvest in the British Virgin Islands remains a problem. Coastal habitats in Puerto Rico have also shown some improvement. Since 1974, mangrove forest acreage has increased by 40%, which will protect coastal erosion and provide nursery habitat for marine fish.

Mississippi River: The Mississippi River is one of the world's major river systems in size, habitat diversity, and biological productivity. Most of the river and its floodplain have been extensively modified for commercial navigation and other human use. The 29 navigation dams constructed between Minneapolis and St. Louis have greatly altered natural features of the river and the floodplain forests that provide valuable bird habitat. Additionally, ecosystems have been lost to agriculture and urbanization such that forest cover now makes up only 14% of the Upper Mississippi River Valley. These alterations, combined with the effects of nonindigenous species and natural processes such as drought, are responsible for continued negative changes in this ecosystem. Wild celery, an important food for waterfowl, has declined significantly in Lake Onalaska since reaching peak abundance in the early 1980's. Similarly, the species richness of pearly-mussels has declined (Fig. 8). In some reaches, fingernail clams have declined, leading to decreases in scaup, which rely on these clams as food. Fish habitat is also diminishing in the system. Sedimentation has reduced water depth, which compromises overwintering habitat for fish. Loss of aquatic vegetation also reduces habitat for young fish. Like the Great Lakes, the Mississippi River suffers from pollution by toxic chemicals, which affected reproduction of eagles and mink, but with better controls of contaminant inputs, these populations have rebounded.

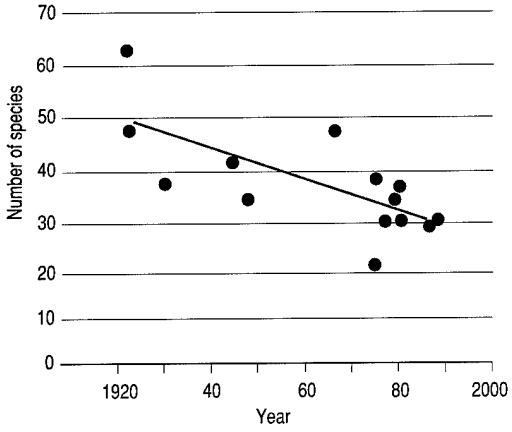

Fig. 8. Species richness of pearly-mussels in the Upper Mississippi River drainage has declined substantially. Data compiled from the following sources: Shimek 1921; Grier and Mueller 1922; Ellis 1931a,b; Dawley 1947; Finke 1966; Coon et al. 1977; Fuller 1978, 1979; Mathiak 1979; Perry 1979; Thiel et al. 1979; Ecological Analysts Inc. 1981; Thiel 1981; Duncan and Thiel 1983; Holland-Bartels 1990.

Coastal Louisiana: Coastal Louisiana ecosystems experience rapid changes due to topography, natural processes such as climate, and human modifications. The result is an annual loss of coastal wetlands of about 25 square miles per year. Most of this loss occurs when vegetated marshland sinks until it is below sea level; eventually the marshland reverts to open water. These wetlands have always been dynamic systems, expanding and shrinking over thousands of years, but human modification has pushed the natural processes into ever-shrinking coastal wetlands. Construction of the levees and associated navigational works of the Mississippi River prevent the overflow of fresh water and sediments from rebuilding marshes during spring floods, which threaten nearly 1200 square miles of habitat important to birds and marine species. A $900-million estuarine fishery and millions of waterfowl (Fig. 9) and other birds rely on this diminishing and rich coastal Louisiana habitat. This system is also impacted by nonindigenous species, such as water hyacinths which impede drainage and navigation and choke out native vegetation in lower reaches of rivers and freshwater marshes. Nutria, an introduced non-native species, are responsible for denuding the vegetation in intertidal flats and for stopping the regrowth of bald cypress.

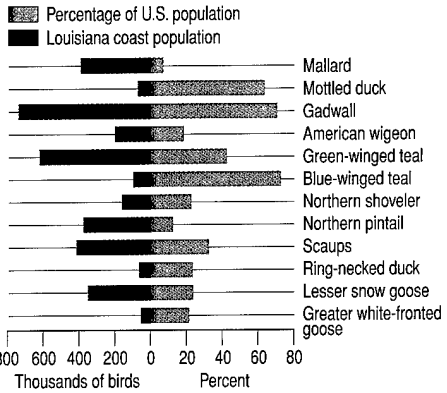

Fig. 9. Number of individuals (1969-1994 mean) of predominant waterfowl species in coastal Louisiana, and for each, the mean percentage of the U.S. wintering population represented by the Louisiana coastal population (Michot 1996).

Grasslands: Grasslands (Fig. 10) are among the most biologically productive of all communities within the United States, but they are also one of the most threatened habitats. In seven states, less than 1% of the native tallgrass prairie habitat remains; losses

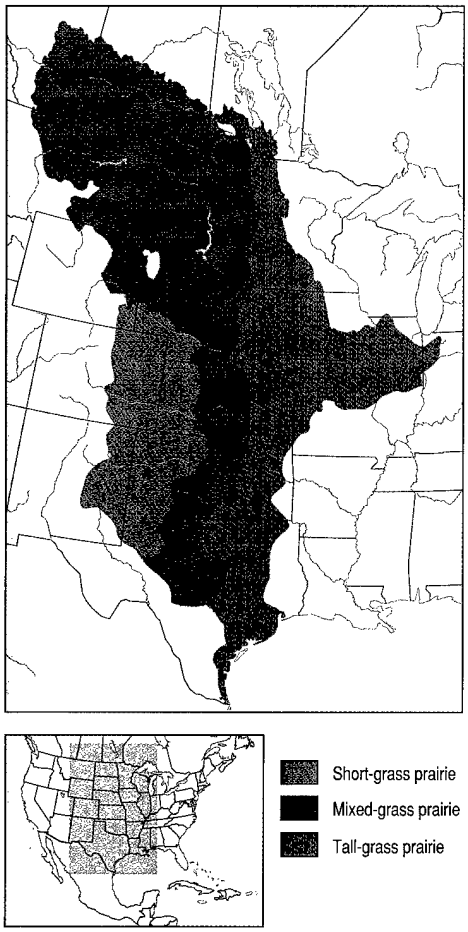

Fig. 10. Extent of historical (pre-European) tall-grass, mixed-grass, and short-grass prairies on the North American Great Plains.

are due to agriculture and grazing, urbanization, and mineral extraction. Erosion threatens the sustainability of grassland soils, and the lack of fire has enabled invasion of nonindigenous species. Frequent fires are essential in maintaining native species diversity in grasslands. Waterways of the prairie potholes have been altered by drainage for agriculture. All of these changes contribute to a habitat loss that has resulted in significant declines in waterfowl breeding areas. Rainfall and predators are other important factors in determining the success of waterfowl in the prairie pothole region. Of the 435 bird species that breed in the United States, 330 breed in the Great Plains. Native grassland bird species have shown more consistent, widespread, and steeper declines than any other group of North American birds.

Rocky Mountains: This region is known for its natural beauty, as well as for its interesting array of biological resources: elk, gray wolves, grizzly bears, bald eagles, Douglas-fir, ponderosa pine, spruce-fir, and many others. Rapid population growth, nonindigenous species introductions, and urban expansion threaten the resources of the region, however. The population in the surrounding areas has greatly increased since 1950; for example, both Utah and Colorado have experienced a 150% population increase. This rapid population growth has increased demands for water and power and has altered habitats. Habitat loss and population-control programs are responsible for an estimated 98% decline in prairie dog populations. Prairie dog ecosystems are valuable in the Rocky Mountain foothills because they support 170 vertebrate species and contain more specialized plants and insects than adjacent areas.

While restoration of greenback cutthroat trout has been successful, three other native cutthroat trout subspecies are extinct. Introductions of nonindigenous fish severely threaten other native fish. The one remaining native trout species is threatened and is a primary post-hibernation food source for grizzly bears. As in other parts of the nation, bald eagles and peregrine falcons are recovering from declines caused by pesticides. At the same time, habitat loss, introduced species, and environmental contaminants are all contributing to declines of amphibians in the Rocky Mountains. For example, western toads now occupy less than 20% of their previous range. Although gray wolves were reintroduced into the Greater Yellowstone ecosystem in 1995 and their status is improving, the species occupies less than 10% of its historical range.

Great Basin-Mojave Desert: This area between the Sierra Nevada, the Transverse Ranges, the Rocky Mountains, and the Columbia and Colorado plateaus harbors a rich biological diversity. Great topographical relief and an arid, continental climate provide conditions for unique plants and animals. Because of the region's arid nature, aquatic habitats are at a premium and are very critical (Fig. 11). More than 75% of the species in the region are strongly associated with riparian, or streamside, vegetation. Unfortunately, much of this vegetation has been degraded by water diversions, agriculture, and grazing. Grazing, in particular, has changed the character of these habitats in the Great Basin, reducing biodiversity and enabling nonindigenous species such as the tamarisk to become dominant. Water diversions for irrigation and urban growth lower levels of surface waters and cause increases in total dissolved solids and some heavy metals, threatening biological resources of Mono and Great Salt Lakes. The unique plant diversity of this region's terrestrial ecosystems is threatened by urbanization, grazing, fire suppression, and nonindigenous species, such as cheatgrass. More than 99% of the sagebrush-grass zone, for example, has been negatively affected by livestock.

Biological populations reflect the impacts on habitats. Of 131 species and subspecies of fish that histori-

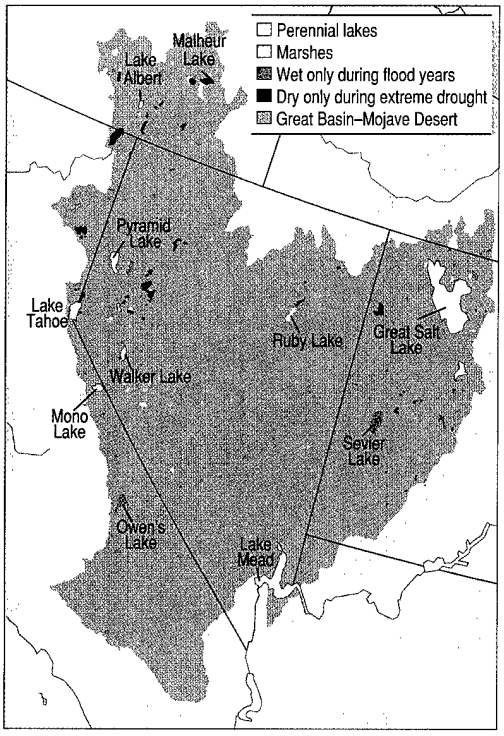

Fig. 11. Terminal wetland ecosystems in the Great Basin—Mojave Desert region.

cally occurred in the Great Basin-Mojave Desert, 10 are extinct and 75 (62%) are listed, candidates for listing, or of concern. The Amargosa toad is a candidate for listing as endangered, but trends of other amphibians are still unknown. Trends in many bird species are unknown because of limited sampling and high variability. Still, because many of the region's species depend on wetland and riparian habitats, which are being destroyed and degraded, researchers are concerned that declines are widespread.

Southwest: The southwestern United States is a land of extremes, and as with the Great Basin, the variation in topography and climate has produced great biological diversity. Widespread grazing of domestic livestock, suppression of natural fire, and commercial forest logging have altered the biological resources of the Southwest. Because of the variation in habitats and their biotic communities, each responds differently to human-induced stress. For example, fire suppression in ponderosa pine forests, which cover extensive portions of the Southwest, have reduced understory plants and have caused a buildup of needles that disrupts nutrient cycling and contributes to poor tree growth. Grazing, which occurs in almost all of these forests, replaces palatable plant species with thorny or poisonous species, thus reducing diversity further. More than 85% of the ponderosa pine forests have been significantly and negatively impacted by grazing and fire suppression. In desert shrublands and semidesert grasslands, which form a diverse mosaic in the arid Southwest, grazing and fire suppression favor a vegetation shift from grasses to shrubland, thus inviting nonindigenous species to become established. Between 1974 and 1987, grassland cover declined by 35%; the nonindigenous honey mesquite shrub now dominates nearly 70 million acres.

As with other arid ecosystems, the Southwest aquatic and riparian habitats are invaluable. Habitat loss due to dams, groundwater pumping, and pollution have contributed to jeopardizing more than 48% of the region's fish fauna. Investigations have also indicated declines in the region's leopard frogs, but the status of many amphibians and reptiles is unknown. The Southwest has the largest number of native mammal species, although several have been extirpated, including the grizzly bear and gray wolf. Smaller mammals may be of even greater concern. For example, of the 30 species of bats, one-third to one-half are now considered sensitive.

California: Because parts of California are included in other chapters, this chapter focuses on westside California, a very distinctive region because of its topography and Mediterranean climate. Ecosystems in California have been heavily altered (Table 1) by agriculture, grazing, urbanization, and timber harvest. More than 85% of the old-growth coast redwood forests have been logged, reducing dependent species. Native California prairie has almost disappeared because it has been converted to agriculture or to nonindigenous annual grasslands. Similarly, more than 95% of the region's historical wetlands have been destroyed or modified. These habitat changes, along with nonindigenous species, have negatively affected species trends—57% of fish species are extinct or on the road to extinction if present trends continue; 40% of the salamanders and 54% of the frogs are given or are in need of some sort of protection. Birds have also declined in California. In the 1970's, for example, 10-12 million waterfowl wintered in or migrated through California, with the great majority relying on Central Valley habitats. More recently, only 2.5 million waterfowl wintered in the Central Valley. Additionally, of the 342 species of land birds in this region, 21.3% are listed as state or federally threatened and endangered species.

Table 1. Human-caused reductions in westside California plant communities and formations (after Noss and Peters 1995).

Community/formation	Vegetation reduced (percent)
Native grasslands	99
Needlegrass steppe	99.9
Southern San Joaquin Valley alkali sink scrub	99
Southern California coastal sage–scrub	70–90
Vernal pools	91
Wetlands	91
Riparian woodlands	89
Coast redwood forest	85

Pacific Northwest: The Pacific Northwest has a wealth of natural resources, which are used for a variety of purposes. This chapter addresses the status of four primary areas of resource concern: old-growth western forests, forests east of the Cascades, eastside rangelands, and aquatic ecosystems. Logging has drastically reduced the amount of old-growth forests; much of the remaining old-growth forests occur in stands smaller than 400 acres. The combination of old-growth forest removal and fragmentation has negatively affected many species. Three of the seventeen bird species that are closely associated with these forests and for which there is reliable population trend information have shown significant long-term downward trends, whereas none show upward trends. In eastside forests, selective harvest, grazing, and fire suppression have greatly altered the forests—in some areas as much as 98% of the old-growth ponderosa pine has been logged or lost. More than 99% of the fertile Palouse Prairie grasslands of southeastern Washington, as well as adjacent areas in Oregon and Idaho, were converted to agriculture, and 2-2.5 million acres of grassland and sagebrush steppe have been replaced by nonindigenous vegetation, primarily because of overgrazing.

Bird species have reacted differently to changes in rangelands. Whereas 25 bird species show downward population trends, especially in

those species associated with grassland and shrub-steppe habitats, several raptor species show long-term upward trends. As of 1992, land managers listed 144 plant species in Oregon and Washington because of their rarity, but few were monitored for trend information. Aquatic habitats have been impacted as well. Ninety-five percent of the streams surveyed throughout Oregon had been moderately or severely degraded, primarily by logging activities, but potential for restoration of some of these streams remains high. The plight of salmon in the Pacific Northwest remains problematic (Fig. 12). Habitat degradation, dams, overharvest, and ocean conditions all contribute to continued declines of salmon. Evidence of the widespread declines in frogs is also found in the Northwest. The spotted frog was once widespread in a variety of habitats on both sides of the Cascades but is now nearly extirpated on the westside.

Alaska: Alaska's vast size, small population, and cold climate have protected the state from many of the negative effects on biological resources seen in the conterminous United States. With limited development, biological resources mostly respond to natural processes—unsuppressed wildfires, climatic events, and natural population variability. However, for many biological resources in Alaska, trend information is nonexistent. Harvest has a major impact in this region, particularly on fishery resources. Freshwater fish stocks in the interior are declining, especially those reachable by road. In the Susina River drainage, for example, the harvest of wild rainbow trout declined by 50% during the last 10 years, despite a doubling of the time spent fishing. Harvests of whitefish in the Tanana drainage dropped from 26,810 fish in 1986 to 739 in 1991. Salmon populations seem to be stable, except for chum salmon in some areas. Wildlife species have experienced some negative effects due to harvest, but many populations, such as some caribou herds, are at record high numbers. Introduced species have caused some problems. For example, the Aleutian Canada goose was nearly extirpated because of predation from introduced foxes, and an introduction of caribou to Adak Island threatened habitat of endangered plants when the caribou population exceeded carrying capacity.

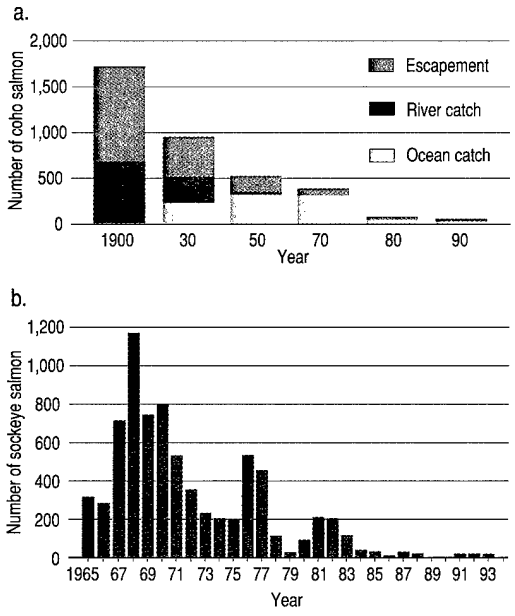

Fig. 12. Examples of declining populations of anadromous salmon: a) estimated abundance of coho salmon on the north coast of Oregon (adapted from Kostow 1997) and b) counts of sockeye salmon at upper dams on the lower Snake River in Idaho (adapted from Hassemer et al. 1997).

Hawaii and the Pacific Islands: The Hawaiian archipelago is the most isolated island group of comparable size and diversity on Earth. This isolation results in a high percentage of unique species. Oceanic islands, however, are quite vulnerable to biological invasions, and the Hawaiian archipelago has been severely affected by nonindigenous species. For example, wild pigs brought to the island cause significant damage to forests by eating tree fern trunks, rare plants, and earthworms, and by helping spread seeds of non-native plants (Fig. 13). Introduced goats also destroy native vegetation to the point

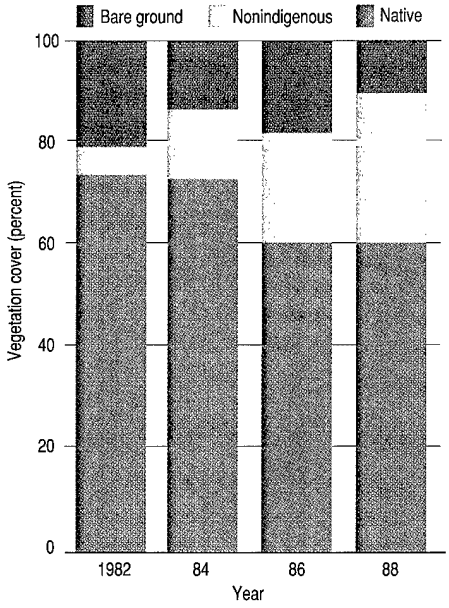

Fig. 13. Graph showing invasion of nonindigenous plants resulting from pig damage to montane bog sites on East Maui, 1982—1988 (from Medeiros et al. 1991).

where high goat densities can result in obliterated landscapes. Eradication efforts for both species are under way in several areas. Mosquitoes, which are not native to the region, are significant invaders because they help spread avian malaria, which has harmed many native birds. About 90 nonindigenous plant species pose significant threats to Hawaiian ecosystems. Some plants, such as miconia, can out-compete native species to create single-species stands or can even alter ecosystems processes.

The most spectacular land-bird assemblage ever found on any remote ocean archipelago evolved in the Hawaiian Islands, but this assemblage has been significantly depleted through human actions. Of the 76 species of perching birds or songbirds that lived in Hawaii, 31 are known only as fossils. Of the remaining 45, 19 are extinct and 18 are federally listed as endangered.

Marine Resources: A range of human activities affects living marine resources, including fishes, marine mammals, and marine birds. Increasingly intensive fishing efforts, in conjunction with the use of more sophisticated fishing gear and electronics, have resulted in gross over-

fishing of some marine populations. Associated with fishing is bycatch, when nontarget animals are taken in fishing operations. Both overfishing and bycatch are problems that have caused marine resource managers to create controlled access to fishing, whereby catch quotas are allocated to individual fishing vessels instead of allowing free and open access. Quota allocation to individual vessels is gaining acceptance.

Habitat alterations in rivers and estuaries, as well as in coastal zones, are a result of urbanization. Urbanization alters freshwater flows, increases erosion, introduces toxic chemicals and other contaminants into the waters, furthers the introduction of nonindigenous species, and degrades the marine habitats essential to living marine resources. Numerous demographic trends suggest that these conditions and threats are not likely to change soon. Some 50% of our population is estimated to live within a 2- or 3-hour drive of major freshwater systems (the Great Lakes) or coastal waters. As the nation grows, there will be further population growth in coastal zones. Our desire to live within sight of the ocean has never abated and, increasingly, urban dwelling areas are being developed on or near shorelines. Often these developments severely and negatively alter coastal and marine ecosystems and harm living marine resources.

Another major issue today is the mitigation necessary to protect endangered or threatened species. A recent example of this situation is with certain salmon runs in Pacific coast streams. The use of river waters for irrigation, power generation, and domestic consumption by large urban areas has compromised these streams and the survival of the salmon runs.

Many natural changes in the dynamics of ecosystems also may exacerbate the effects of the factors just listed. For instance, attention to global warming over the past two decades is now culminating in data that show widespread climatic effects on living marine resources. Articles in recent issues of major scientific publications indicate a progressive subtle warming of Pacific coastal waters and, consequently, an extirpation of certain species that would have been found in these waters a half-century ago. Similar trends have been speculated about and, to some degree, measured in shelf waters as well as in the coastal zone of the northwest Atlantic.

On the whole, the outlook for the welfare of the nation's living marine resources is guarded, with a need to remain vigilant. The crash of some groundfish fisheries, the poor welfare of some Pacific coast salmon stocks, and declines in some marine mammal populations are examples of situations that need special attention. Although many other of the nation's marine resources are in good condition, they too must be attentively managed and conserved under a suite of federal laws and international treaties. The science of the marine environment and the state of its resources must be improved, for without reliable scientific knowledge, resource use and management must necessarily be more conservative.

This is an executive summary and the full report may be cited as follows:
Mac, M. J., P. A. Opler, C. E. Puckett Haecker, and P. D. Doran. 1998. Status and trends of the nation's biological resources. 2 vols. U.S. Department of the Interior, U.S. Geological Survey, Reston, Va.

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The Status and Trends of our Nation's Biological Resources

EXECUTIVE SUMMARY

The Status and Trends of Our Nation's Biological Resources is a report that synthesizes current information on status and trends of biological resources with a historical perspective of ecosystems across the country to assess how the nation's resources are changing. The report was produced by the U.S. Geological Survey's Biological Resources Division with contributions from nearly 200 experts from federal government, academic, and nongovernmental communities, including a section on Marine Resources written by the National Marine Fisheries Service. The 1,000-page, peer-reviewed, full-color, two-volume report is written in non-technical language to be usable by policy makers and interested citizens as well as natural resource professionals.

The report is organized into two parts. Part One details seven major factors affecting biological resources nationwide: Natural Processes, Land Use, Water Use, Climate Change, Nonindigenous Species, Environmental Contaminants, and Harvest. Part Two describes the status and trends of biological resources in different regions of the country, the ecosystems in that region, and how these resources have been affected by the factors described in Part One. The regions covered are the Northeast, Great Lakes, Southeast, Caribbean Islands, Mississippi River, Coastal Louisiana, Grasslands, Rocky Mountains, Great Basin-Mojave Desert, Southwest, California, Pacific Northwest, Alaska, Hawaii and the Pacific Islands, and Marine Resources.

Part 1: Factors Affecting Biological Resources

Of the seven factors detailed in the report, six are human-induced and one, natural processes, covers natural events such as fire, hurricanes, and even precipitation extremes that induce changes in physical habitat. These natural processes, when not extremely severe or highly regular in their occurrence, can promote biodiversity by varying physical habitat. Hurricanes can provide some benefits to ecosystems by distributing sediment to coastal wetlands. Similarly, biological populations can respond surprisingly fast in areas devastated by volcanos (Fig. 1).

Land use, water use, and nonindigenous species are the three factors that have had the greatest broad-scale effects

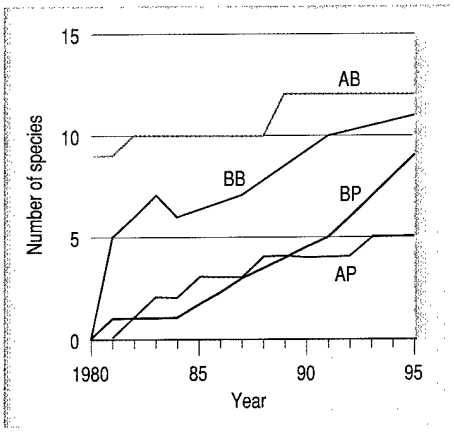

Fig. 1. Changes in number of bird and amphibian species in the blowdown and pyroclastic flow zones following the eruption of Mount St. Helens. AB = amphibians in the blowdown zone, BB = birds in the blowdown zone, BP = birds in the pyroclastic flow zone, and AP = amphibians in the pyroclastic flow zone.

on biological resources. Urbanization, conversion of lands to agriculture, draining of wetlands, and the fragmentation of forests are some of the land-use changes repeatedly cited in Part Two as major forces negatively affecting the health of biological resources. Changes in our nation's waterways to accommodate navigation, irrigation, hydroelectric power generation, and municipal use have drastically altered the biological integrity of aquatic environments. Consequently, aquatic organisms now dominate lists of imperiled species. Changes in land and water use have altered habitats so that they are more favorable for the establishment of nonindigenous species, which are posing increasing threats because of our more global economy and increased international travel. The invading spe-

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cies become established in habitats that have no natural competitors or predators, and thus, these species can thrive to the extent that they may significantly harm the habitat (Fig. 2).

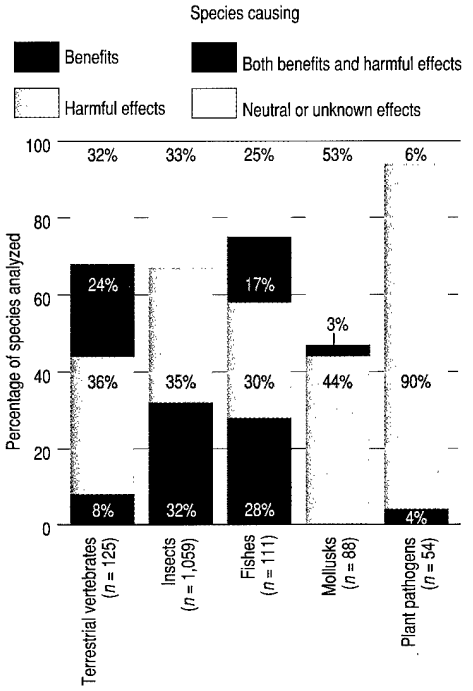

Fig. 2. Percentage of nonindigenous species that cause beneficial, harmful, both beneficial and harmful, and neutral or unknown effects (Office of Technology Assessment 1993).

The impacts on biological resources due to environmental contaminants and climate change are often not as obvious as the effects of a dammed river or a drained wetland, but potential effects can be severe. Birds, for example, accumulate selenium from used irrigation water, which decreases their reproductive success, and acid drainage from abandoned mines reduces the diversity of thousands of miles of freshwater streams. Climate change also has the potential to alter the geographic ranges of species and to possibly change habitats significantly enough to cause species endangerment.

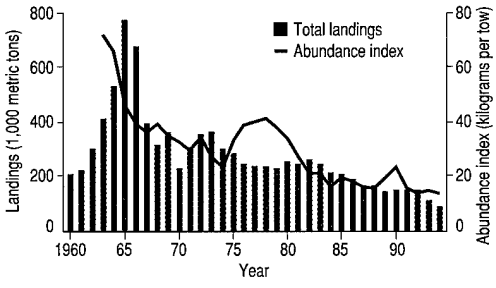

Fig. 3. Landings and abundance index of principal Northeast flounders and groundfishes, 1960—1994 (from National Oceanic and Atmospheric Administration 1996).

The effects of harvest, both economically and biologically, are most apparent in the depletion of marine resources (Fig. 3). Harvest also affects genetic diversity when population size is reduced, but the relation between diminished genetic diversity and the ability of a population to sustain harvest is not well understood. Consideration of harvest effects must go beyond focusing on the single harvested population and toward considering all related members of the community.

This report articulates the status and trends of individual species and particular habitats, which, if lost, can threaten the ecosystem functions on which humans depend. In the face of environmental change, biodivesity may provide the stability that buffers ecosystems against the collapse of ecological function.

Part 2: Regional Trends of Biological Resources

Northeast: This region is the most heavily populated and hence has been negatively impacted by urbanization and fragmentation of remaining forests. Over the last century the region has become increasingly forested because of declines in agriculture. Consequently, populations of some woodland bird species have grown. The forests, however, are somewhat changed from the native forests not only in their size, but also in their composition; elm and beech have declined, and chestnut trees have disappeared-all due to nonindigenous diseases. As these forests have matured, there are fewer early successional forests, which has negatively affected birds that inhabit scrub habitats, such as the woodcock. (Fig. 4). Alterations of aquatic habitats in the Northeast have resulted in the listing of 13 species of freshwater mussels as endangered. In addition, nonindigenous species

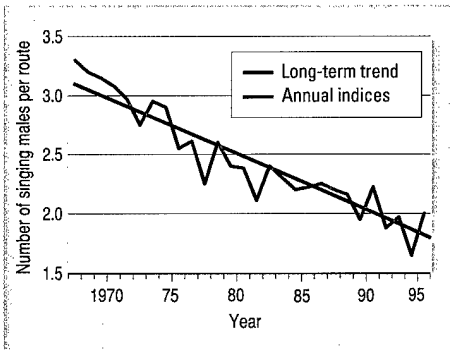

Fig. 4. Long-term trend and annual indices of the number of woodcock heard on the woodcock singing-ground survey in the eastern region, 1968—1995 (Bruggink and Kendall 1995)

have also impacted aquatic habitats; purple loosestrife, for example, has degraded habitats in many wetlands, the zebra mussel is established in the Finger Lakes, and sea lamprey and several nuisance plants have invaded Lake Champlain. A number of valuable resources have severely declined in the Northeast because of the combination of harvest, lost or degraded habitat, and disease; these resources include the black duck (Fig. 5), blue crab, oysters, and submerged aquatic vegetation in the Chesapeake Bay. Conversely, some populations have made successful comebacks, such as striped bass. Many species that adapt well to urbanized environments, such as Canada geese, white-tailed deer, and beavers, are even becoming nuisance species because of their dense numbers.

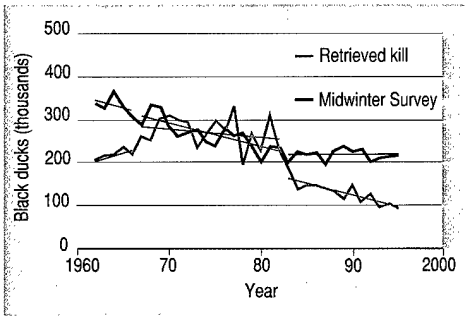

Fig. 5. Retrieved kill and Midwinter Survey counts of American black ducks for the Atlantic Flyway, 1962—1995. Three regression lines each, for black duck retrieved kill and the Midwinter Survey data, represent the periods 1962—1966, when hunting regulations were most liberal; 1967—1982; and 1983—1995, when hunting regu lations were most restrictive.

Great Lakes: The biological resources of the Great Lakes and their connecting waterways have been drastically affected by nonindigenous species and historical commercial fishing. Non-native species entered the Lakes because of the man-made connections to the ocean. At least 25 non-native fish species, as well as numerous other invasive aquatic organisms, have become established in the Great Lakes, resulting in a fishery that is highly managed by stocking nonindigenous salmonids. While commercial fishing contributed to the demise of the native lake trout and whitefish fisheries, (Fig. 6) these two species are being restored. The Great Lakes have also suffered from environmental pollution; inputs of nutrients and toxic chemicals negatively affected a number of fish and wildlife species between the 1950's and 1970's. Clean-up efforts have been successful in reducing the levels of persistent toxic chemicals and have contributed to the restoration of bald eagles. Reduced nutrients in Lake Erie have also sparked the resurgence of burrowing mayfly populations, a critical food for vertebrates.

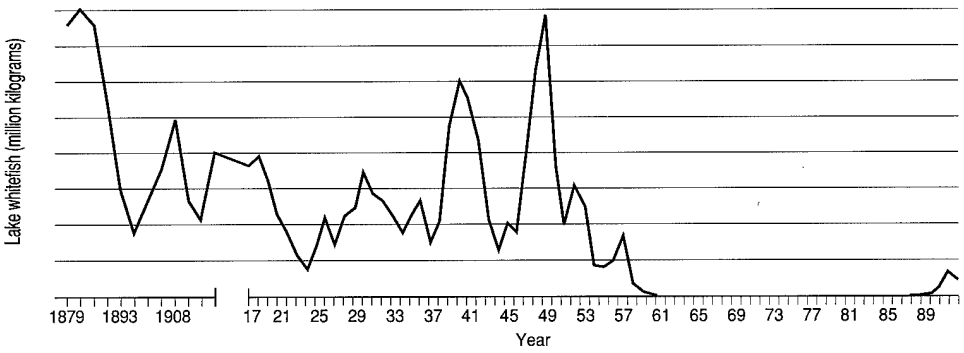

Fig. 6. Commercial catch of lake whitefish in U.S. waters of Lake Erie, 1879—1992 (Baldwin et al. 1979).

The coastal shore of the Great Lakes provides unique habitat in the dunes that are found in the upper lakes. Dune communities support more localized native species than any other part of the basin. Forests in the Great Lakes region have significantly changed. Much of the forest in the southern part of the region has been lost to agriculture and urban development, greatly affecting the native oak forest and savanna habitats. In the north, public ownership of lands has protected some forests, although the make-up of these forests has changed.

Southeast: Variation in climate, topography, and soil provide the Southeast with a rich diversity of habitats. The result is that a number of taxonomic groups reach continental high points of species richness. Amphibians, fishes, mollusks, aquatic insects, and crayfish have more species in the Southeast than anywhere else in North America. Because the Southeast has little public land and a fast-growing human population, this diversity is at significant risk due to land and water use. Nearly all major stream systems have been channelized or dammed, thus eliminating another important natural process—flooding—and adversely affecting stream habitat. As many as 144 major reservoirs have been built in this region, and the effects of these dams on the wealth of aquatic biodiversity are dramatic—19% of the freshwater fish species are threatened or endangered, and 73% of the freshwater mussels are at risk. Nonindigenous species have also had a great impact on aquatic habitats.

Although 55% of the land in the Southeast is forested, almost all is second-growth. Forests have been affected by nonindigenous species such as gypsy moths, wild pigs, and chestnut blight—an invasive disease that has decimated the American chestnut tree. Southeastern ecosystems have also been harmed by the absence of an important natural process, fire. Natural fires have been suppressed across the country, not only because of their potential danger, but also because they were viewed as being harmful to forest resources. Ecological research has shown that fire is important to the maintenance of many ecosystems and species in the Southeast and elsewhere. More than 50% of the rarest plants in the region depend on a natural frequency of fire.

Caribbean Islands: Island ecosystems are more vulnerable to change than continental systems, and land use and nonindigenous species have severely affected the Caribbean Islands. Forest habitats across much of the Caribbean were decimated by early settlement, but on some islands, most notably Puerto Rico and St. Johns, reforestation is occurring. These islands now have 38% and 75% forest cover, respectively. In Puerto Rico, 118 species of nonindigenous plants have become established, competing with native species and altering habitats. Almost two-thirds of Puerto Rico's endemic amphibians are declining, in part due to habitat destruction and introduced mammals such as the black rat. However, as in other locations around the world, some amphibian declines have been noted in areas with protected natural habitat, such as the Caribbean National Forest in Puerto Rico.

Puerto Rico and the Virgin Islands include significant marine resources that, similar to the marine resources of the mainland U.S.A., are increasingly stressed. Coral reefs of the Virgin Islands, for example, have declined because of diseases, hurricanes, sedimentation from coastal development, and destruction by boat anchors. Efforts to restore populations of threatened and endangered sea turtles that nest in the Vir-

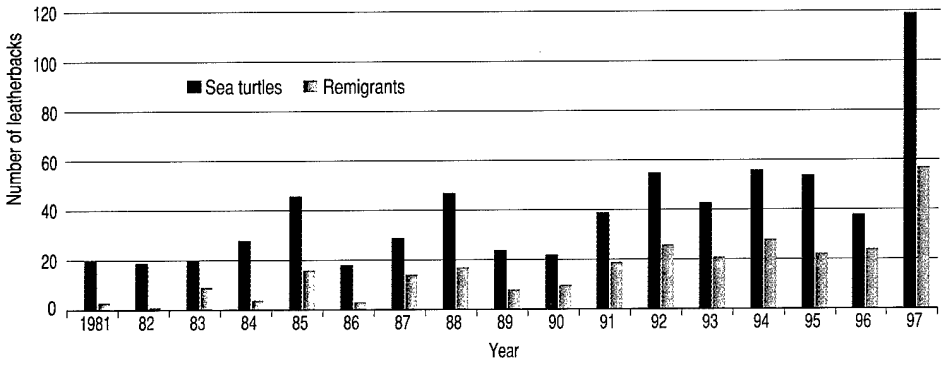

Fig. 7. The number of leatherback turtles and leatherback remigrants (that is, a nesting female who returns to nest at a particular site in subsequent nesting seasons) returning to nesting grounds at Sandy Point, St. Croix, U.S. Virgin Islands, 1981 to 1997 (modified from Boulon et al. 1994).

gin Islands have met with some success (Fig. 7), although commercial harvest in the British Virgin Islands remains a problem. Coastal habitats in Puerto Rico have also shown some improvement. Since 1974, mangrove forest acreage has increased by 40%, which will protect coastal erosion and provide nursery habitat for marine fish.

Mississippi River: The Mississippi River is one of the world's major river systems in size, habitat diversity, and biological productivity. Most of the river and its floodplain have been extensively modified for commercial navigation and other human use. The 29 navigation dams constructed between Minneapolis and St. Louis have greatly altered natural features of the river and the floodplain forests that provide valuable bird habitat. Additionally, ecosystems have been lost to agriculture and urbanization such that forest cover now makes up only 14% of the Upper Mississippi River Valley. These alterations, combined with the effects of nonindigenous species and natural processes such as drought, are responsible for continued negative changes in this ecosystem. Wild celery, an important food for waterfowl, has declined significantly in Lake Onalaska since reaching peak abundance in the early 1980's. Similarly, the species richness of pearly-mussels has declined (Fig. 8). In some reaches, fingernail clams have declined, leading to decreases in scaup, which rely on these clams as food. Fish habitat is also diminishing in the system. Sedimentation has reduced water depth, which compromises overwintering habitat for fish. Loss of aquatic vegetation also reduces habitat for young fish. Like the Great Lakes, the Mississippi River suffers from pollution by toxic chemicals, which affected reproduction of eagles and mink, but with better controls of contaminant inputs, these populations have rebounded.

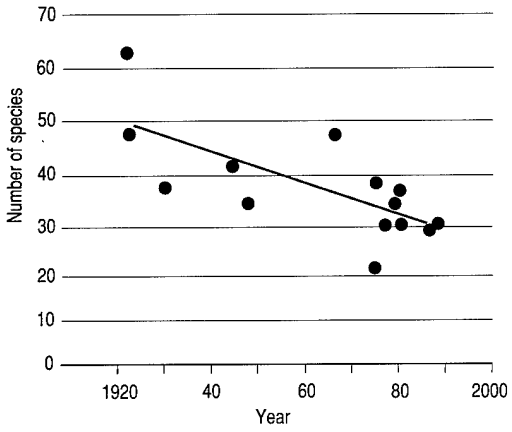

Fig. 8. Species richness of pearly-mussels in the Upper Mississippi River drainage has declined substantially. Data compiled from the following sources: Shimek 1921; Grier and Mueller 1922; Ellis 1931a,b; Dawley 1947; Finke 1966; Coon et al. 1977; Fuller 1978, 1979; Mathiak 1979; Perry 1979; Thiel et al. 1979; Ecological Analysts Inc. 1981; Thiel 1981; Duncan and Thiel 1983; Holland-Bartels 1990.

Coastal Louisiana: Coastal Louisiana ecosystems experience rapid changes due to topography, natural processes such as climate, and human modifications. The result is an annual loss of coastal wetlands of about 25 square miles per year. Most of this loss occurs when vegetated marshland sinks until it is below sea level; eventually the marshland reverts to open water. These wetlands have always been dynamic systems, expanding and shrinking over thousands of years, but human modification has pushed the natural processes into ever-shrinking coastal wetlands. Construction of the levees and associated navigational works of the Mississippi River prevent the overflow of fresh water and sediments from rebuilding marshes during spring floods, which threaten nearly 1200 square miles of habitat important to birds and marine species. A $900-million estuarine fishery and millions of waterfowl (Fig. 9) and other birds rely on this diminishing and rich coastal Louisiana habitat. This system is also impacted by nonindigenous species, such as water hyacinths which impede drainage and navigation and choke out native vegetation in lower reaches of rivers and freshwater marshes. Nutria, an introduced non-native species, are responsible for denuding the vegetation in intertidal flats and for stopping the regrowth of bald cypress.

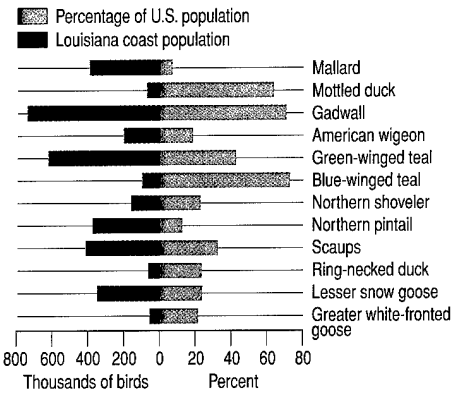

Fig. 9. Number of individuals (1969-1994 mean) of predominant waterfowl species in coastal Louisiana, and for each, the mean percentage of the U.S. wintering population represented by the Louisiana coastal population (Michot 1996).

Grasslands: Grasslands (Fig. 10) are among the most biologically productive of all communities within the United States, but they are also one of the most threatened habitats. In seven states, less than 1% of the native tallgrass prairie habitat remains; losses

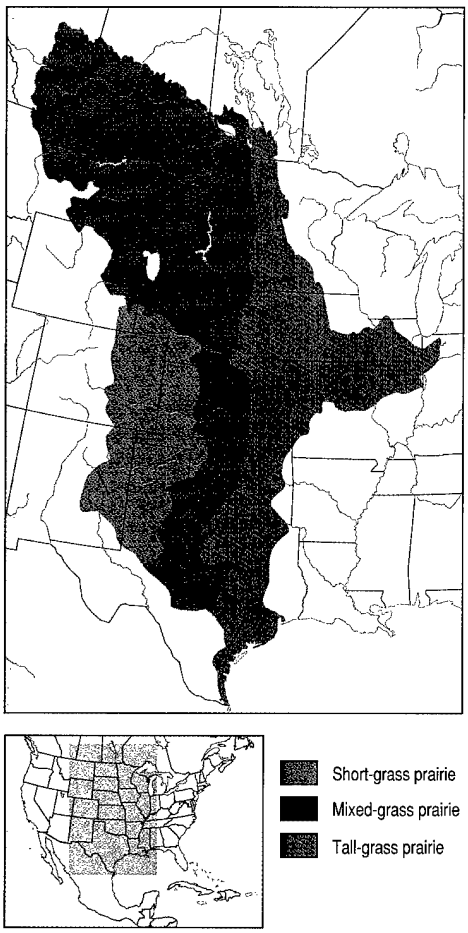

Fig. 10. Extent of historical (pre-European) tall-grass, mixed-grass, and short-grass prairies on the North American Great Plains.

are due to agriculture and grazing, urbanization, and mineral extraction. Erosion threatens the sustainability of grassland soils, and the lack of fire has enabled invasion of nonindigenous species. Frequent fires are essential in maintaining native species diversity in grasslands. Waterways of the prairie potholes have been altered by drainage for agriculture. All of these changes contribute to a habitat loss that has resulted in significant declines in waterfowl breeding areas. Rainfall and predators are other important factors in determining the success of waterfowl in the prairie pothole region. Of the 435 bird species that breed in the United States, 330 breed in the Great Plains. Native grassland bird species have shown more consistent, widespread, and steeper declines than any other group of North American birds.

Rocky Mountains: This region is known for its natural beauty, as well as for its interesting array of biological resources: elk, gray wolves, grizzly bears, bald eagles, Douglas-fir, ponderosa pine, spruce-fir, and many others. Rapid population growth, nonindigenous species introductions, and urban expansion threaten the resources of the region, however. The population in the surrounding areas has greatly increased since 1950; for example, both Utah and Colorado have experienced a 150% population increase. This rapid population growth has increased demands for water and power and has altered habitats. Habitat loss and population-control programs are responsible for an estimated 98% decline in prairie dog populations. Prairie dog ecosystems are valuable in the Rocky Mountain foothills because they support 170 vertebrate species and contain more specialized plants and insects than adjacent areas.

While restoration of greenback cutthroat trout has been successful, three other native cutthroat trout subspecies are extinct. Introductions of nonindigenous fish severely threaten other native fish. The one remaining native trout species is threatened and is a primary post-hibernation food source for grizzly bears. As in other parts of the nation, bald eagles and peregrine falcons are recovering from declines caused by pesticides. At the same time, habitat loss, introduced species, and environmental contaminants are all contributing to declines of amphibians in the Rocky Mountains. For example, western toads now occupy less than 20% of their previous range. Although gray wolves were reintroduced into the Greater Yellowstone ecosystem in 1995 and their status is improving, the species occupies less than 10% of its historical range.

Great Basin-Mojave Desert: This area between the Sierra Nevada, the Transverse Ranges, the Rocky Mountains, and the Columbia and Colorado plateaus harbors a rich biological diversity. Great topographical relief and an arid, continental climate provide conditions for unique plants and animals. Because of the region's arid nature, aquatic habitats are at a premium and are very critical (Fig. 11). More than 75% of the species in the region are strongly associated with riparian, or streamside, vegetation. Unfortunately, much of this vegetation has been degraded by water diversions, agriculture, and grazing. Grazing, in particular, has changed the character of these habitats in the Great Basin, reducing biodiversity and enabling nonindigenous species such as the tamarisk to become dominant. Water diversions for irrigation and urban growth lower levels of surface waters and cause increases in total dissolved solids and some heavy metals, threatening biological resources of Mono and Great Salt Lakes. The unique plant diversity of this region's terrestrial ecosystems is threatened by urbanization, grazing, fire suppression, and nonindigenous species, such as cheatgrass. More than 99% of the sagebrush-grass zone, for example, has been negatively affected by livestock.

Biological populations reflect the impacts on habitats. Of 131 species and subspecies of fish that histori-

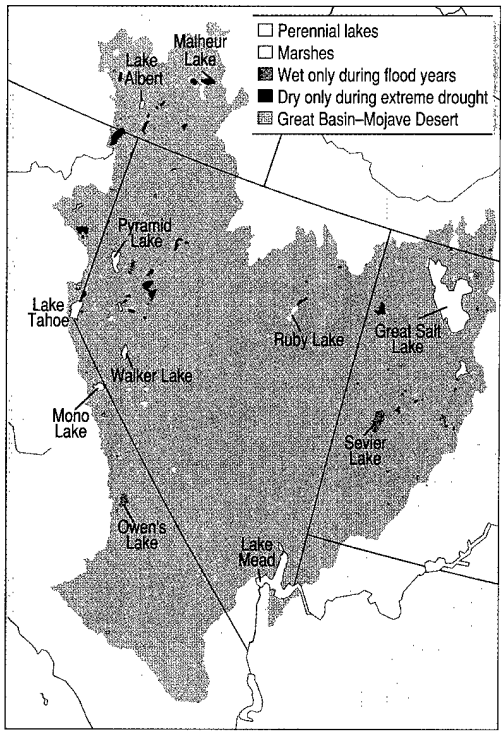

Fig. 11. Terminal wetland ecosystems in the Great Basin—Mojave Desert region.

cally occurred in the Great Basin-Mojave Desert, 10 are extinct and 75 (62%) are listed, candidates for listing, or of concern. The Amargosa toad is a candidate for listing as endangered, but trends of other amphibians are still unknown. Trends in many bird species are unknown because of limited sampling and high variability. Still, because many of the region's species depend on wetland and riparian habitats, which are being destroyed and degraded, researchers are concerned that declines are widespread.

Southwest: The southwestern United States is a land of extremes, and as with the Great Basin, the variation in topography and climate has produced great biological diversity. Widespread grazing of domestic livestock, suppression of natural fire, and commercial forest logging have altered the biological resources of the Southwest. Because of the variation in habitats and their biotic communities, each responds differently to human-induced stress. For example, fire suppression in ponderosa pine forests, which cover extensive portions of the Southwest, have reduced understory plants and have caused a buildup of needles that disrupts nutrient cycling and contributes to poor tree growth. Grazing, which occurs in almost all of these forests, replaces palatable plant species with thorny or poisonous species, thus reducing diversity further. More than 85% of the ponderosa pine forests have been significantly and negatively impacted by grazing and fire suppression. In desert shrublands and semidesert grasslands, which form a diverse mosaic in the arid Southwest, grazing and fire suppression favor a vegetation shift from grasses to shrubland, thus inviting nonindigenous species to become established. Between 1974 and 1987, grassland cover declined by 35%; the nonindigenous honey mesquite shrub now dominates nearly 70 million acres.

As with other arid ecosystems, the Southwest aquatic and riparian habitats are invaluable. Habitat loss due to dams, groundwater pumping, and pollution have contributed to jeopardizing more than 48% of the region's fish fauna. Investigations have also indicated declines in the region's leopard frogs, but the status of many amphibians and reptiles is unknown. The Southwest has the largest number of native mammal species, although several have been extirpated, including the grizzly bear and gray wolf. Smaller mammals may be of even greater concern. For example, of the 30 species of bats, one-third to one-half are now considered sensitive.

California: Because parts of California are included in other chapters, this chapter focuses on westside California, a very distinctive region because of its topography and Mediterranean climate. Ecosystems in California have been heavily altered (Table 1) by agriculture, grazing, urbanization, and timber harvest. More than 85% of the old-growth coast redwood forests have been logged, reducing dependent species. Native California prairie has almost disappeared because it has been converted to agriculture or to nonindigenous annual grasslands. Similarly, more than 95% of the region's historical wetlands have been destroyed or modified. These habitat changes, along with nonindigenous species, have negatively affected species trends—57% of fish species are extinct or on the road to extinction if present trends continue; 40% of the salamanders and 54% of the frogs are given or are in need of some sort of protection. Birds have also declined in California. In the 1970's, for example, 10-12 million waterfowl wintered in or migrated through California, with the great majority relying on Central Valley habitats. More recently, only 2.5 million waterfowl wintered in the Central Valley. Additionally, of the 342 species of land birds in this region, 21.3% are listed as state or federally threatened and endangered species.

Table 1. Human-caused reductions in westside California plant communities and formations (after Noss and Peters 1995).

Community/formation	Vegetation reduced (percent)
Native grasslands	99
Needlegrass steppe	99.9
Southern San Joaquin Valley alkali sink scrub	99
Southern California coastal sage–scrub	70–90
Vernal pools	91
Wetlands	91
Riparian woodlands	89
Coast redwood forest	85

Pacific Northwest: The Pacific Northwest has a wealth of natural resources, which are used for a variety of purposes. This chapter addresses the status of four primary areas of resource concern: old-growth western forests, forests east of the Cascades, eastside rangelands, and aquatic ecosystems. Logging has drastically reduced the amount of old-growth forests; much of the remaining old-growth forests occur in stands smaller than 400 acres. The combination of old-growth forest removal and fragmentation has negatively affected many species. Three of the seventeen bird species that are closely associated with these forests and for which there is reliable population trend information have shown significant long-term downward trends, whereas none show upward trends. In eastside forests, selective harvest, grazing, and fire suppression have greatly altered the forests—in some areas as much as 98% of the old-growth ponderosa pine has been logged or lost. More than 99% of the fertile Palouse Prairie grasslands of southeastern Washington, as well as adjacent areas in Oregon and Idaho, were converted to agriculture, and 2-2.5 million acres of grassland and sagebrush steppe have been replaced by nonindigenous vegetation, primarily because of overgrazing.

Bird species have reacted differently to changes in rangelands. Whereas 25 bird species show downward population trends, especially in

those species associated with grassland and shrub-steppe habitats, several raptor species show long-term upward trends. As of 1992, land managers listed 144 plant species in Oregon and Washington because of their rarity, but few were monitored for trend information. Aquatic habitats have been impacted as well. Ninety-five percent of the streams surveyed throughout Oregon had been moderately or severely degraded, primarily by logging activities, but potential for restoration of some of these streams remains high. The plight of salmon in the Pacific Northwest remains problematic (Fig. 12). Habitat degradation, dams, overharvest, and ocean conditions all contribute to continued declines of salmon. Evidence of the widespread declines in frogs is also found in the Northwest. The spotted frog was once widespread in a variety of habitats on both sides of the Cascades but is now nearly extirpated on the westside.

Alaska: Alaska's vast size, small population, and cold climate have protected the state from many of the negative effects on biological resources seen in the conterminous United States. With limited development, biological resources mostly respond to natural processes—unsuppressed wildfires, climatic events, and natural population variability. However, for many biological resources in Alaska, trend information is nonexistent. Harvest has a major impact in this region, particularly on fishery resources. Freshwater fish stocks in the interior are declining, especially those reachable by road. In the Susina River drainage, for example, the harvest of wild rainbow trout declined by 50% during the last 10 years, despite a doubling of the time spent fishing. Harvests of whitefish in the Tanana drainage dropped from 26,810 fish in 1986 to 739 in 1991. Salmon populations seem to be stable, except for chum salmon in some areas. Wildlife species have experienced some negative effects due to harvest, but many populations, such as some caribou herds, are at record high numbers. Introduced species have caused some problems. For example, the Aleutian Canada goose was nearly extirpated because of predation from introduced foxes, and an introduction of caribou to Adak Island threatened habitat of endangered plants when the caribou population exceeded carrying capacity.

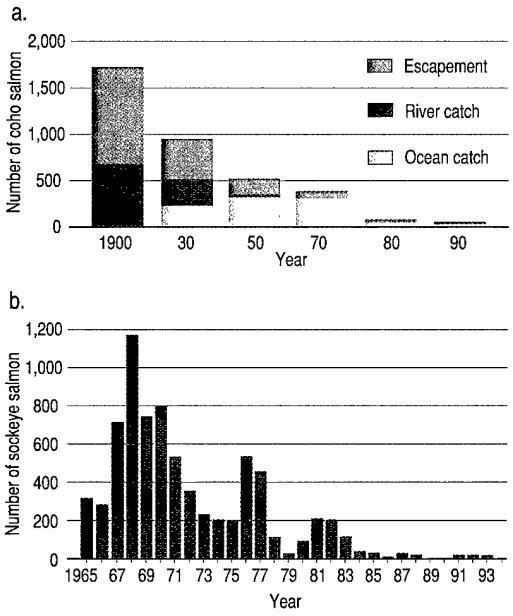

Fig. 12. Examples of declining populations of anadromous salmon: a) estimated abundance of coho salmon on the north coast of Oregon (adapted from Kostow 1997) and b) counts of sockeye salmon at upper dams on the lower Snake River in Idaho (adapted from Hassemer et al. 1997).

Hawaii and the Pacific Islands: The Hawaiian archipelago is the most isolated island group of comparable size and diversity on Earth. This isolation results in a high percentage of unique species. Oceanic islands, however, are quite vulnerable to biological invasions, and the Hawaiian archipelago has been severely affected by nonindigenous species. For example, wild pigs brought to the island cause significant damage to forests by eating tree fern trunks, rare plants, and earthworms, and by helping spread seeds of non-native plants (Fig. 13). Introduced goats also destroy native vegetation to the point

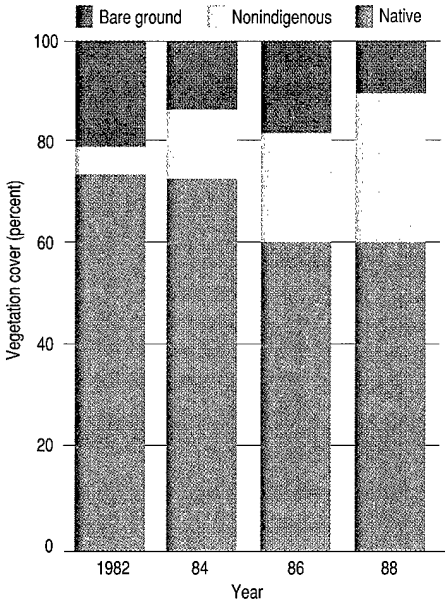

Fig. 13. Graph showing invasion of nonindigenous plants resulting from pig damage to montane bog sites on East Maui, 1982—1988 (from Medeiros et al. 1991).

where high goat densities can result in obliterated landscapes. Eradication efforts for both species are under way in several areas. Mosquitoes, which are not native to the region, are significant invaders because they help spread avian malaria, which has harmed many native birds. About 90 nonindigenous plant species pose significant threats to Hawaiian ecosystems. Some plants, such as miconia, can out-compete native species to create single-species stands or can even alter ecosystems processes.

The most spectacular land-bird assemblage ever found on any remote ocean archipelago evolved in the Hawaiian Islands, but this assemblage has been significantly depleted through human actions. Of the 76 species of perching birds or songbirds that lived in Hawaii, 31 are known only as fossils. Of the remaining 45, 19 are extinct and 18 are federally listed as endangered.

Marine Resources: A range of human activities affects living marine resources, including fishes, marine mammals, and marine birds. Increasingly intensive fishing efforts, in conjunction with the use of more sophisticated fishing gear and electronics, have resulted in gross over-

fishing of some marine populations. Associated with fishing is bycatch, when nontarget animals are taken in fishing operations. Both overfishing and bycatch are problems that have caused marine resource managers to create controlled access to fishing, whereby catch quotas are allocated to individual fishing vessels instead of allowing free and open access. Quota allocation to individual vessels is gaining acceptance.

Habitat alterations in rivers and estuaries, as well as in coastal zones, are a result of urbanization. Urbanization alters freshwater flows, increases erosion, introduces toxic chemicals and other contaminants into the waters, furthers the introduction of nonindigenous species, and degrades the marine habitats essential to living marine resources. Numerous demographic trends suggest that these conditions and threats are not likely to change soon. Some 50% of our population is estimated to live within a 2- or 3-hour drive of major freshwater systems (the Great Lakes) or coastal waters. As the nation grows, there will be further population growth in coastal zones. Our desire to live within sight of the ocean has never abated and, increasingly, urban dwelling areas are being developed on or near shorelines. Often these developments severely and negatively alter coastal and marine ecosystems and harm living marine resources.

Another major issue today is the mitigation necessary to protect endangered or threatened species. A recent example of this situation is with certain salmon runs in Pacific coast streams. The use of river waters for irrigation, power generation, and domestic consumption by large urban areas has compromised these streams and the survival of the salmon runs.

Many natural changes in the dynamics of ecosystems also may exacerbate the effects of the factors just listed. For instance, attention to global warming over the past two decades is now culminating in data that show widespread climatic effects on living marine resources. Articles in recent issues of major scientific publications indicate a progressive subtle warming of Pacific coastal waters and, consequently, an extirpation of certain species that would have been found in these waters a half-century ago. Similar trends have been speculated about and, to some degree, measured in shelf waters as well as in the coastal zone of the northwest Atlantic.

On the whole, the outlook for the welfare of the nation's living marine resources is guarded, with a need to remain vigilant. The crash of some groundfish fisheries, the poor welfare of some Pacific coast salmon stocks, and declines in some marine mammal populations are examples of situations that need special attention. Although many other of the nation's marine resources are in good condition, they too must be attentively managed and conserved under a suite of federal laws and international treaties. The science of the marine environment and the state of its resources must be improved, for without reliable scientific knowledge, resource use and management must necessarily be more conservative.

This is an executive summary and the full report may be cited as follows:
Mac, M. J., P. A. Opler, C. E. Puckett Haecker, and P. D. Doran. 1998. Status and trends of the nation's biological resources. 2 vols. U.S. Department of the Interior, U.S. Geological Survey, Reston, Va.

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Ecosystem Recovery Following a Catastrophic Disturbance: Lessons Learned from Mount St. Helens

On 18 May 1980, the eruption of Mount St. Helens volcano removed or leveled 350 square kilometers of old-growth and younger-aged forests and dramatically altered all types of ecosystems within this area (Fig. 1). Before the eruption, this landscape was typical of those found throughout mountainous regions of the Pacific Northwest: dense, temperate coniferous rain forests, with large areas partially modified by timber harvest activity, and sparse alpine vegetation occurring at higher elevations above treeline. Crystal clear lakes and cold, fast-flowing streams were common. In contrast, the eruption created a starkly barren landscape that bore little resemblance to preeruption conditions.

Although the eruption resulted in catastrophic loss of human life, wildlife, and forests, subsequent study of ecosystem recovery has revealed important insights regarding the role of natural disturbance in regulating the productivity and biodiversity of a variety of Northwest ecosystems. The range of disturbance caused by the eruption and the resulting spatial mosaic of disturbance types provided a unique opportunity for ecologists to study how large-scale disturbances influence natural ecosystems.

Volcanism and Western Montane Ecosystems

Within the scale of a single human lifetime, the eruption of Mount St. Helens appears to be an extraordinary and unique event, a disturbance that dramatically altered the local environment but also an event so unusual that it would seem to have little relevance to understanding the "normal" processes that generally shape ecosystems of the Pacific Northwest. Closer inspection, though, has revealed that such eruptions have greatly affected ecosystems throughout the mountainous regions of the Cascade Mountains and the Sierra Nevada. For example, Mount St. Helens has erupted more than 20 times within the last 4,500 years, an average of once every 225 years (Crandall and Mullineaux 1978). Before 1980, Mount St. Helens last erupted 123 years ago. These periods are well within the 500–600 years that it takes to produce an old-growth Douglas-fir forest (Franklin and Hemstrom 1981).

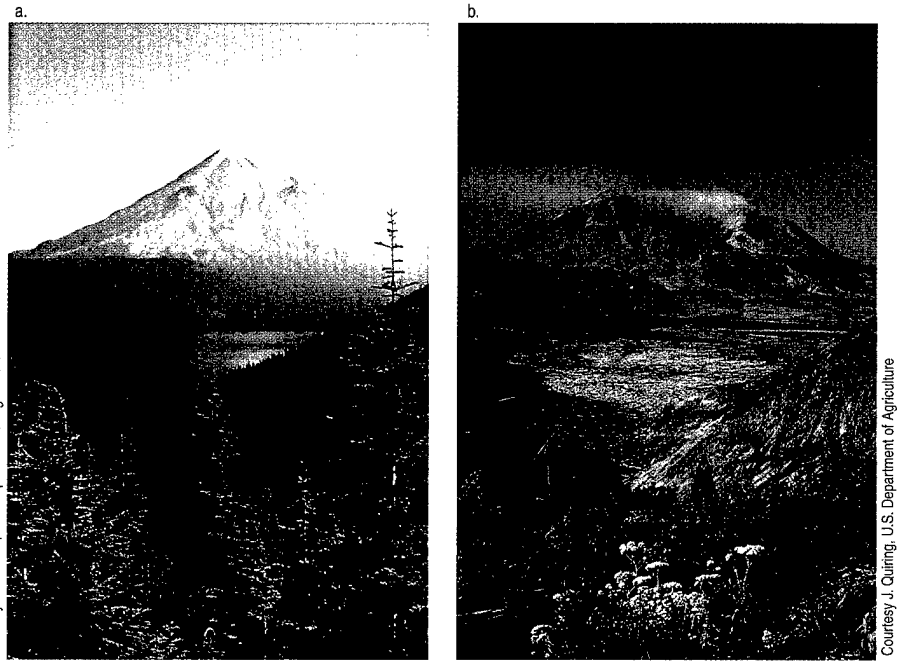

Fig. 1. The landscape from Bear Pass, Mount St. Helens a) before and b) after (1992) the 1980 eruption. The volcano is in the background; Spirit Lake is in the middle of each picture.

Natural Disasters, Biodiversity, and Ecosystem Recovery

The eruption of Mount St. Helens instantly created a large-scale natural experiment that ecologists could use to evaluate theoretical ideas about how entire communities recover from disturbance and the mechanisms most important in recovery. We present some examples of the lessons ecologists have learned by conducting long-term studies of both terrestrial and aquatic ecosystems after the eruption. These examples illustrate situations in which theory accurately predicted observed recovery or in which we learned something fundamentally new.

Terrestrial Vegetation

Ecologists recognize that several mechanisms may act singly or in concert to influence the development of plant assemblages. It is not always clear, though, under what conditions different processes will dominate. The eruption of Mount St. Helens had highly variable effects on vegetation. In general, both initial plant survival and rates of recovery were inversely related to disturbance intensity. It is important to recognize, however, that the dramatic visual differences between pre- and posteruption landscapes were due to the removal or leveling of a few tree species. Vegetation responses differed considerably within two distinct zones of disturbance—the blowdown zone and the pyroclastic flow zone.

In the blowdown zone, overstory trees were either blown down or snapped off, and understory species were buried under as much as a meter of ash. Wind-dispersed herbs, such as fireweeds and composites, colonized the barren surfaces of the blowdown zone during the first year following the eruption. Since then, they have spread by seeds and vegetative growth and dominated many areas within 4 to 7 years (Halpern et al. 1990). In general, this pattern fits classic ecological theory—early successional species colonize and exploit nutrient-poor, disturbed substrates that retain little water.

Not all patterns were this predictable. In several upland areas of the blowdown zone, the recovering plant assemblages are bizarre mixtures of late-successional understory and pioneering species—assemblages we never would have expected to encounter (Halpern

et al. 1990; C. M. Crisafulli, U.S. Forest Service, Amboy, Washington, unpublished data). The reasons for these kinds of assemblages are related to the survival of a few late successional species and the colonization of other species. Although our initial inspection suggested that no species survived, some local patches escaped complete destruction. Four factors appeared to increase the probability that individual plants would survive in these locations: (1) patches of late-lying snow shielded some plants from the blast; (2) plants living on the lee sides of ridges were not exposed to the main force of the blast; (3) some plants survived in soils on the exposed rootwads of large blown-down trees; and (4) some plants were able to resprout from perennial root stock on steep slopes where erosion quickly cut through ash deposits (Frenzen and Crisafulli 1990; Halpern et al. 1990).

Of the individuals which survived the initial eruption, some flourished, whereas others perished quickly because of the dramatic change in conditions. Because the overstory that had formerly intercepted nearly all sunlight had been removed, surviving saplings of Pacific silver fir and mountain hemlock previously in the forest understory experienced tremendous growth and were producing cones by 1993. The survival of these few individuals will greatly accelerate the overall recovery process, because seeds will not have to arrive from distant sources beyond the disturbed area. These new conditions, though, created an intolerable stress for other survivors. Shade-adapted understory herbs, such as wintergreen and fawn lily, were unable to tolerate the posteruption conditions of increased light, temperature, and desiccating winds, and soon perished.

In contrast to the slow recovery of upland vegetation, most riparian areas recovered rapidly. Bank erosion quickly re-exposed some buried shrubs and trees such as salmonberry and willow. Fragments of some species—such as willows—were swept downstream of their original locations and then sprouted. Surviving plants quickly produced wind- and water-dispersed seeds that colonized wet shorelines.

Within the pyroclastic flow zone, no individuals survived. Considering the intensity of destruction, classical successional theory predicts a long successional recovery in which mosses, liverworts, and lichens or wind-dispersed herbs establish first, followed by shrubs and then conifers. Which species colonize and when they actually establish are theoretically governed by their dispersal abilities, subsequent alteration of the site by colonizing species, and competition among late-establishing species. Studies conducted on the pumice plain within the pyroclastic flow zone, however, show that this classical pattern of succession has not necessarily happened. Many areas within the pyroclastic flow zone remain sparsely vegetated 15 years after the eruption, and late successional species (5 species of conifers, sword ferns, and lady ferns) have colonized along with wind-dispersed herbs such as fireweed and pearly everlasting (del Moral and Wood 1993; Crisafulli, unpublished data). Still, only two main types of plant assemblages have developed here: willow–herb communities that are restricted to a few springs and seeps, and patches of lupines (C. M. Crisafulli, W. M. Childress, E. Rykiel, Jr., and J. A. MacMahon, Amboy, Washington, unpublished manuscript).

Although the prairie lupine lacks specialized structures for long-distance dispersal, this short-lived perennial herb was among the first species to arrive on the pumice plain and has profoundly influenced the first 15 years of succession (Fig. 2). A few critical attributes appear responsible for its successful establishment. First, lupine has a mutualistic relationship with a root bacteria that fixes nitrogen, and the soils of the pumice plain have extraordinarily low amounts of nitrogen (Halvorson et al. 1991). Second, because this species produces prodigious amounts of seed, populations are spreading at a rapid rate from centers of initial establishment (Crisafulli, Childress, Rykiel, and MacMahon, unpublished manuscript). When these populations are dense and growing vigorously, they inhibit colonization by other species, but once they die, they leave a nutrient-rich substrate where other species can thrive (Morris and Wood 1989).

The establishment of several species of conifers also appeared to defy conventional wisdom. Conifers are poor long-distance dispersers because they have heavy seeds, and they require the presence of symbiotic soil fungi called mycorrhizae to survive. Scientists did not believe that the barren soils of the pumice plain could support these fungi, but the fact that these species arrived and are persisting suggests that we do not fully understand either their dispersal dynamics or the conditions they require to successfully establish.

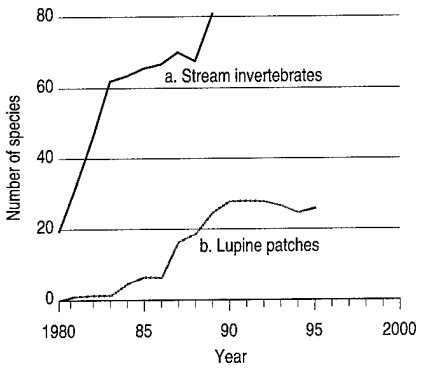

Fig. 2. Changes following the 1980 eruption in a) the number of invertebrate taxa in Clearwater Creek within the blowdown zone, and b) the number of terrestrial plant species within lupine patches of the pyroclastic flow zone.

Birds

Ecologists probably know more about birds than any other group of animals, and many ecologists would predict that two factors strongly influence the development of a bird community: structural complexity of the environment should affect species diversity, and the type and abundance of resources should influence the types of birds occurring in an area. Monitoring over a 12-year period generally confirmed theoretical predictions, although there were a few species-specific surprises. When we consider the natural history of each species, even these surprises were understandable, although not necessarily predictable.

Undisturbed forests in this area have about 15 species of birds. No bird species survived in either the blowdown or pyroclastic flow zones, so recovery of the avifauna in both areas started in the complete absence of birds. The pattern of recovery differed greatly between blowdown and pyroclastic flow zones over a 13-year period (1980–1993; Crisafulli and MacMahon, unpublished data; Fig. 3), an anticipated result considering that the two zones differed greatly in structural complexity following the eruption and recovery rates of vegetation.

The physical environment of the blowdown zone following the eruption was complex but offered few food items for birds. Habitat consisted of tangled trees and their branches embedded in a deep layer of ash and pumice. Little living aboveground vegetation existed. Bird colonization in this zone occurred in two phases. Within a year of the eruption, seven species had colonized (dark-eyed junco, white-crowned sparrow, northern flicker, hairy woodpecker, mountain bluebird, American kestrel, and Vaux's swift); these species are either ground foragers that nest on the ground or in cavities, or species that fly from perches to forage. These birds occur in open landscapes with sparse vegetation, though colonization by Vaux's swift was initially surprising, because it traditionally had been thought to occur in association with mature or old-growth forests (Manuwal 1991). Its establishment suggested that what the swifts require is snag habitat, and not old-growth forest per se.

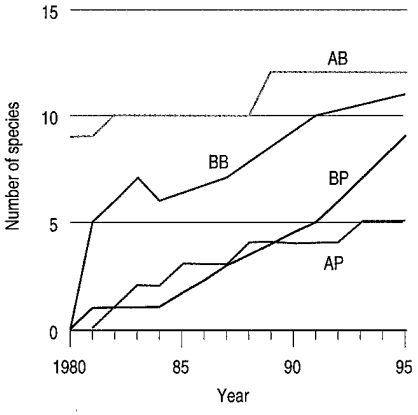

Fig. 3. Changes in number of bird and amphibian species in the blowdown and pyroclastic flow zones following the eruption. AB = amphibians in the blowdown zone, BB = birds in the blowdown zone, BP = birds in the pyroclastic flow zone, and AP = amphibians in the pyroclastic flow zone.

The second recovery phase occurred about 7 years after the eruption and was directly associated with the colonization and expansion of erect, woody vegetation (alder, willow, and cottonwood) along water courses. At this time, an entirely new assemblage of species colonized the blowdown zone, including yellow warblers, orange-crowned warblers, MacGillivray's warblers, willow flycatchers, and warbling vireos. The new species were added to those present rather than replacing them; all these species nest in deciduous shrubs and trees and forage either by gleaning insects from the surface of vegetation or by catching flying insects on the wing. After 15 years, the bird species richness was 70% that of undisturbed forest, but the species composition remains markedly different from the undisturbed forest.

Bird colonization in the pyroclastic flow zone, where no remnants of the preeruption landscape remained, was slower than in the blowdown zone (Fig. 3) and involved different species. This new landscape is stark and open, with undulating pumice hills and complex networks of rills and gullies; it presently supports bird assemblages with only 46% of the species richness of undisturbed forest. The assemblage that developed in this area was not initially anticipated, but its establishment makes sense in hindsight. These species comprised three subgroups, each with strong affinities for completely different habitat types. Red-winged blackbirds and savannah sparrows usually inhabit low-elevation wetlands or pastures; horned larks, rock wrens, and western meadowlarks are associated with shrub-steppe habitats; and gray-crowned rosy-finches and water pipits are normally found in high-elevation, alpine conditions. None of these species are normally found within montane coniferous forests, but the pyroclastic flow zone provided a new set of habitat conditions that mimicked conditions typically found in other locations.

Stream Ecosystems

Until recently, succession in stream ecosystems was thought to occur mainly in response to vegetation changes in the surrounding watersheds and riparian zones, which are known to influence both habitat features in streams and the abundance and type of food available to aquatic animals. Succession caused by competition and predation was thought unimportant since annual floods disturbed streams too frequently for biotic interactions to influence long-term successional dynamics. Research at Mount St. Helens has shown that succession in streams can be a long and ecologically complex phenomenon.

Three months after the eruption, we began an annual monitoring program of several streams in which disturbance varied from complete elimination of living things to a modest reduction in their abundance and diversity (Hawkins 1988). Data from the most severely disturbed streams show that invertebrate species richness increased very rapidly over the first 5 years following the eruption and continued to increase, though at a slower rate, up to 1990, the last year for which data have been compiled (see Anderson 1992; Fig. 2). By 10 years after the eruption, these streams had recovered about 80% of the invertebrate species typically found in an undisturbed stream.

Five species of vertebrates occurred in many of our study streams before the eruption (cutthroat trout, brook trout, shorthead sculpin, tailed frog, and Pacific giant salamander). Although at least a few individuals of most of these species were observed soon after the eruption, recovery of densities varied greatly among species (Fig. 4). In many streams, all of these animals appeared to have been completely extirpated, but within 5 years of the eruption, modest to abundant populations of tailed frog tadpoles and sculpins existed even in heavily disturbed streams. We recorded the highest densities of tailed frog tadpoles and shorthead sculpins ever reported by 4 and 5 years after the eruption (Hawkins et al. 1988; C. P. Hawkins, Utah State University, Logan, unpublished data). In contrast, the recovery of trout and giant salamanders has been slow; 15 years after the eruption, their densities are only 5% to 10% of those observed in undisturbed streams (Hawkins, unpublished data).

We believe the existence of protected refugia was largely responsible for preserving a few individuals in even severely disturbed streams. These refugia appear to be the source of the populations that established later. The eruption occurred in late May when there was still snow cover on some hillslopes and ice on some lakes. At least a few trout are known to have survived

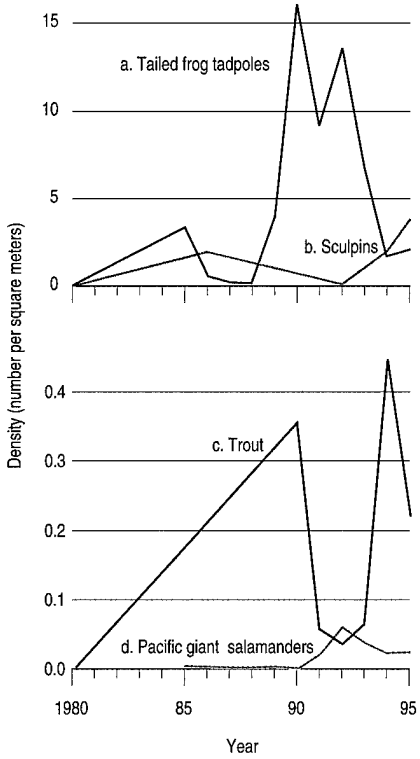

Fig. 4. Changes in densities of a) tadpoles of the tailed frog, b) shorthead sculpin, c) trout (cutthroat trout and brook trout), and d) Pacific giant salamander in heavily disturbed streams in the blowdown zone.

in the ice-covered lakes (Crawford 1986) that served as sources of colonists for many streams. Second, we believe that a few sculpins and adult tailed frogs survived in small springs that were also probably snow-covered and topographically shielded from the full force of the eruption.

One clear lesson that emerged from these studies was that appearance of the surrounding landscape is not necessarily related to the quality of stream habitat. Although the floodplains and hillslopes surrounding many of these streams were still largely barren, conditions within streams quickly recovered sufficiently to support an abundant and diverse fauna (Hawkins 1988; Anderson 1992). In general, amphibians are thought to be highly sensitive to landscape alterations that affect either adult habitat conditions (temperature, humidity) or the availability of breeding sites. We thought amphibians would have been exterminated by the eruption, but we have found that many species survived and in some cases

recovered rapidly (MacMahon 1982; Zalisko and Sites 1989; Crisafulli, Hawkins and MacMahon, unpublished manuscript; Fig. 3).

Aquatic species generally had higher survival rates than terrestrial species, and among aquatic species, pond breeders fared better than stream dwellers. At the time of the eruption, aquatic species were present as both terrestrial adults and aquatic larvae. Because ice, snow, and cold water buffered the aquatic biota in many high-elevation lakes and streams from the impact that devastated neighboring terrestrial environments, some individual animals that were in water or under snow survived (frogs and toads that were hibernating, tadpoles of the tailed frog, and larval and neotenic salamanders). We think these individuals served as a source of colonists to lakes and streams at lower elevations where aquatic biota appeared to have been completely extirpated. Dispersal of colonists therefore appears to have radiated from epicenters of survival within the blast zone rather than from distant, unaffected populations.

One of the most astonishing events that we observed was that four species of frogs and toads and one species of pond-breeding salamander had colonized all available lake habitats within 5 years of the eruption even though absolutely no dispersal corridors existed between lakes. These animals were dispersing great distances over nonforested, barren pumice substrates. Another surprise was that the eruption may have actually created more aquatic habitat than existed before the blast.

In contrast to the aquatic species, three species of salamanders in the family Plethodontidae, which is a largely terrestrial family, seem to have been eliminated from the entire disturbed landscape. The only species of this family to survive was a semiaquatic species. Because all three of the extirpated species are thought to have low mobility and require mesic forest conditions, we expect these species to be absent from this landscape for decades or centuries.

Not only has the eruption of Mount St. Helens provided many insights into the vulnerability of many types of plants, animals, and ecosystems to a catastrophic disturbance, but it has also shown us that many of our ideas about succession and the factors that influence the colonization and establishment of species need refinement. In almost every case in which we were surprised at a response, we had lacked sound information on the basic biological attributes of a species. If nothing else, the study of biotic recovery at Mount St. Helens has convinced us that we must continue to describe, document, and quantify the basic biological features of this nation's flora and fauna.

See end of chapter for references

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The blowdown at Tionesta Scenic Natural Area is another example of a natural disturbance—a particularly large and spectacular one. Similar large disturbances have occurred elsewhere. The famous fires in Yellowstone National Park in 1988 are an example, and the history of that landscape reveals that such fires have been a periodic occurrence (Romme 1982; Turner and Romme 1994). The effects of Hurricane Hugo in 1989 (Walker et al. 1991) and the eruption of Mount St. Helens in 1980 (del Moral 1993; also see box on Mount St. Helens) are also notable examples. Other landscapes, such as the boreal forests of the Boundary Waters Canoe Area Wilderness, the coastal sage shrublands of California, and the Pinelands of Long Island, have a history of periodic fire (Fig. 26). Forests of the Midwest and Southeast are affected by tornadoes, some leaving swaths of downed trees up to 1.6 kilometers wide (Pickett and White 1985).

There are many other kinds of natural disturbances; some are restricted to particular landforms. Flooding reworks the channels in broad, seemingly slow-moving rivers, in small brooks, and in desert arroyos (Fisher et al. 1982). Floods lay down new surfaces, uproot or bury existing plants, and bring new seeds. The animal communities of streams can be severely affected as well, with populations of insect

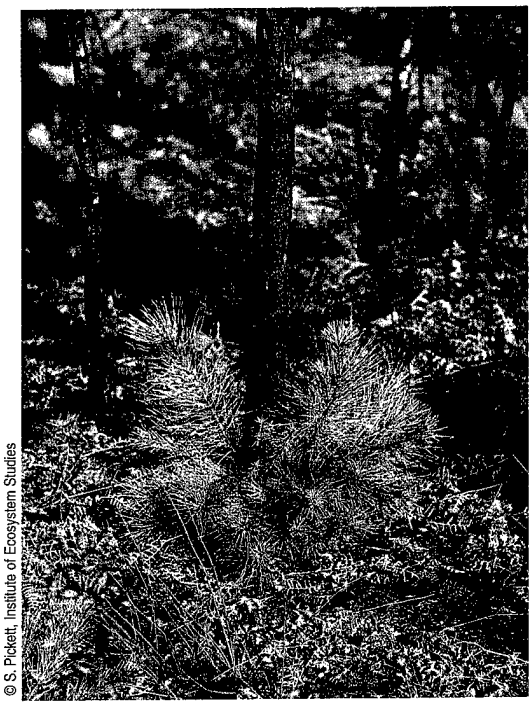

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Fig. 26. A burned pitch pine resprouting after a fire. Pitch pine is one of the few pine species capable of resprouting from root crown and stem, contributing to its dominance in frequently burned pinelands and barrens in the eastern United States. The other woody species in this community in the New Jersey Pinelands, such as bear oak and the heath species, are also capable of resprouting after fire.

larvae swept downstream and fish displaced (Fig. 27). Landslides and snow avalanches can affect mountainous regions. Sometimes mass movements of soil and rock or of snow can be set off by earthquakes, heavy rains, or by instability in the mass itself. Diseases and herbivorous insects can occasionally open gaps by causing mortality of the largest organisms in a community (Knight 1987; Pacala and Crawley 1992). So the range of events and the variety of sizes of the openings they create in communities are large. Patches of early successional communities, open space, and resource-rich patches often owe their existence to natural disturbance. Thus, disturbance is a widespread, if periodic, source of some of the heterogeneity to which biological diversity is a response (Pickett 1976; Huston 1979).

Disturbance can also be generated as a result of long-standing natural stresses in a community. For example, long periods of drought can ultimately lead to the deaths of many individuals in an ecosystem, create openings in the community, and alter the availability of other resources such as nutrients. The dust bowl of the 1930's is an example of disturbance in a human-managed system triggered in part by extreme climatic fluctuation. Of course, that natural stress would not have had such severe effects without the intense human use of the systems. However, even in unplowed prairie, the extreme droughts of the 1930's had significant ecological effects by changing the proportions of the species in the communities (Weaver and Albertson 1943). Such disturbances can be thought of as diffuse compared with the precise opening of a community by, for example, a lightning strike.

An important characteristic of disturbance remains to be explored here. Disturbances of a particular type have a generally characteristic distribution through time in a specific system and climate. Larger, more intense events (Fig. 28) are less frequent in time, ranging from many centuries to a millennium for huge blowdowns at a spot in eastern forests (Pickett and Thompson 1978; White 1979). In contrast, single tree gaps are formed on average about every 120 years in moist eastern deciduous forests. Large, lasting floods are less frequent than small, temporary spates. Huge crown fires are low-frequency events because of their dependence on high fuel accumulations and extremely dry weather.

The mixture of disturbance types, their characteristics, and their temporal and spatial patterns in a particular landscape and climate, can be defined as a disturbance regime. Disturbance regimes are complex because they have so many aspects. A disturbance regime is characterized by the spatial and temporal distribution of type, size, shape, and temporal frequency of disturbance. The term regime should not be taken to mean that the patterns are rigid. Rather, the patterns are probabilistic—distributed with some unpredictability in time and space. Exactly when a given spot on the ground will experience a disturbance of a certain kind and intensity is somewhat unforeseeable. What is absolutely certain, however, is that such natural disturbances will occur (Bormann and Likens 1979; Denslow 1980; Bazzaz 1983).

The pattern of natural disturbance molds the biological diversity of a region. Plants and

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Fig. 27. A creek in the Inner Bluegrass region of Kentucky. Although calm when this photograph was taken, the stream is subject to intense flooding during the spring freshet and after particularly heavy thunderstorms in summer. Such intense floods scour the channel and greatly alter the community of stream invertebrates. The altered sediment conditions can also affect algae and diatoms that grow on the rock surfaces.

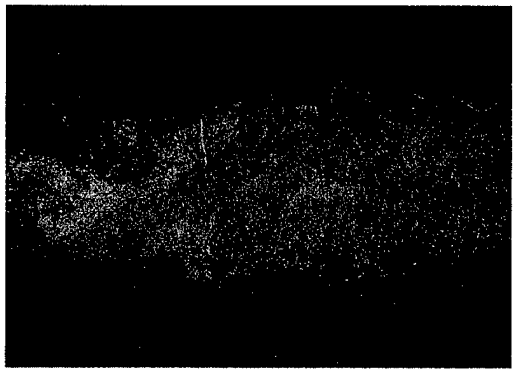

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Fig. 28. A false-color infrared aerial photograph of a portion of the tornado blowdown at the Tionesta Scenic Natural Area, Pennsylvania. This photograph was taken by U.S. Forest Service personnel 2 weeks after the tornado in 1985. The red color indicates intact and healthy plant canopies. Careful examination of the photograph reveals the spiral pattern of downed logs within the blowdown, reflecting the rotary motion of the tornado winds. The tornado began to touch down just to the left of the frame of the photograph.

animals must respond to the disturbance regimes in the areas they inhabit. In fact, the assemblage of organisms in a region reflects the disturbance regime to a large extent (Denslow 1980). A large or permanent change in the disturbance regime is expected to alter the kinds and numbers of organisms in a landscape (Clark 1986). This is one of the key insights of ecology, indicating that biological diversity depends on processes rather than just static conditions (Loucks 1970; Reiners 1983; Walker 1989). In fact, static conditions are rare or nonexistent.

Very severe disturbances can reduce biological diversity. Likewise, disturbances that promote the establishment of invasive exotic species that in turn reduce native biological diversity have a negative influence. Very frequent disturbances tend to reduce the number of species, because few species have the short life span and rapid growth to be able to respond within the intervals between disturbances. Nevertheless, ecologists must understand how disturbance fits with the other ecological factors that affect biological diversity. This view of organisms and the assemblages and ecosystems of which they are a part—responding to ever-changing landscapes—can be summarized as patch dynamics (Pickett and White 1985). The natural world is punctuated by disturbances and other episodic events, creating patches in which environments differ from their surroundings. Different organisms die, leave, survive, or invade at characteristic rates in the opened patches, and the assemblages in those patches change through time, undergoing succession (Whittaker and Levin 1977; Bormann and Likens 1979). Organisms may migrate between patches, exploiting those that match their requirements or offer them shelter from predators and other consumers. Organisms may avoid or be extirpated from those patches that do not satisfy their requirements or where the successional change in the patch moves the environment beyond the range of tolerance of the organisms.

Patchy landscapes can be reflected in the structure of populations. Populations can be subdivided into units that occupy separate patches, and migration among the patches may be an important feature in the persistence of the entire population. Geographically subdivided populations that are connected by migration, either directional or reciprocal, are called metapopulations (Pulliam 1988). Metapopulations can function in several ways (Pulliam 1988; McLaughlin and Roughgarden 1993; Harrison 1994). One mode is for the whole array of patches to serve as a joint, interconnected reservoir of organisms. Alternatively, some of the patches can act as sinks, siphoning individuals from more suitable patches. Finally, there can be a persistent core that supplies satellite populations. Patch dynamics can interact with all of these subdivided population structures. Knowing the nature of patch dynamics and the degree and nature of population subdivision is necessary for successful management or maintenance of biological diversity (Heinselman 1973; Gilbert 1980; McNaughton 1989; Menges 1990).

Homogenization

So far, the processes and patterns in nature that contribute heterogeneity to physical and biological aspects of the environment have been presented. Heterogeneity is the primary ecological filter that enhances biological diversity. The rich history of evolution has generated a diverse array of organisms that can respond to the heterogeneity of the natural world. Many features and behaviors of organisms create additional heterogeneity. But biological diversity is not only the result of processes that generate heterogeneity—homogenizing forces play a role too, but a negative role (Huston 1979; Pickett 1980). Homogenization reduces the number of opportunities for different species to exist in an area, thereby counteracting the generation and maintenance of heterogeneity. To fully understand biological diversity, the relative balance between homogenizing and diversifying forces must be assessed (Huston 1994).

There are natural and human-generated processes that cause homogeneity in nature. The natural force behind homogeneity that has been most often demonstrated by ecologists is competition. Competition is the joint use by two or more organisms of the same resource that is in short supply. If two competitors are unevenly matched, the one that captures the most of the resource in a place and over some interval will "win." The winner will displace the less effective exploiter of the resource. This observation has been generalized as the *competitive exclusion principle* (Hardin 1960; Aarssen 1983; Tilman and Wedin 1991): within an environment that supplies a uniform amount of a limiting resource, two competitors for that resource cannot coexist at equilibrium. There are many ways to state this important principle, but they all involve the assumptions that organisms are not perfectly matched in their competitive relations, that the competitive relations are direct, and that the environment is uniform in resource supply and the environmental factors that affect resource use by the organisms.

The competitive displacements suggested by the competitive exclusion principle are observed in many situations. One compelling example is in succession. The sequence of species reflects a ranking of competitive ability

for one or more resources with the more effective competitors becoming important in older communities (Bazzaz 1987). For example, successional turnover can be seen as reflecting different demands for light (Horn et al. 1989). The species that are important early in succession require high levels of light. In turn, the species that become important later in succession can tolerate lower levels of solar radiation. Thus, light becomes, in effect, less limiting to the plants. At the same time, other resources such as nitrogen build up in the soil. Therefore, the identity of the limiting factors shifts through succession, and the changes in species composition reflect the shift because species that are better competitors for light give way to species that are better competitors for nitrogen (Tilman 1988). The physiological, morphological, and architectural trade-offs mentioned in the first section of this chapter (explaining why organisms respond to heterogeneity) underlie the successional and competitive replacements. A species cannot effectively use the contrasting resource levels that appear in early versus late successional communities. Such trade-offs are universal features of organisms and drive competitive displacement.

Another factor that can drive homogenization—under certain specific conditions—is consumption. Predation, herbivory or browsing, and parasitism are three main ways consumption is expressed in nature (Fig. 29). If a consumer tends to use prey indiscriminately, then consumption can reduce diversity because all prey in an area are equally targeted and equally susceptible. In such a situation, all species are reduced in numbers, and the rare ones may be extirpated because they are all consumed, they exist in such low densities that they are unable to find mates, or because unpredictable variations in the environment kill them all.

Some disturbances can reduce biological diversity through homogenizing the environment—for instance, very large or very frequent disturbances. In the case of extremely large disturbances, especially those that are quite intense, environmental conditions can be made uniform over a large area. A relatively few species may find such sites suitable. Likewise, very frequent disturbances can exclude many species that take a long time to grow and mature. The high frequency of disturbances synchronizes an area so that few species match the conditions there.

The processes tending toward homogenization in nature are rarely unopposed (Denslow 1985). The fact that they are counteracted by a variety of physical and biotic interactions is what keeps our world so interesting, diverse, and functioning in a sustainable way. The homogenization that results from monotonous succession, competitive displacement, indiscriminate consumption, or large, frequent disturbances is opposed by a variety of processes. Fine-scale and moderate disturbance (Loucks 1970), differential predation and herbivory on the dominant or most abundant organisms (Petraitis et al. 1989), and the basic variability in the physical environment (Chesson 1985) counteract the tendency toward uniformity. The factors that generate homogeneity and the types and natures of the factors that oppose them are specific to an environment and time. Whether a factor shows up in the homogenizing or in the diversifying side of the ledger depends on the species that are present in the system, the resources available in the system, and possibly the role of humans. Let me give some examples.

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Fig. 29. A tree felled by beaver, illustrating plant consumption, a factor that can drive homogenization.

The dominant organisms—the ones that give the conspicuous structure to the community—can be struck down in patches by wind and fire or by herbivore outbreaks. American beech, which casts a shade that most other tree species cannot tolerate, is toppled by a severe windstorm after having stood in the canopy for perhaps two centuries. Suppressed saplings of other tree species take advantage of the light, water, and nutrients released in the gap. The dense, aromatic canopy of chaparral shrubs, which has been inhibiting the germination of wildflower seeds, is burned by the first severe fire in as much as 40 years (Fig. 30; also see California chapter). The next growing season, there is a raucous bloom. On a rocky seacoast, a dense, thick bed of mussels is battered and partially removed by a log carried in a storm surf. A variety of algae and sessile invertebrates, which had been excluded from the spot for years, now can attach to the rock and exploit the light or consume the plankton carried in by the tide. Rabbits that had been excluded from a formerly rich grassland are reintroduced, and species not seen for years now prosper and flower. All these types of heterogeneity—and many others—interact so that homogenization is foiled at every turn. The twists, convulsions, and surprises in nature generate opportunity for diversity.

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Fig. 30. Recently burned chaparral in southern California.

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Fig. 31. Plumed seeds of little bluestem. These seeds are awaiting dispersal by the wind, a biotic factor that can contribute to heterogeneity. Although the seeds are light and copiously plumed, most of them fall within a few meters of the plant that produced them.

Other biotic factors can contribute to heterogeneity as well. Dispersal might be thought of as a uniform, unrestricted phenomenon in nature. However, the patchiness that results from gravity, from the narrow focus of dispersing animals, or from the vagaries of wind and water flow, means that few organisms are distributed evenly in nature. For example, fish larvae, although microscopic and buoyant, can be captured in eddies, or the light, plumed seeds of many plants can be blown away in a single concentrated gust (Fig. 31). In short, dispersal is a chancy and nonuniform business in nature (McLaughlin and Roughgarden 1993).

But there is another source of homogeneity that is, in many cases, as strong or stronger than the ability of nature to generate variety. Human sources of homogeneity are many and pervasive (Goudie 1990). They include novel disturbances and stresses, alterations of natural disturbance regimes, and changes in the structure of landscapes, among others. They work on many scales, as well, from the global to the backyard.

Consider the backyard: the unbroken neighborhood lawn, one of the unique contributions of American landscape architecture and regional planning, is a potent force for homogeneity. The ideal lawn has been viewed as one comprising one or a few species—often Kentucky bluegrass—maintained at great investment of cost, energy, and chemicals (Bormann et al. 1993). The lawn may be bordered by a small number of evergreen shrubs, either cultivated varieties of natives or, more likely, exotic species. Perhaps in spring, bulbs of plants bred from ancestors in the Middle East—tulips and daffodils—will appear. But most of the growing season, there is an unremitting carpet of uniform green. Looking up the street, we shift to a coarser scale but still see a landscape of a homogeneous grid of blocks that disregards natural topography and hydrology (Fig. 32). Modifying the grid into sweeping suburban curves and quiet cul-de-sacs is no more biologically heterogeneous than the ancestral grid inherited from the Roman Empire.

Other examples of human homogenization abound (McDonnell and Pickett 1993). Parks bristle with tree species from Europe and Asia, resound with the songs of exotic birds, and burble with fountains supplied from reservoirs hundreds of miles away. Our farm fields grow perhaps one or two of the handful of cultivated species that feed most of the people on Earth, and they are laid out in huge uniform rectangles convenient to mammoth plows and combines. The hedgerows (Fig. 33), which may have harbored native plants and animals, have retreated to the house, where they persist as islands of shrubs and ornamentals in which domestic cats stalk and a mongrel dog lounges. Hilltops are shorn off to make way for houses and so reduce topographic heterogeneity, while interstate highways shrink the distances between ecologically different climatic regions. And indeed, in many places, the homogeneous farm fields give way to even more homogeneous parking lots for malls. Large clear-cuts are cleaned up so they look nothing like the regrowing biotic jumble at Tionesta Scenic Natural Area, and they are filled from the top to the bottom of their slopes with seedlings of the same tree species. The annual pulse of streams—rising in spring and falling in summer, with variation from year to year—is smoothed out to provide reliable navigation, water supply, and electrical power. Landscapes are manicured to maintain the same view year after year.

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Fig. 33. A hedgerow bordering a farm field in central Illinois. Agglomeration of family farms into larger units often is associated with the removal of hedgerows, which are corridors for the movement of wildlife and habitat for a variety of species. Hedgerows can also affect the flows of nutrients and water in landscapes.

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Fig. 32. A portion of the city of Poughkeepsie, New York. The regular grid has cut through hills and obliterated the valley of a small tributary to the Hudson River.

The lesson is clear. Industrial agriculture and forestry, uniform town planning, accidental or intentional transport of species, provision of energy, and expansion of the land base for housing are all homogenizing influences. Of course, all the services and amenities that these homogenizing processes generate are widely desired.

Biological diversity is a net outcome of processes favoring heterogeneity and processes favoring homogeneity (Pickett 1980; Huston 1994). Much of what humans do, either intentionally or accidentally, shifts the balance toward homogeneity and thus decreases

biological diversity. Biological diversity is a nonrenewable natural resource in the short term of human resource exploitation. Can human activities enhance or preserve heterogeneity? Can human land uses mimic better the heterogeneity that is such a key part of the natural world? Can development plans become more appropriately *patchy*? These questions emerge from the ecological understanding of the natural processes that determine biological diversity.

Research Needs

Understanding the natural processes maintaining the biological diversity of the United States may at first glance seem to require little additional work. The scientific literature provides a good basis for the overall picture of diversity as a net response to the processes generating heterogeneity on the one hand and those that reduce the crucial heterogeneity of the environment on the other. There is, however, need for much better knowledge about the subject of biological diversity itself, the processes affecting it, and the relation between the two (Pickett et al. 1994).

The most basic research need is to deepen the understanding of the biological diversity of the United States. I have taken the evolutionary richness of biological diversity as a given, but the biological diversity we see today is, in fact, a part of an ongoing evolutionary process. The ecological understanding summarized in this chapter rests on where the biological diversity has originated and how it has changed in time and space. The knowledge of evolutionary relations, geographic patterns, and the physical, chemical, and behavioral characteristics of organisms is the very foundation for conservation and use of the wild living resources of the United States. Improving the understanding of the basic raw material of biological diversity will require sustained research into the systematics of organisms. The needs are particularly pressing for taxonomic groups for which experts are few or collections of specimens are sporadic. Even in the case of well-known groups, the collections must be well-maintained in museums and herbaria and the catalogs made available to digital networks. Thus, a priority for best understanding the natural processes underpinning biological diversity is the health of modern biosystematic research and curation of specimens.

A second major need is the better use of quantitative data in understanding the patterns and changes in biological diversity in the United States. Quantitative measurement of the heterogeneity of the environment needs to be more extensive and must involve a greater variety of spatial scales. For example, how regional and local processes interact in determining the biological diversity of particular areas is still an open question for most taxonomic groups and sites. In addition, measurements of the characteristics of biological diversity must be made both in areas that are relatively pristine and in those that have been extensively modified by humanity. Measurements in a broad array of situations will allow the relations between various amounts of spatial heterogeneity and biological diversity to be statistically evaluated. Examining situations in which homogenizing processes are also at work to varying degrees is necessary to complete the quantitative models suggested by the overview presented here. In particular, the agents, intensities, frequencies, and spatial extents of natural disturbance regimes and their modifications by humans need to be measured. Infrequent events and episodic processes require special focus because they are likely to be missed by short-term or casual observation.

A range of reference sites and situations for biological diversity must be amassed. The array of sites must include not only those of unusual composition and aesthetic merit but also representatives of more common assemblages and ecosystems. These are needed to assess intentional and unintentional changes in biological diversity caused by human activities; they are also needed to inform realistic goals for restoration and management. Existing sites that have suffered relatively less from human effects as well as historical reference sites whose past environmental controls can be determined are required. Historical and paleoecological analyses are both required for successful establishment of benchmark natural systems.

Biological diversity exists in both a naturally and a human-generated changing environmental context. Natural climate change has been a major control of biological diversity, albeit with the flexibility allowed by evolution and migration. Therefore, the climate changes predicted as a result of human-generated changes are a special concern for the future of biological diversity. Long-term ecological studies, retrospective studies, and intelligent monitoring are all required to document the changes in the systems and to determine what the causes may be. To begin to determine causes of changes in biological diversity in particular areas, small-scale experiments and concomitant measurements of environmental resources, stresses, and disturbances must be made.

It is clear that biological diversity and ecosystem and landscape function are related, because the elements of biological diversity are the elements that compose these other kinds of ecological systems. There is, however, an urgent

need to quantify the linkages between biological diversity and functional attributes of various ecological systems and to conduct experiments on the relationships. In the past, biological diversity and ecosystem research have intersected rather little, given the importance of the linkage.

The Flux of Nature

I have presented an overview of the key ecological processes that maintain biological diversity by generating natural heterogeneity. I close with two images of modern ecology to summarize these processes. One is of a simple graph showing how biological diversity is the outcome of the opposing processes that generate heterogeneity and homogeneity (Fig. 34). Throughout nearly the entire history of the Earth, that battle has been fought without a human referee. Even when humans were part of

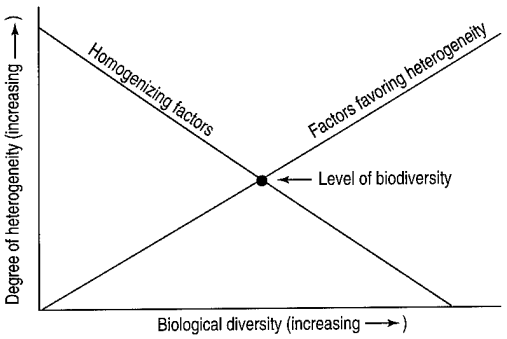

Fig. 34. A conceptual model indicating the opposing influence on biological diversity of factors that generate heterogeneity and those that generate homogeneity. The level of biological diversity is a net result of the factors that make opportunities available for different species, as opposed to those that remove opportunities. The introduction of aggressive exotic competitors that are more generalized and can preempt the place of more specialized or limited native species or the introduction of disease or consumer organisms that directly remove the native species from the systems because of deaths can cause additional deficits in diversity beyond those reflecting loss of heterogeneity.

the game, until the invention of hydraulic agriculture or the massive use of fire, the ecological game swirled about them, little perturbed by their presence. Now humans are referees and coaches, seeming to favor the processes that foster homogeneity (Turner et al. 1990). Some of this is inevitable and desirable, while some of it is avoidable and perhaps even unnecessary. These issues deserve careful consideration in the public sphere. The science is clear: biological diversity is part of the machinery of this planet (Wilson 1992). It is the result of a trade-off between factors that promote heterogeneity and factors that promote homogeneity; the natural world is overwhelmingly heterogeneous. When the mix of homogenization and "heterogenization" is altered, biological diversity is altered. The awkward word in the previous sentence has a point: there is no readily available, simple, and familiar term for the process of creating heterogeneity. Heterogenization—or some better, simpler term capturing this idea—needs to be a part of our everyday language if we are to better deal with our national heritage of natural biological diversity.

The second image that emerges from the insights reviewed in this chapter is the one of the natural world as dynamic. Successions wax and wane; natural disturbances punctuate the lives of organisms and the structures of communities, ecosystems, and landscapes; and climate change and migrations move organisms and change the rate of transforming matter and energy in ecosystems. Many of the important interactions that are key parts of this machinery are usually hidden from us because they depend on microbes or tiny organisms in the soil. Many of the processes become obvious only when we examine systems for long periods or delve into their long histories. Nevertheless, whether invisible or infrequent, such processes and organisms are as much a part of the systems that sustain us and provide important services as are the more obvious and sometimes seemingly static structures.

This view of the natural world is of ecological systems in flux. The flux has some components that are continual, while others are episodic; some components of flux are obvious while others are subtle. But, to echo the words of the ancient Greek philosopher Heraclitus, all is flux. Rather than envisioning the natural world as being in simple balance, which unfortunately connotes stasis and permanence, the persistence of natural systems is founded on flux. So the flux of nature is an ecologically appropriate metaphor (Pickett and Ostfeld 1995). If there is a balance, it is a dynamic and changeable balance derived from the interaction of fluxes that generate heterogeneity and the opposing fluxes that generate homogeneity. Biological diversity is founded on dynamics yielding heterogeneity, and this is the key to understanding our natural heritage. Maintaining the heterogeneity on which natural diversity is founded while preventing the extreme homogenizing tendencies of humans is the key to maintaining that nonrenewable natural heritage.

Acknowledgments

I am grateful to M. L. Cadenasso, B. Maurer, and an additional reviewer for helpful readings and comments on the manuscript. This paper is a contribution to the program of the Institute of Ecosystem Studies, with partial support from the Mary Flagler Cary Charitable Trust.

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Land Use

Land-use change in the United States represents an enormous uncontrolled experiment in the ways habitat changes influence plants and animals. When cities were built, land was plowed, or forests were cut, the effects on our native biota were not considered. Of course, humans have influenced the flora and fauna of North America over the ages. Native Americans established settlements, practiced agriculture, hunted, and used fire to induce vegetation changes (Denevan 1992). Land-use changes, however, have been particularly profound since Europeans settled North America three centuries ago. Landscapes have become mosaics of natural and human-influenced patches, and once-continuous natural habitats are becoming increasingly fragmented (for example, Burgess and Sharpe 1981; Harris 1984). Our nation's lands experienced tremendous changes in response to human activities, but our understanding of how land-use history affected the plants and animals in our modern landscapes is incomplete.

The term *land-use change* has several meanings; we use it to include changes in both land cover and land use. *Land cover* refers to the habitat or vegetation type present, such as forest, agriculture, and grassland. Land-cover change describes differences in the area occupied by cover types through time. Both losses and gains are included. For example, changes in how much forest occurs across a landscape may reflect additions as croplands or rangelands are abandoned and forests regrow. Forest cover may also be lost to harvest or to development. In addition to tracking the amount of cover types, land-cover change also describes shifts in the spacing of cover types across the landscape over time. For example, forest may occur in a large block, or it may exist as several smaller parcels. Land use is usually defined more strictly and refers to the way in which, and the purposes for which, humans employ the land and its resources (Meyer 1995). For example, a place that is in forest cover may be used for low-density housing, logging, or recreation. Land-use change encompasses all those ways in which human uses of the land have varied through time.

Land-use patterns have important influences on biological diversity—that is, the abundance, variety, and genetic constitution of native animals and plants—for several reasons. First, land-use activities may alter the relative abundances of natural habitats and result in the establishment of new land-cover types. The introduction of new cover types can increase the variety of species by providing a greater diversity of habitats. Natural habitats, though, are often reduced, leaving less area available for native species. Species that are not native to the locale may gain a foothold and out-compete the native species (see chapter on Nonindigenous Species). Second, the spatial pattern of habitats may be altered, often resulting in the fragmentation of once-continuous habitat. The effects of habitat fragmentation on animals, plants, and their habitats are numerous (see summaries by Saunders et al. 1991 and Noss and Csuti 1994), and the biological diversity of native species is almost always reduced. Third, land-use activities may change the natural pattern of environmental variation, especially by causing changes in natural disturbance patterns. For example, the environment may be changed directly when fire control and logging alter the frequency and extent of natural fires. Environmental scientists understand that natural disturbances create and maintain biological diversity by creating a mosaic of habitats (see chapter on Natural

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Processes). In general, the chances of losing native animal and plant species and disrupting ecological functions increase when the patterns of natural habitats are altered.

The relation between land-use change and animal and plant communities sets the stage for understanding our present-day fauna and flora and for managing our lands. Both worldwide and in the United States, land cover today is altered principally by direct human use: agriculture, raising of livestock, forest harvesting, and construction (Meyer 1995). Our human society relies on natural habitats for a variety of services including productivity, recycling of nutrients, breakdown of wastes, and maintenance of clean air, water, and soil. The rate and quality of these services, and their capacities to recover from stress, often depend directly on communities of native plants and animals (Schulze and Mooney 1993; Tilman and Downing 1994; Mooney 1996). The ways in which plants and animals respond to new kinds of human-caused environmental disturbances can help us learn more about the tolerances of species and their needs. We present a historical perspective on land-use change and its effects on biological diversity in the United States and consider what this may teach us and what to anticipate from current land-use trends.

Historical Perspective on Land Use and Biological Diversity

The vegetation in our nation's landscapes is the result of a combination of environmental characteristics (such as soils, climate, and topography) and land-use history (Foster 1992; White and Mladenoff 1994; Meyer 1995). At the time of European settlement, forests covered about half the present lower 48 states. Most of the forestland was in the more moist East and Northwest regions, and it had already been altered by Native American land-use practices (Williams 1989). Clearing of forests for fuel, timber, and other wood products and opening the land for crops led to a widespread loss of forest cover that lasted through the early 1900's (Fig. 1). So extensive was this loss that by 1920 the area of virgin forest remaining in the contiguous United States was only a tiny fraction of that present in 1620 (Fig. 2).

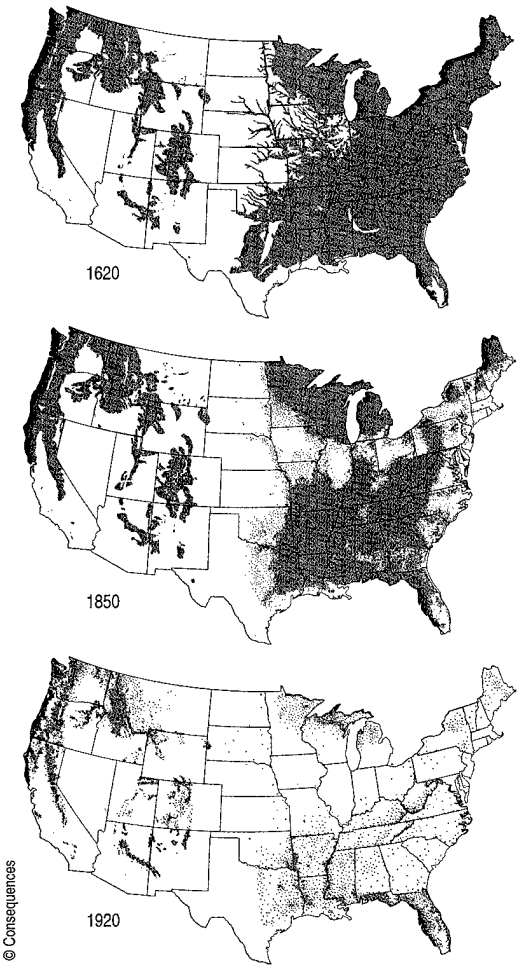

Fig. 2. Approximate area of virgin old-growth forest in the contiguous United States in 1620, 1850, and 1920. Note that this does not depict total forest area because forests that have regrown after clearing are not shown (from Meyer 1995).

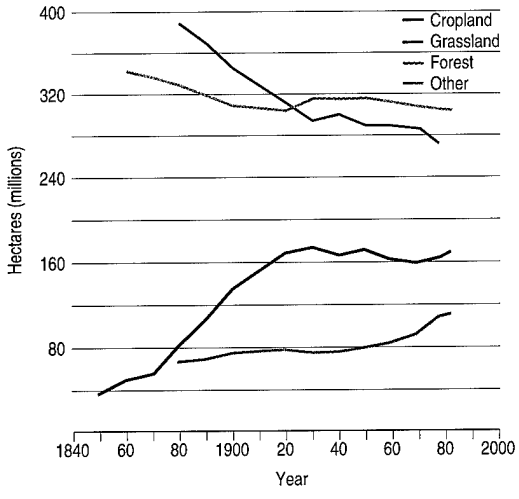

Fig. 1. National trends in the amount of land in different uses for the contiguous United States since the mid-1800's. Data obtained from Powell et al. (1993) and Fedkiw (1989). The amount of forest in 1630 was about 423 million hectares (Powell et al. 1993), and the amount of cropland in 1800 was probably less than 8.1 million hectares (Fedkiw 1989).

Cropland increased at the expense of other land covers throughout much of American history (Meyer 1995). Cropland reached a peak in the 1930's and has since fluctuated around 162 million hectares (Fig. 1). Irrigated cropland became significant only in the late 1800's, and it increased rapidly after 1945, primarily in the drier West, with the advent of more advanced technologies like center pivot irrigation. By 1980, about one-eighth of all cropland was irrigated. While dry cropland was being irrigated, however, wetlands were being drained for agriculture. Between the 1780's and 1980's, 53% of American wetlands were converted to other

uses (Meyer 1995). Between the 1950's and 1970's alone, nearly 4.5 million hectares were lost. Grasslands also experienced a net decline (Fig. 1).

Developed land in the United States has expanded as the population has grown. Most of the population of the United States now lives in cities, towns, and suburbs rather than on farms. Americans spread out across the land as transportation technologies improved, especially as the automobile became the primary mode of transportation. Present-day patterns of settlement involve more land per person than in the past, and homes and subdivisions are more dispersed across the landscape. A frontier of rapid and sometimes chaotic land-use change surrounds urban areas (Meyer 1995). Trends in developed land are unique because they run in only one direction—that is, developed land expands and does not revert to other categories. Thus, the distribution of developed land across our nation will leave a long-lasting footprint on our landscapes.

Ninety-seven percent of the nation's surface area is land, and consequently most of the water that enters streams and lakes is affected by activities on land (National Research Council 1992). Declines in stream and river conditions in the United States are well documented (Naiman et al. 1995). Of the 1 billion hectares of land in the contiguous United States, nearly half have been cultivated or grazed by livestock (Bureau of the Census 1990). Changes in drainage and erosion that accompany agriculture have substantial effects on fresh waters (National Research Council 1992). Urban areas account for only 3% of the land in the United States, but the effects of densely settled areas on our water resources are extreme. As cities are built, natural wetlands and floodplains are replaced with surfaces such as asphalt, cement, and buildings that cannot absorb water. Flash flooding becomes common, and additions of waste and pollutants to downstream waters increase (National Research Council 1992). Thus, land-use change affects not only the land but also the waters.

Regional Variation in Historical Land-Use Change

The timing and sequence of land-use changes in the United States have varied among regions. Territories of the United States were acquired from east to west as land was purchased and treaties were signed (Fig. 3). Settlement patterns also followed this trend as new lands were acquired by an expanding nation and people were encouraged to move

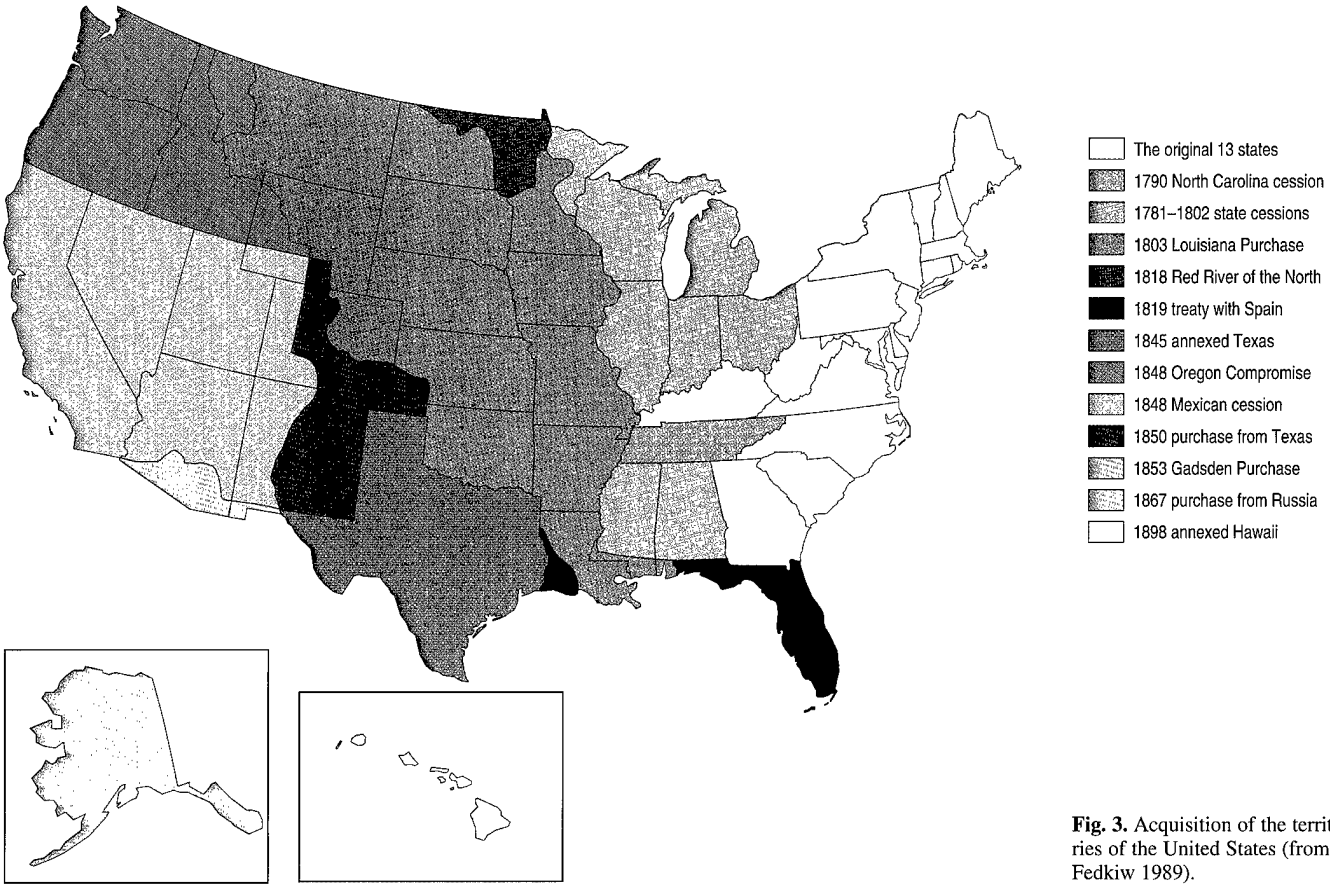

Fig. 3. Acquisition of the territories of the United States (from Fedkiw 1989).

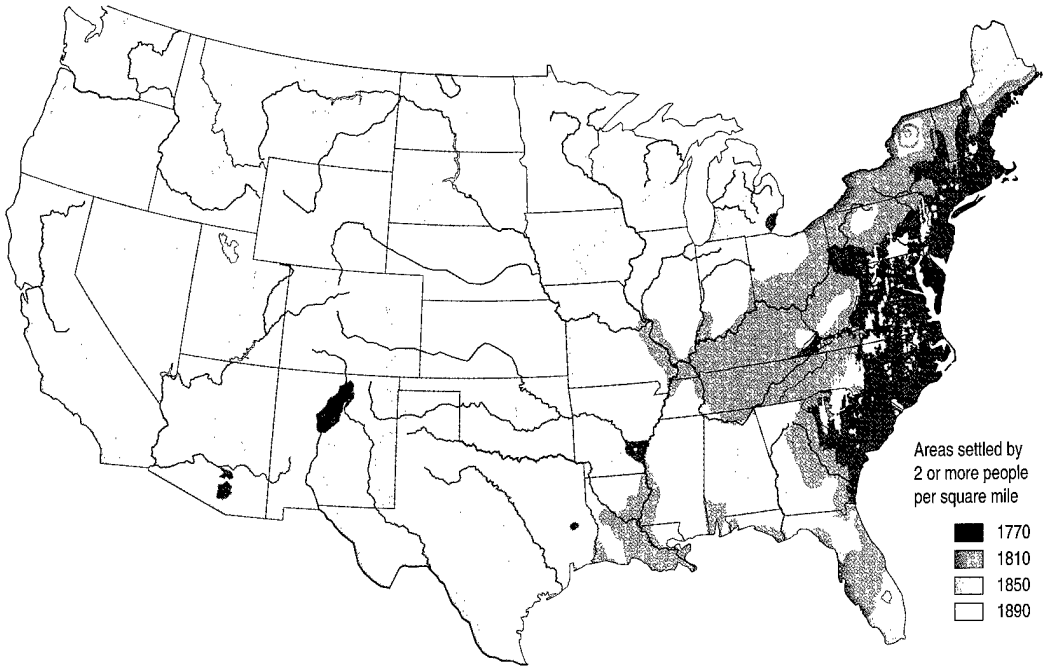

Fig. 4. The progress of settlement of the contiguous United States from 1770 to 1890. The Eastern Seaboard was settled first, but westward movement was rapid (from Fedkiw 1989).

westward (Fig. 4). Clearing of forests rapidly followed settlement, beginning in the East and proceeding westward. Some originally cleared areas—such as New England, the Southeast, and the upper Midwest—have now become reforested because of lack of cultivation (Fig. 5). In other regions, clearing for agriculture has been more permanent (for example, the lower Midwest), or harvest of virgin forest has continued until recent times (Pacific Northwest). In this section, regional patterns of land-use change are compared to illustrate the diversity of changes across the country.

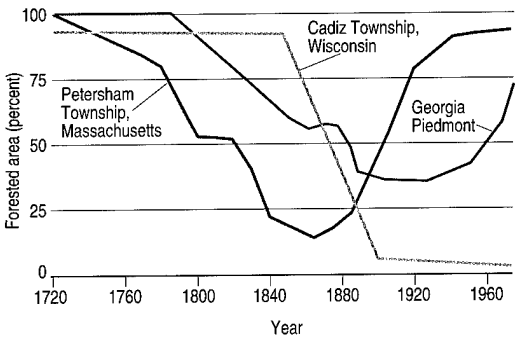

Fig. 5. Postsettlement changes in forest cover for several regions of the United States. Initial deforestation occurred in the Northeast (for example, Petersham Township, Massachusetts [Foster 1992]), with the South (for example, the Georgia Piedmont [Johnson and Sharpe 1976]) and Midwest (for example, Cadiz Township, Wisconsin [Dunn et al. 1991]) following later.

Deforestation and Reforestation in the Eastern United States

The eastern United States has undergone dramatic changes in the area covered by forest during the past 250 years. Foster's (1992) analysis of land-use change in Petersham Township, central Massachusetts, illustrates the cycle of forest clearing and regrowth that was typical of much of the Northeast. Forest clearing by European settlers began around 1730 and proceeded at a pace of 1%–4% of the original forest per year. Open land covered half of Petersham Township in 1800, and nearly 85% of the land was open by 1850 (Figs. 5 and 6). Remaining uncleared forests generally occurred in less accessible locations, such as steep slopes, but were still used for grazing, timber, and fuelwood. Farming became unprofitable and farm abandonment commenced in the mid-1800's; thereafter, forests gradually grew back on neglected fields. This process led to the broad-scale establishment of forest cover over the entire region. Most recently (1920–1990), Petersham Township is characterized by residential development and almost no agriculture.

The patterns described by Foster (1992) were generally repeated throughout the northeastern United States. Ninety-five percent of Dutchess County, New York, was in farmland as late as 1880, but farming had declined dramatically by the 1930's (Glitzenstein et al. 1990). Indeed, much of New York State followed a similar pattern (Hill 1985; Nyland et al. 1986; Smith et al. 1993). Forest regrowth, however, was not always the rule. Forest cover in Franklin Township, New Jersey, increased between 1880 and 1943 but then declined; only 16% of the area was forested in 1986 (White et al. 1990).

The Southeast underwent a similar cycle of forest clearing and regrowth that occurred about 50 years later than in the Northeast (Turner 1987; Fig. 5). For example, before European settlement the vegetation of Georgia was primarily forest, although it had been modified for centuries by Native Americans (Stewart 1956). Following European settlement, Coastal Plain

forests were cut between 1866 and 1890, and stands of virgin pine were completely cut by 1895. Indeed, only 2% of the original longleaf pine forest that covered much of the Coastal Plain remains throughout the Southeast (Noss 1989). Upland broadleaf forests were cleared continuously for farming during the 1800's, and by 1930, more than 80% of the Piedmont had been cleared at least once. A great many farms were abandoned following the boll weevil infestation of cotton during the early 1900's. Most of the abandoned farms reverted through succession to pine (primarily loblolly pine and shortleaf pine), and some of the Piedmont pine forests are now making the transition to broadleaf forest (Turner 1990).

Deforestation of the Midwest

The oak–hickory forests that range from the Ozark Mountains to the Appalachian Mountains owe their current condition largely to human activity, which began with Native American activity before 1600 (DeVivo 1990; Denevan 1992). Native peoples used fire to move game animals, to open up the forest, and to clear underlying brush and saplings. The native peoples also cleared land for agriculture in river valleys and on flat, moist upland sites (Parker 1991). Their use of fire and forest clearing affected the types of trees found in the forest communities, so that the widespread dominance of oak and hickory most likely had its origin in Native American practices.

The European settlers who began to arrive in the Midwest in the late 1700's initially adopted Native American methods of clearing forests. Much of the land cleared in the early 1800's was abandoned as soil fertility declined and settlers moved farther west. But as technology developed by the mid-1800's, forests were permanently cleared. In Illinois, for example, only 31% of the forest area present in 1820 exists today (Iverson 1991; Fig. 7). Until 1860 forests were the sole source of potential cropland, and by 1860 the timber industry was thriving in Illinois. Iverson (1991) makes a striking comparison of deforestation rates in Illinois from 1820 to 1923 and recent rates of forest clearing in three tropical countries (Table 1). It is instructive to note that deforestation in the United States was of a similar magnitude as present-day deforestation rates in the tropics.

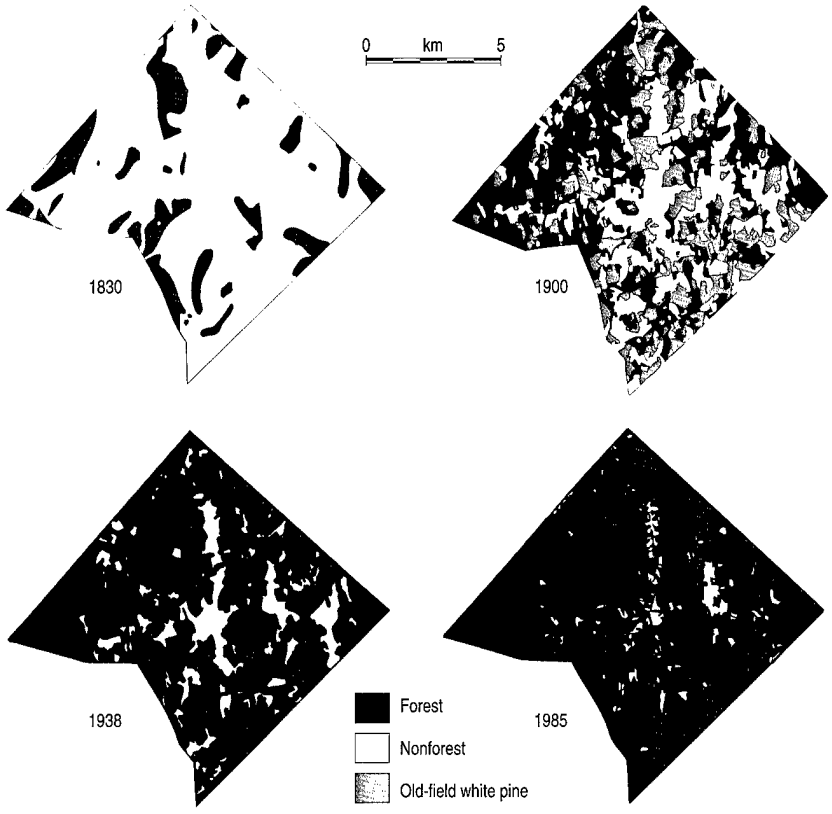

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Fig. 6. Spatial pattern of forest-cover changes reconstructed for Petersham Township, Massachusetts (by Foster 1992). Small isolated patches of forest were present in 1830, but by 1985, secondary succession had resulted in extensive connected forest cover.

Overhunting and fragmentation of the midwestern forest into smaller pieces caused the disappearance of many wide-ranging mammals by 1860 (for example, black bear, gray wolf, mountain lion), and even the white-tailed deer was eliminated from some areas by 1900 (Reeves 1976), but most plant and animal species were able to persist in habitat fragments. Clearing and widespread grazing continued until the late 1930's, but since that time continued disturbance of the land has been greatly reduced (Parker 1991). Land used for grazing in the central Midwest has decreased from 70% in the 1930's to around 30% today. Reforestation has occurred on the hilly portions in the south and west of the region, while intensive agriculture is still practiced in the relatively flat northern areas.

The central hardwood forest ecosystem of the Midwest is diverse and resilient. The region apparently has survived massive human disturbance with the disappearance of few native species. Some species are rare because their

Location	Land cover	From (year)	Area (hectares)	To (year)	Area (hectares)	Percent cleared per year
Rondonia, Brazil	Forest	1978	239,800	1987	208,800	1.47
Malaysia	Forest	1972	48,970	1982	36,870	2.47
Costa Rica	Forest	1940	34,210	1983	8,710	1.73
Illinois, U.S.	Forest	1820	55,870	1870	24,290	1.13
	Forest	1870	24,290	1923	90	0.87
Illinois, U.S.	Prairie	1830	87,550	1860	10	3.33

Table 1. Comparison of recent deforestation rates in the tropics with conversion of forest and prairie in Illinois during the settlement period as presented by Iverson (1991).

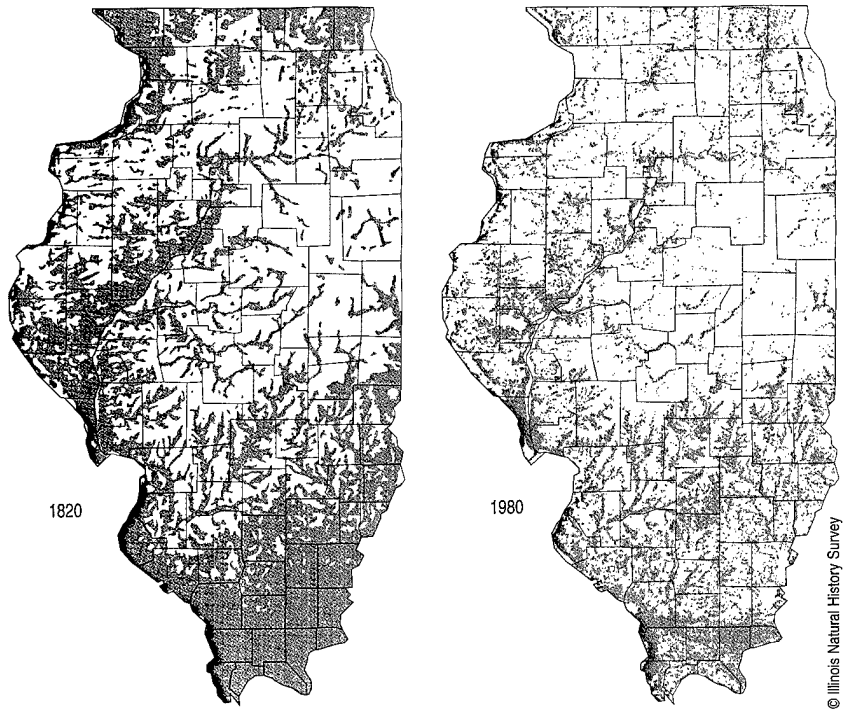

Fig. 7. The distribution of forest cover in Illinois in 1820 and 1980. Most remaining forests in Illinois occur within 300 meters of rivers and streams (from Iverson 1991).

habitat has declined or because they were harvested by humans. Many other species are rare because of a reduction in environmental patchiness (see chapter on Natural Processes) due to natural disturbances such as periodic fires and storms (Anderson and Schwegman 1991).

The Plains and the Loss of Native Prairie

Along the boundary between forests and prairies, it was the forested lands that were first settled. Settlers believed that the prairie was unsuitable for settlement because of lack of wood and drinking water, lack of protection from winter storms, and the lack of trees, which was thought to be caused by infertile soils (Latta 1938; Anderson 1970). Settlement began in the early 1800's, but even as late as 1836 only small prairies near woodlands were settled, despite the invention of plows capable of tilling the thick prairie sod and the high crop yields obtained from prairie soils (Anderson 1970). After the railroads were established in the 1850's and 1860's, crops and supplies could be transported economically, and the prairies were then rapidly settled (Barrows 1910; Anderson 1970).

Before 1800, Illinois was nearly two-thirds prairie grassland and one-third forest, but by 1850 prairie habitat was reduced by 75% (Graber and Graber 1963). Although natural prairie became extremely rare by 1920, diversified commercial farming that included rotation farming and livestock production allowed grasslands to remain common between 1900 and 1950, and many prairie vertebrates thrived (Warner 1994). The development of high-yield mechanical and chemical cultivation practices led to intensive row cropping by the 1960's, and grassland habitats declined sharply (Warner 1994). Only about 0.01% of the original unplowed prairie now remains (Iverson 1988), which has led to significant changes in the abundance of prairie birds between 1850 and the present (Table 2), with some bird species increasing and others declining.

Cattle raising was largely a frontier activity, and by 1865 the cattle industry had moved to Illinois, Iowa, and Missouri and was pushing farther west. Spanish cattlemen introduced herds to both Texas and California before 1865 (Rasmussen 1974). Herds of cows roamed freely on the plains with little tending and by the 1880's had expanded throughout the northern plains (Fedkiw 1989). After World War I, ranch farming became more common because it reduced some of the economic hazards of herding. Cattle numbers on the plains have varied widely in this century because of unpredictable markets and weather. Range conditions were probably at their worst in the late 1920's.

The decline in grasslands (Fig. 1) was primarily due to a shift to cropping, mostly wheat. Beginning in the 1880's, dryland farming and irrigation development in the semiarid West were encouraged by the government and by the railroad companies. By 1920 more than 75 million hectares had been added to annual cropland, mostly west of the Mississippi (Fedkiw 1989). Today, very little of the original extensive native prairies remains.

Pacific Northwest Forests

Cutting of forests in the Pacific Northwest began in the 1800's when European settlers arrived in the region. The extensive forests covering the lowlands and river valleys were viewed as blocks to progress and were systematically burned and cleared for agriculture (Forest Ecosystem Management Assessment Team 1993). In the late 1800's and early 1900's, commercial logging began to increase on the uplands but did not begin in earnest on federal lands until after World War II. European methods of forest management were gradually adopted on most federal and private lands—techniques such as clear-cutting, removal of logs and snags, slash burning, thinning, and planting stands of a single species. The assumption was that forests managed in this manner could be cut and regrown at relatively short intervals (for example, 40–80 years) without negatively affecting water quality, fish, soils, or land animals. Stream and riparian ecosystems in the region first suffered damage from grazing and mining that occurred from the 1860's to 1910, and then from the logging, roads, fire

Species	Before 1900[a]	1906–1909[b]		1956–1958[c]		1987–1989[d]		USFWS[e]
		Percent	Rank	Percent	Rank	Percent	Rank	Percent change
Eastern meadowlark[f]	Abundant	25.5	2	20.0	2	11.8	2	-67.0
Dickcissel	Abundant	13.1	3	8.7	4	7.7	5	-46.7
Grasshopper sparrow	Abundant	5.9	5	5.3	6	8.6	4	-56.0
Bobolink	Abundant	25.8	1	9.7	3	11.4	3	-90.4
Henslow's sparrow	Abundant	<1.0	15	<1.0	14	1.6	12	*g
Red-winged blackbird	Very common	9.9	4	36.2	1	26.8	1	-18.8
Greater prairie-chicken	Very common	<1.0	13	0.0	16	0.0	16	*g
Upland sandpiper	Very common	2.3	9	<1.0	12	<1.0	13	-16.8
Vesper sparrow	Common	1.3	11	1.4	10	<1.0	15	+12.1
Horned lark	Common	4.9	6	4.8	7	<1.0	14	0.0
Field sparrow	Common	4.0	7	2.9	9	5.6	7	-52.6
Song sparrow	Common	2.6	8	1.0	11	3.3	10	-29.3
Savannah sparrow	Common	2.3	10	5.8	5	3.5	9	-58.9
American goldfinch	Common	1.2	12	3.1	8	4.7	8	-42.8
Common yellowthroat	Common	<1.0	14	<1.0	15	5.8	6	-8.8
Sedge wren	Common	<1.0	16	<1.0	13	2.8	11	-22.5

[a] Relative abundance before 1900 based on the works of Nelson (1876) and Ridgway (1873, 1889, 1895).
[b] Relative abundance 1906–1909 based on censuses of Gross and Ray from about 380 hectares of ungrazed grass, mixed-hay, and pasture in northern and central Illinois (Forbes 1913; Forbes and Gross 1922).
[c] Relative abundance 1956–1958 based on censuses of Graber and Graber (1963) from approximately 290 hectares of ungrazed grass, mixed-hay, and pasture in northern and central Illinois.
[d] Relative abundance from present study (1987–1989) based on censuses of about 400 hectares of ungrazed prairie and agricultural grasslands in northeastern and east-central Illinois.
[e] Estimated population change within Illinois between 1967 and 1989 based on the U.S. Fish and Wildlife Service's Breeding Bird Survey (U.S. Fish and Wildlife Service, unpublished data).
[f] For 1906–1909 and 1956–1958, relative abundance estimates are for eastern and western meadowlarks combined.
[g] Present on too few routes for accurate trend analysis.

Table 2. Relative abundance of prairie birds within Illinois, 1850 to 1989 (from Herkert 1991).

management, and irrigation that occurred in the twentieth century (Wissmar et al. 1994).

As a result of more than a century of logging and fire control, the forests of the Pacific Northwest presently consist of a highly fragmented mosaic of clear-cuts, thinned stands, and young (and often single species) plantations interspersed with uncut natural stands. In addition, the development of extensive road systems to access the forests has further modified the landscape. The road density often equals or exceeds the density of natural stream channels in the basin—more than 2.5 kilometers of road per square kilometer. Only about 15% of the 10 million hectares dominated by Douglas-fir remains as ancient forests in the 12 national forests studied by Morrison et al. (1991); the percentage appears to be less on private and state lands. The remaining ancient forest, for the most part, occurs in highly fragmented stands and is subjected to greater damage from windstorms and human intrusions caused by edge effects and the extensive road system. Many of the remaining stands are in small patches (less than 30 hectares) and within 125 meters of roads or clear-cuts, significantly decreasing their value as habitat for native plants and animals.

The Olympic Peninsula in Washington state provides a regional illustration of the changes that have taken place throughout the Pacific Northwest (Fig. 8). Since 1940 nearly 76% of the Olympic Peninsula's ancient forests have been logged (Fig. 8a). In 1940, 87% of the ancient forest was in patches greater than 4,000 hectares, whereas by 1988, the forest was so fragmented that 60% of the ancient forest occurred in patches of fewer than 40 hectares (Fig. 8b). In addition, very little of the low-elevation forest remains today. In the Pacific Northwest, many species are only found below elevations of 1,200 meters and others are only found below 600 meters. Most of this species-rich lowland forest occurs in small stands or fragmented webs with the natural communities endangered by their proximity to forest edge (Fig. 8c).

The West and Southwest

In the late 1870's, following serious efforts by European immigrants to subdue the Native Americans, much of the Southwest was opened to settlement (Cooper 1960). The history of settlement and vegetation change of southwestern pine forests since settlement has been documented by Cooper (1960). Early accounts of these forests stressed the open nature of the woods, luxurious grass swards, and lack of gullying. It is likely that the open nature of the forest was maintained, in part, by use of fire by Native Americans. Some tribes, such as the Navajo, also maintained extensive herds of stock. The introduction and subsequent mismanagement of livestock in the West, however, produced profound changes in plant cover (Cooper 1960). Deterioration of watershed condition was rapid following settlement, reaching its worst state by the turn of the century and leading to serious concern over water supply. The adverse ecological effects of overgrazing are well known (for example, see West 1993).

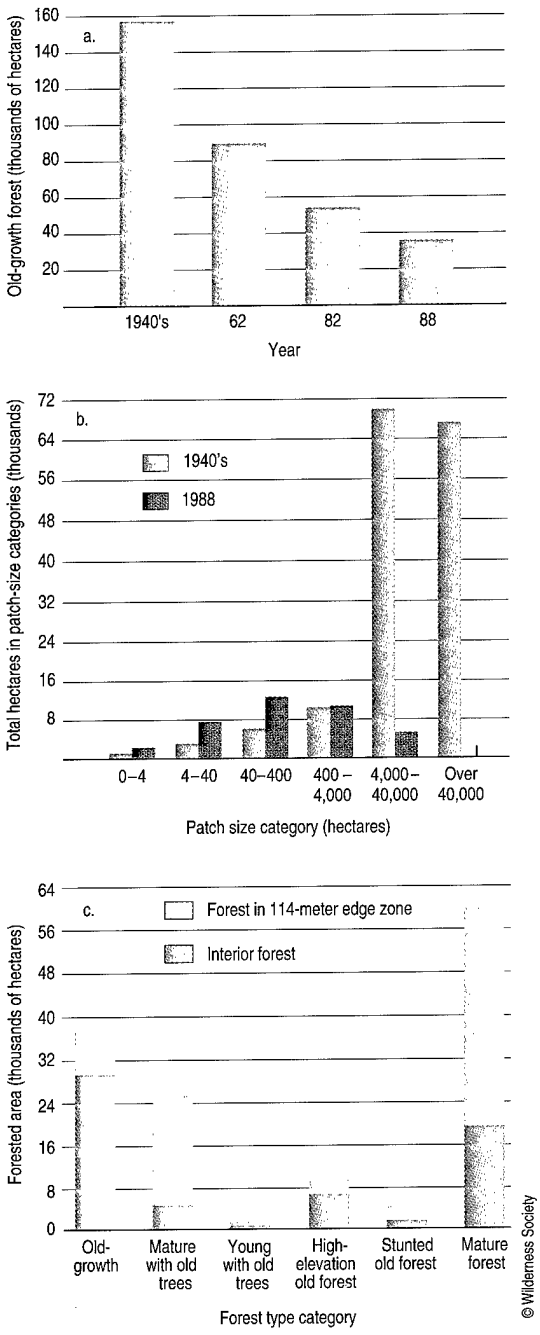

Fig. 8. Recent historical changes in abundance and landscape structure of old-growth forest on the Olympic Peninsula, Washington (from Morrison et al. 1991): a) area of old-growth forest through time; b) frequency distribution of old-growth by patch size in the 1940's and 1988 indicates the dramatic shift from large contiguous old-growth forest to small isolated tracts; and c) area of different forest types considered interior forest (more than 114 meters from a patch edge) and occurring within the edge zone (less than 114 meters from a patch edge) in 1988 illustrates that a considerable proportion of the present forest is subject to edge effects.

Cumulative effects of land-use changes in the Southwest since settlement include a decrease in grass cover, a shift in composition of herbaceous vegetation, and an increased density of pine trees. Two factors appear primarily responsible for these changes (Cooper 1960). First, heavy grazing led to a reduction of native bunchgrasses and, in some cases, replacement by nonindigenous annual plants. The second factor was the exclusion of fire from the forests and grasslands. Frequent surface fires that maintained an open understory in the pine forests were typical before settlement by those of European ancestry. More intense crown fires were rare during this time.

In the northern Rocky Mountains, the post-1860 rush of miners greatly accelerated land-use change. Madison Valley, Montana, offers a good example of settlement patterns (Wyckoff and Hansen 1991). Although Native Americans had migrated through the area, they had not maintained permanent settlements in the valley. Permanent settlement of the region by European immigrants began around 1870; these settlers introduced large numbers of livestock to the land, resulting in deleterious effects on many habitats. As range conditions deteriorated, fescue and wheatgrasses declined and were replaced by rabbitbrush, grama grasses, and sagebrush. Seasonal overgrazing by livestock caused particular damage to sensitive riparian and subalpine habitats (Wyckoff and Hansen 1991).

Recent land-use changes in the West are dominated by increased demand for housing development. In California, for example, the human population increased 25% between 1980 and 1990, leading to urbanization of 123,000 hectares of previously undeveloped land (Charbonneau and Kondolf 1993). Smaller cities in the Rocky Mountain states are also experiencing intense developmental pressure. Residential development is occurring nearer and nearer to large private and public landholdings; this geographic proximity makes forest and wildland management problematic. For example, management of natural fire becomes more of an issue when homes and businesses are nearby. In addition, dispersed residential development leads to extensive natural habitats becoming increasingly fragmented at fine scales. The sizes and connectivity of native habitats become reduced, making wildlife management more difficult.

Land-Use Change and Trends in Biological Diversity

The composition of plant and animal communities across the United States has undoubtedly changed continuously over the past 400 years as human uses of the land have changed. When Europeans arrived in North America, there were approximately 1.9 million people occupying the vast continent (Ubelaker 1988 *in* MacLeish 1994). The level of human activity on the land diminished rapidly in the sixteenth century as the large Native American populations dwindled following the introduction of European diseases (Denevan 1992). Human activity then increased rapidly as Europeans settled the landscape in the seventeenth and eighteenth centuries (Whitney 1994).

A clear picture of changes in biological diversity since European settlement is very difficult to obtain. Existing information suggests

Table 3. Loss of native vascular plant species for selected states (from Whitney 1994).

State	Number of native species	Native species extirpated or extinct	
		Number	Percent
Maine	1,500	84	5.6
Massachusetts	1,700	53	3.1
New York	2,000	59	3.0
Pennsylvania	2,100	62	3.0
Illinois	2,000	50	2.5
Indiana	1,900	22	1.2
Iowa	1,350	49	3.6
Ohio	1,800	84	4.7
Wisconsin	1,700–1,800	13	0.7

that many states have lost between 1% and nearly 6% of their flora (Table 3) and between 2% and 20% of their fauna (Table 4). Many of the plants that were lost were growing at the edges of their ranges. Others that were lost were associated with habitats that are now rare—like Coastal Plain wetlands and grasslands—or habitats that were associated with fire (Whitney 1994). Although many species were lost from portions of their ranges, relatively few have become extinct. Many species that are still present, though, have undergone dramatic changes in abundance.

Table 4. Summary of losses of native vertebrates for selected states (from Whitney 1994).

State or region	Number of native species having bred in region[a]	Native species extirpated or extinct	
		Number	Percent
Mammals			
New England	70	6	9
Massachusetts	58	8	14
Pennsylvania	70	8	11
Ohio	65	13	20
Indiana	65	13	20
Illinois	67	8	12
Iowa	68	10	15
Missouri	70	3	4
Michigan	66	6	9
Minnesota	78	5	6
Birds			
Massachusetts	186	3	2
Pennsylvania	180[a]	8	4
Ohio	188[a]	8	4
Indiana	180[a]	15	8
Illinois	215[a]	16	7
Iowa	160[a]	15	9
Missouri	184	32	17
Michigan	214[a]	5	2
Minnesota	245[a]	8	3
Wisconsin	220[a]	4	2
Fish			
Connecticut	40	1	2
Massachusetts	41	1	2
Pennsylvania	180	28	15
Ohio	154	9	6
Indiana	168	10	6
Illinois	186	10	6
Iowa	140[a]	12	9
Wisconsin	155	9	6

[a] Approximate number.

Effects of Fire Suppression on Ecosystems and Diversity

Fire suppression has been one of the great success stories of wildland management organizations. Over the last 100 years or so, public fire-fighting agencies such as the U.S. Forest Service, the Bureau of Land Management, the Bureau of Indian Affairs, and the National Park Service have developed an impressive array of fire-fighting technologies that have remarkably reduced acreage burned by wildfires (Pyne 1982).

In California, fires ignited naturally and by Native Americans before European settlement burned as much as 13% of the state in any one year (Martin and Sapsis 1992). With effective fire suppression beginning in the early twentieth century, burned acreage plummeted to 15% of presuppression values. Since 1970, however, suppression efforts have become less effective. California, for example, has experienced a doubling in acreage burned by wildfires, while the number of wildfires in the state has increased only slightly (Martin and Sapsis 1992). Other western states have also seen sharp increases in burned acreage. In recent years, fires that burned tens and hundreds of thousands of acres have occurred in California, Idaho, Montana, Oregon, Washington, and Wyoming (Martin and Sapsis 1992; Agee 1993; Covington et al. 1994; Johnson et al. 1994). While most ecosystems occasionally experience very large fires (Romme and Despain 1989), the present-day frequency of such large fires appears unprecedented.

Ecosystems respond differently to fire suppression. Ecosystems that tend to be particularly cool and moist, such as certain boreal and subalpine ecosystems, burn so infrequently that the interval between fires is longer than the 75–100 years of effective fire suppression. Ecosystems that are extremely dry, such as deserts or cold, dry alpine ecosystems, are so unproductive that they accumulate fuel too slowly to have been affected by fire suppression (Martin 1982). Temperate ecosystems, where frequent, low-intensity wildfires had occurred in the past, are more likely to have been adversely affected by fire suppression (Agee 1993).

In these temperate, productive ecosystems, average fire size and severity have increased dramatically. Decades of fire suppression have left a legacy of increased fuel loads and ecosystems choked with an understory of shade-tolerant, late-successional plant species (Figs. 1 and 2). These structurally homogeneous ecosystems are conducive to the large, severe fires, especially during hot, dry, windy periods in late summer or early fall. Such ecosystems have fewer structural breaks to retard fire spread and intensity, and their increased accumulations of live and dead fuels may burn longer and more completely. Plant and animal mortality in these ecosystems is relatively high following the large stand-replacing fires that are now much more likely to occur in these ecosystems.

Ecosystem recovery following stand-replacing fires potentially follows four stand-development stages: stand initiation, stem exclusion, understory reinitiation, and old-growth (Oliver 1981; Larson 1990; Oliver and Larson 1990; Fig. 3). Stand initiation is a period in which a site is reoccupied by an influx of colonizing species combined with a diverse mix of late successional species. During stem exclusion, competition induces self-thinning of weakened plants, leading to a marked decline in species richness and structural diversity. Forest canopies close, leaving understory species with

Fig. 1. Effects of fire exclusion in a Douglas-fir forest of western Montana 1909, 1928, 1938, and 1948 (from Gruell et al. 1982).

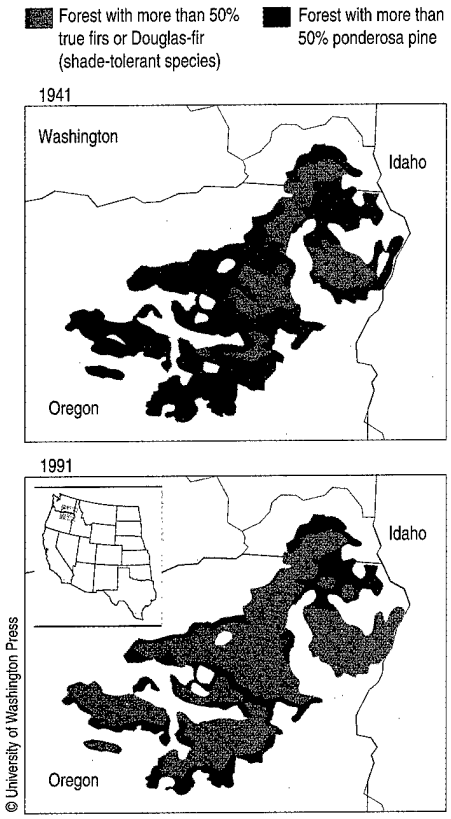

Fig. 2. Forest composition differences between 1941 and 1991 in the Blue Mountains of Oregon and Washington. Douglas-fir and true fir abundance have increased with fire suppression (from Langston 1995).

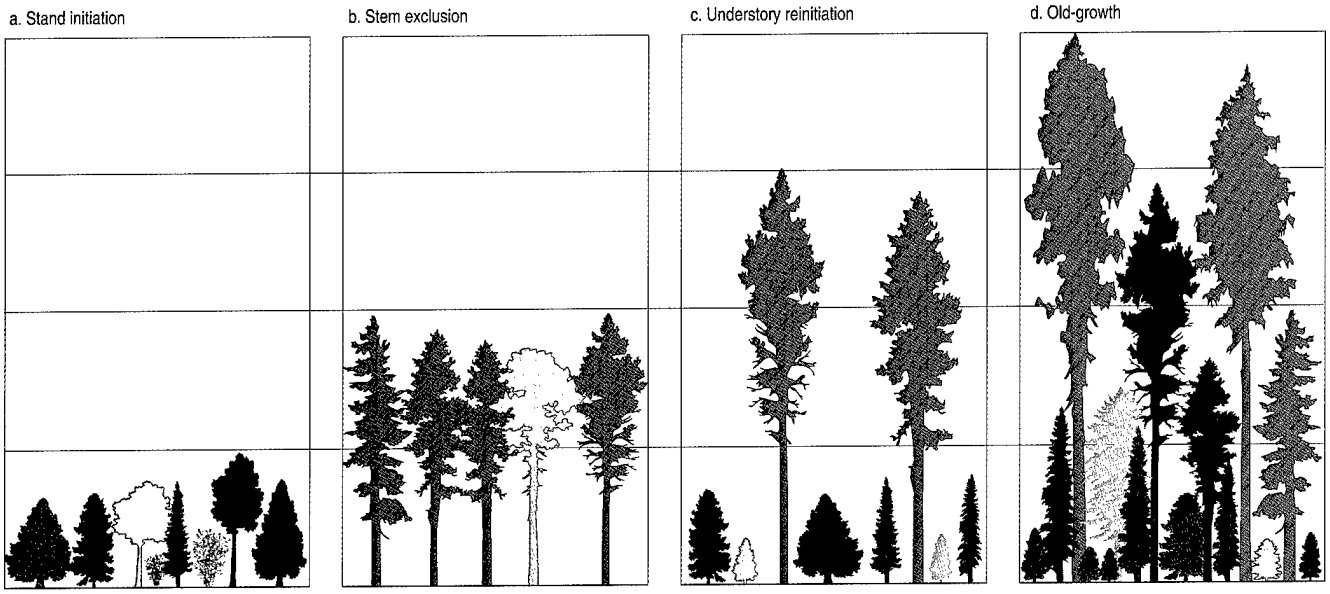

Fig. 3. Hypothetical stand development sequence. Note that all the species are present during a) stand initiation, a period of high species richness. Which species colonize following a disturbance depends strongly on which species were present, even in tiny populations, before the disturbance. Species richness drops during the intense competition of the b) stem exclusion stage, then increases again as succession proceeds toward c) understory reinitiation, and d) old-growth. Note the structural diversity as well as species richness in the old-growth stage. The timing of these stages following disturbance varies considerably with the ecosystem; the old-growth stage may be reached in 200 years or as long as 1,000 years.

inadequate light. Understory reinitiation begins once larger trees die, leaving holes in the canopy large enough for light to reach the forest floor, where late-successional, shade-tolerant species can grow and survive. Over time, an old-growthlike forest develops with characteristic multiple-age classes of trees and multiple canopy layers. Plant species richness peaks during the stand initiation stage, declines during stem exclusion, then slowly increases as growing space is provided by individual tree mortality and the reestablishment of an understory (Schoonmaker and McKee 1988; Stuart et al. 1993). In contrast, structural diversity peaks during old-growth, allowing for a greater richness of epiphytes and invertebrates (Schowalter 1989).

Before fire suppression, ecosystems accustomed to frequent, low-severity wildfires supported diverse landscapes composed of a variety of plant communities and successional stages. The resulting landscape mosaic typically burned irregularly. Some landscape patches had light, discontinuous fuel and burned cool and quickly; others had heavy, continuous fuel and burned hot and slowly or did not have enough available fuel to burn at all. Recovery from fire was equally varied. Patches that burned hot resembled small stand-replacing fires with stand development patches dominated by shade-intolerant species. In contrast, few to no overstory trees were killed and only some of the understory plants were killed in cool-burning patches. Shade-tolerant species reestablished themselves in the understory. Stands harboring complements of both early and late successional species represented islands of high biological diversity.

The greatest effect of fire suppression on biological diversity is not on the diversity within a particular habitat (Whittaker 1977), but on the diversity of habitats across a landscape. Landscapes with high diversity resulting from fire perpetuate high species diversity by providing opportunities for the establishment and maintenance of early successional species and communities (Connell 1978; Reice 1994). Fire suppression, on the other hand, increases uniformity in habitats as competition eliminates early successional species, leaving only shade-tolerant understory plants to reproduce. For example, in the Klamath Mountains of northern California, recently burned landscapes had more (46–48) distinct habitat types that were more evenly distributed than equal-sized unburned areas (31) (Fox et al. 1992). Burned landscapes included habitat types dominated by early successional pines, shrubs, or herbaceous species, whereas unburned landscapes were more uniform in their cover of later successional fir-dominated communities.

Fire suppression has helped change the ecosystem dynamics of communities adapted to frequent, low-intensity wildfire. Complex landscapes are made simpler, some early and midsuccessional plants and animals are extirpated, shade-tolerant tree populations rapidly expand, and the relative importance of fire as a disturbance agent is reduced, while the importance of insects and pathogens is elevated (Covington et al. 1994). During droughts, for example, excessively dense forests become further stressed, enabling pathogens and insects to reach high population levels (Johnson et al. 1994). Trees killed by drought, insects, or pathogens create abundant fuel that exacerbates fire hazard. When fire occurs in such a system, it is often larger and more severe than one expected in areas with a natural fire regime. Such a scenario is being played out in the forests in the Blue Mountains of eastern Oregon and southwestern Washington (Langston 1995).

Re-creating the natural fire regimes of ecosystems adapted to frequent, low-severity fire seems an obvious management choice if we want to enhance biological diversity and reduce the risk of catastrophic wildfire. Paradoxically, while fires help maintain native biological diversity, they also create opportunities for invasive alien species to become established. In many cases, these species are superior competitors, predators, or parasites on our native flora and fauna (Hobbs and Huenneke 1992) and could actually reduce native biological diversity. Thus, restoring a more natural fire regime will have to be carefully considered to maximize ecosystem benefits while minimizing biological and social costs.

See end of chapter for references

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In hindsight, the overall changes in many animal species proceeded in a predictable way. The large animals, especially predators such as wolves and mountain lions, disappeared soon after settlement. Numbers of furbearers diminished as they were trapped for their pelts. As forests were opened and prairies were plowed, forest edge and pioneering species replaced the forest-interior and grassland-interior species. Overharvesting and changes to freshwater habitats led to losses of many fishes.

Although these general trends are conspicuous, remarkably few studies have addressed the changes in species abundance or composition associated with land-use change since Europeans came to America. The kinds and proportions of trees in forests can sometimes be reconstructed from historical records such as General Land Office surveys and compared with the makeup of present-day forests. Although past land use can be compiled from deed and tax documents, there is little numerical information on the abundance and distribution of most nonwoody plants and most animals. Birds are the best-studied animals, yet most information on them does not extend back farther than the 1950's.

Composition of Forest Communities, Then and Now

Are present-day forests similar in composition to the forests encountered by the early settlers? Dramatic changes in forest cover have occurred throughout the eastern United States and upper Midwest during the past two centuries, suggesting that our forests displayed considerable resilience—that is, the ability to recover from disturbance. On a regional basis, the distribution of forest types closely resembles the presettlement patterns, but on closer inspection, there are substantial differences in present-day forests.

In the 1700's in Petersham Township, Massachusetts, regional forest communities

were distributed along slopes and valleys much as they are today (Foster 1992). Trees such as birch, red maple, and oaks, which are found in young forests or which can resprout, have increased in number, however. At the same time, there has been a decline in long-lived, shade-tolerant species such as eastern hemlock and sugar maple. At a local scale within a forest, the effects of land use are dominant. For example, the variety and abundance of different trees vary substantially among areas that were permanent woodlots, pastured, or cropped (Foster 1992).

When species composition is examined, even patches of forest that seem mature and stable may be very unlike the forests that existed before the arrival of European settlers (Foster et al. 1992). A single woodland that remained forested throughout the settlement period has changed profoundly in tree species composition and structure during the past 250 years. The dominant species in the canopy have changed at least three times. Surprisingly, many of the trees that were common before European settlement are now rare within the woodland and uncommon in the landscape. Sugar maple and American beech have been almost completely eliminated locally because of land-use changes (Foster et al. 1992).

According to detailed vegetation and land-use analyses (White and Mladenoff 1994), similar transitions in forest composition have taken place in northern Wisconsin. Old-growth eastern hemlock and mature hardwood dominated a 9,600-hectare study landscape during the mid-1800's. By 1931, after large-scale logging and burning of the slash left behind, young forests covered more than 50% of the landscape. By 1989, the area was covered by a mixture of second-growth hardwood and conifer types. Regionally, the regrowing young forest closely resembles presettlement forest distribution, but the variety of trees has changed. A return to the formerly dominant hemlock forest in northern Wisconsin is not likely, based on current trends. Rather, there are two likely alternative directions leading toward either northern hardwoods or a boreal forest dominated by spruce, fir, and pines. Other midwestern oak forests are being converted to forests dominated by maples, black cherry, and yellow-poplar. This trend of reduced oak regeneration has also been documented in Pennsylvania (Abrams and Nowacki 1992) and Illinois (Iverson and Schwartz 1994). Thus, modern forests have not returned to their presettlement composition (Foster et al. 1992). Although the total area covered by forest has increased since 1900 across much of the eastern United States, today's forests are very different from those of the 1700's.

Forest Changes and Forest Animals

Animal communities have been profoundly affected by the removal and regrowth of forests—we know that animals inhabited places that would surprise us today (see MacLeish 1994). Bison used habitats ranging from the Great Plains all the way to Florida, grizzly bears ranged the Midwest, and elk roamed New England. Passenger pigeons, now extinct, flew in great flocks. Qualitative changes in the presence and abundance of animals during the past few centuries have been described. For example, predators such as wolves and furbearers such as beaver declined dramatically following settlement. French and Dutch fur traders in the Northeast took 30,000 beaver pelts in 1620 and almost 300,000 in 1690 (MacLeish 1994), but few such quantitative data exist. Although species have been lost and gained over past centuries, detailed studies have been conducted only in the past several decades.

Forest removal and regrowth create a series of young forest stages that change in space and time. Much of the young successional forest that dominated the landscape earlier during this century has declined markedly as these secondary forests approach maturity (Brooks and Birch 1988; Powell et al. 1993). Animals that thrive in early successional habitats also increased in abundance early in the century and are now declining. For example, as forest cover across the New England states increased to 75%–90% during the past century (Irland 1982), the New England cottontail declined substantially throughout its range (Chapman and Stauffer 1981); the pattern of decline correlated with losses of old fields and young forest habitats (Litvaitis 1993). Bobcats in New England experienced a simultaneous decline related to the decline of their early successional prey species (Litvaitis 1993).

Changes in bird abundances correlate with changes in early successional and forest cover. During the 1937–1989 period of reforestation in Massachusetts, 8 of 18 migratory bird species that declined are known to nest in early successional habitats (Hill and Hagan 1991). Since 1966 the eastern towhee—a species that prefers shrub cover, including abandoned agricultural fields—has declined 13% in the eastern United States (Hagan 1993). Between 1966 and 1988 in coastal New England, 9 of 18 species of nesting land birds associated with early successional habitats have declined (Witham and Hunter 1992). Agricultural land decreased by 9% and early successional habitats by 12% during the same period, while rural housing area increased 23% and urban–industrial land use increased 4%. Additionally, many New England breeding birds that winter in the Southeast have declined

significantly in recent years. It is possible that land-use change in the Southeast may be an important factor contributing to this decline as well (Hagan et al. 1991).

In contrast, forest birds may be rebounding as open habitats diminish. Nine of 15 species in coastal New England that have increased in numbers since 1966 were associated with closed canopy forests (Witham and Hunter 1992). From 1953 to 1976, changes in the bird community of a Connecticut forest preserve were correlated with changes in the abundance of forest in the surrounding landscape (Askins and Philbrick 1987). Forest birds in the preserve declined with forest removal in the surrounding landscape but began to increase again when forest cover increased. Bird species that thrive in residential areas also increased as the surrounding suburb expanded.

Although forested habitat has increased in some areas, today's forested habitats may not be as suitable for some native species when compared to the forested habitats of presettlement times. For example, the extensive deciduous forest that covered the southeastern Piedmont has been replaced by pine forests, which do not provide the conditions needed by various species—forest understory wildflowers and birds such as the red-eyed vireo—that thrived in the original deciduous forests. In the Midwest, old-growth forests and disturbed forests differ substantially in their spatial pattern across the landscape (Mladenoff et al. 1993). Compared with the large, continuous old-growth forests, the disturbed forests have numerous smaller patches of simple shape. Furthermore, certain habitat combinations—such as eastern hemlock forests aligned next to other conifer forests—occurred in the old-growth forest but are absent in the disturbed forests. Such habitat alignments are important for species that use edges or obtain resources from different habitat types (Dunning et al. 1992).

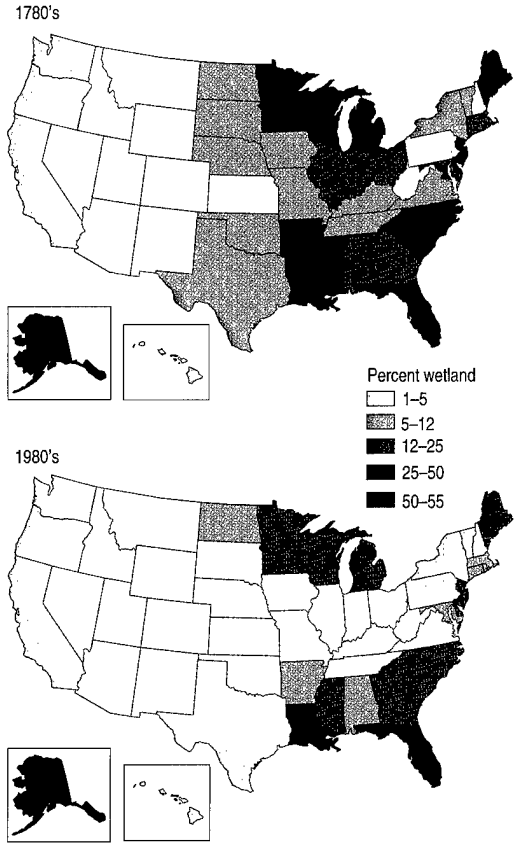

Fig. 9. Percentage of the areas of each state occupied by wetlands in the 1780's and the 1980's (adapted from Dahl 1990).

Aquatic and River Forest Losses Resulting From Land-Use Change

Wetlands, floodplains, and riparian vegetation zones have often been altered by agricultural and urban development (Fig. 9). Woody riparian vegetation once covered an estimated 30–40 million hectares in the contiguous United States (Swift 1974); at least two-thirds of that area has been converted to nonforest land uses, and only 10–14 million hectares remained in the early 1970's. Floodplain clearing for agriculture, urbanization, and water-resource development (especially channel modification and impoundment; see chapter on Water Use) is responsible for much of the loss of riparian forests. In many states of the arid West, the Midwest, and the Lower Mississippi River valley, riparian forests have been reduced by more than 80% (Swift 1974).

Sedell and Froggatt (1984) provide a classic example of the loss of riparian forest for the Willamette River, Oregon. Before 1850 the streamside forest extended up to 3 kilometers on either side of a river characterized by multiple channels, sloughs, and backwaters. By 1967 government-sponsored programs for forest clearing, snag removal, and channelization (channel deepening and straightening) reduced the Willamette River to a single uniform channel that had lost more than 80% of its forest and land-water edge habitats. Fresh waters are especially sensitive to changes in these adjacent lands (Osborne and Kovacic 1993). About 30% of the wetlands of the 50 states and 53% of the wetlands of the contiguous 48 states have been lost (Dahl 1990). The former wetlands slowed the flow of water, and their loss greatly increases the chances and severity of flooding. Wetland conversion also leads to loss of plant, wildlife, and fish species.

Fresh waters are degraded by increasing inputs of silt, nutrients, and pollutants from agriculture, forest harvest, and cities (Carpenter et al. 1996). Lakes and reservoirs fill more rapidly with mud from these sources. Moreover, the growth of nuisance plants, including toxic blue-green algae, is promoted by the increased silt and nutrients, a process called eutrophication. Within a lake or reservoir,

eutrophication is accompanied by a loss of desirable plants as the water becomes increasingly murky. Loss of native plants and chemical changes in the water lead to loss of animal species, including fishes and waterfowl. Regional changes in land use cause widespread eutrophication of many lakes on the landscape, thereby making the lakes more similar because they are all dominated by the same set of species that can tolerate eutrophic conditions. Thus, the diversity of lake types within a landscape is reduced as all lakes become eutrophic and harbor similar species (Carpenter et al. 1996).

Lake Mendota, Wisconsin, illustrates the losses of aquatic species that accompany land-use change in watersheds (Figs. 10–14). Before the advent of the plow in the 1830's, the watershed vegetation (Fig. 10) of this lake was prairie, oak savanna, and forest (Curtis 1959). Studies of dated layers of mud from sediment cores from the bottom of the lake show that the water quality of the lake was high before the rich prairie soils of the lake's drainage were plowed (Brock 1985; Hurley et al. 1992; Kitchell and Sanford 1992). By the 1870's the conversion of native vegetation to agriculture was essentially complete (Fig. 11), and towns were growing around the lake. Large blooms of annoying blue-green algae were common by the 1880's (Brock 1985), and dramatic changes in Lake Mendota's food web also occurred as the native plant communities were replaced by agriculture (Kitchell and Carpenter 1993). The most severe declines in water quality occurred after World War II (Lathrop 1992a) when the use of agricultural fertilizers increased substantially (Fig. 12). Cities also expanded to fill about 9% of the watershed (Fig. 13), and increasing amounts of sewage were added to the lake, intensifying eutrophication (Lathrop 1992a).

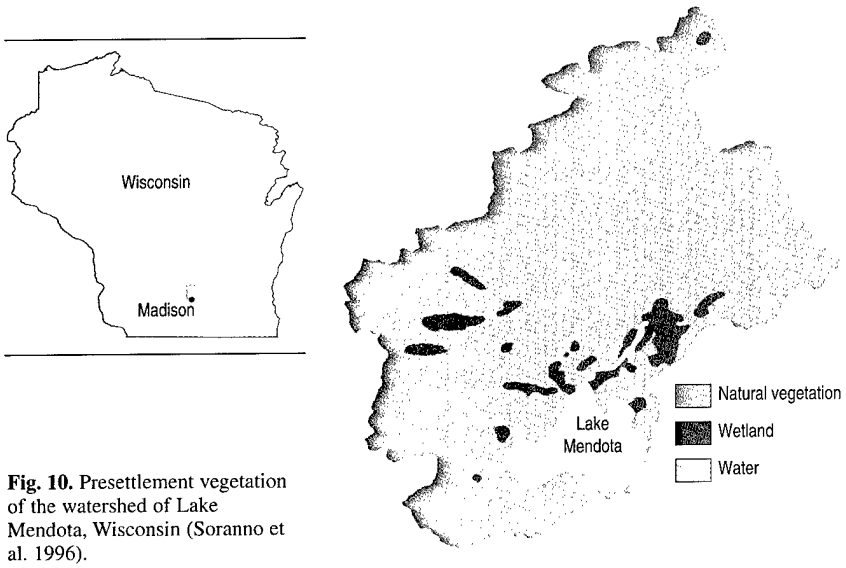

Fig. 10. Presettlement vegetation of the watershed of Lake Mendota, Wisconsin (Soranno et al. 1996).

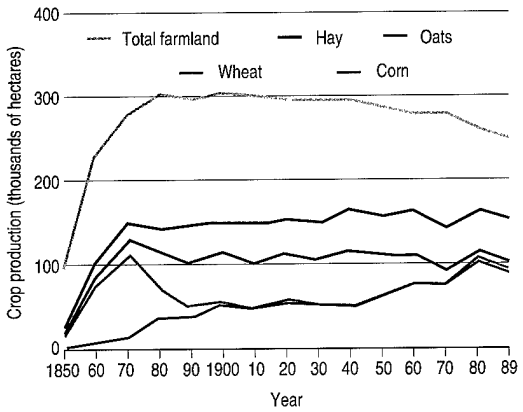

Fig. 11. Area of agricultural land use since 1850 in Dane County, Wisconsin, which includes the watershed of Lake Mendota (Lathrop 1992a).

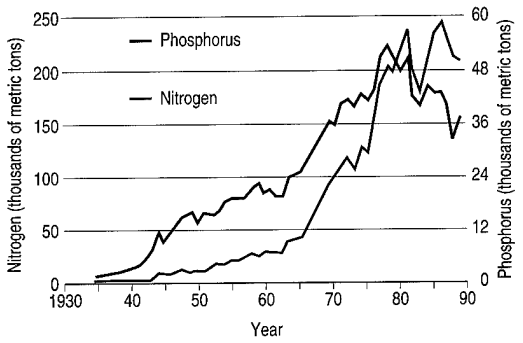

Fig. 12. Fertilizer use in Wisconsin from 1934 to 1989 (Lathrop 1992a).

Although losses of aquatic animals and plants have many interacting causes, most of the species losses from Lake Mendota occurred at the same time as did severe eutrophication, which was caused by increased cultivation, crop fertilization, and expansion of cities (Figs. 11–14). In 1946 the diversity of higher aquatic plants had probably changed little from presettlement times (Nichols et al. 1992), but by 1989, about half the species of aquatic plants were gone. The beds of wildcelery that once supported canvasbacks and other migratory waterfowl were lost, and the native pondweeds crucial for fish reproduction had also disappeared. These beneficial native plants were largely replaced by coontail and by Eurasian watermilfoil, a non-indigenous species, both of which have low food value for fishes and wildlife. Beginning around 1950, deepwater insect populations of Lake Mendota began a steep decline (Lathrop 1992b), and insect larvae—especially midges—that formerly supported fish production were almost absent from the deep waters of the lake by the mid-1960's. The long fingernailclam also disappeared. By the 1920's, six fish species had been eliminated because of intensive fishing and habitat loss. An additional five fish species

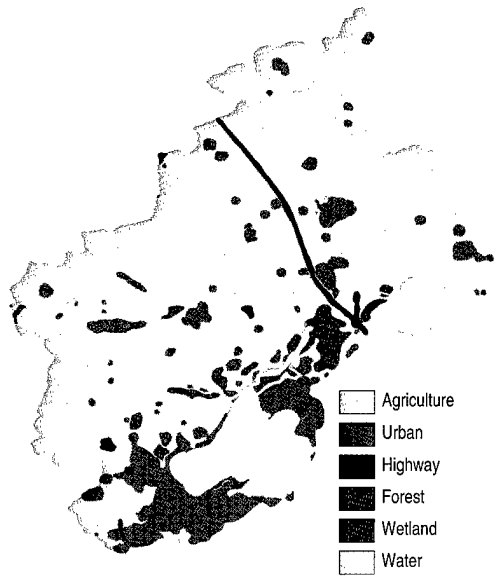

Fig. 13. Land-use patterns in the Lake Mendota, Wisconsin, watershed in 1990 (Soranno et al. 1996).

were lost by 1989 because of the disappearance of native aquatic plants and the stocking of predatory fish. Although 11 of the 37 fish species originally present in Lake Mendota have been extirpated, the lake now contains 37 fish species—the extirpated native species have been replaced by the introductions of fishes not native to the lake (Magnuson and Lathrop 1992).

Loss of native plants and animals is widespread in our nation's lakes, rivers, and other waters. The threat of a diminished variety of aquatic animals and plants is more serious than that for the variety of land animals and plants or even for the variety of organisms in tropical rain forests (Naiman et al. 1995). From 11% to 15% of the birds, mammals, and reptiles in the United States are classified as rare to extinct, but the proportion of aquatic animals and plants similarly classified is much higher—34% for fishes, 65% for crayfishes, and 75% for pearly-mussels (Master 1990). Of 214 stocks of Pacific salmon, 74% have a high or moderate risk of extinction (Nehlsen et al. 1991), primarily due to habitat loss from dams, logging, roads, and grazing (Forest Ecosystem Management Assessment Team 1993). Almost half (44%) of our nation's native clams and mussels are either extinct or endangered (Bogan 1993). Land-use-induced impoundment and inundation of riffle habitat in major river systems (such as the Ohio River, Tennessee River, Cumberland River, and Mobile Bay) and the disappearance of host fish species are responsible for the massive loss of native clams and mussels. About 82% of fishes in the United States are adversely affected by poor water quality, often resulting from habitat loss and fragmentation (Miller et al. 1989). Secondary causes of fish decline are also important, including invasions of nonindigenous species, effects of pollutants, and overfishing. Of the 27 species and 13 subspecies of freshwater fishes that have become extinct in North America during the last century, habitat degradation contributed to at least 73% of these extinctions. The losses of aquatic plants and animals may not be apparent to the casual observer (Noss et al. 1995), but present-day lakes, rivers, and streams are substantially different from those encountered by the early settlers.

Implications of Present Land-Use Patterns for Biological Diversity

Past, present, and future land-use patterns will continue as a dominant influence on biological diversity in the United States. What general themes emerge from our understanding of past land-use changes, their effects on plants and animals, and their importance for understanding the effects of current land-use patterns? We highlight four related issues regarding land use and biological diversity that will continue to be important in coming decades: pervasive effects of habitat fragmentation, indirect effects of land-use change, the importance of landscape context, and land-use practices.

Pervasive Effects of Habitat Fragmentation

Continued habitat fragmentation is one of the most important results of recent land-use changes. Agricultural land conversion has indeed slowed during recent decades, although suburban development, which accelerated nationwide after World War II, still continues unabated. Urban and suburban developments have resulted in loss and fragmentation of natural habitats in many regions of the United States. Resource extractions such as logging, mining, and oil drilling have also resulted in habitat fragmentation.

Adverse effects of fragmentation on biological diversity have been documented by many studies (see Saunders et al. 1991; Noss and Csuti 1994). Of course, species may be directly eliminated from portions of the landscape where habitat has been converted to other uses, but the size of remaining fragments of habitat influences the number of species that can live within each fragment. Small forest patches in Maryland had fewer nesting bird species than larger patches (Whitcomb et al. 1981; Lynch and Whigham 1984); furthermore, species that nested in interior regions of a forest (that is,

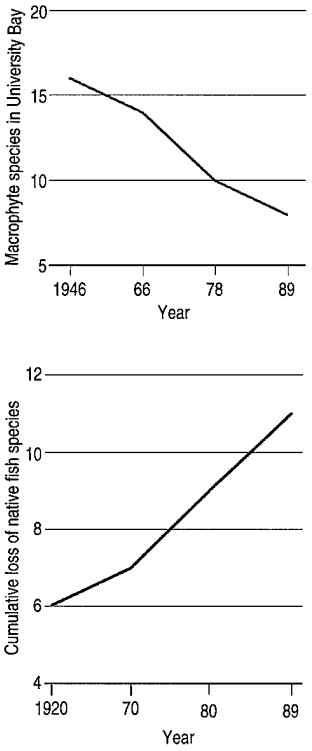

Fig. 14. Change in species richness of aquatic plants and cumulative loss of fishes from Lake Mendota, Wisconsin, during the 1900's (Magnuson and Lathrop 1992; Nichols et al. 1992).

away from the forest edge) were unlikely to inhabit forest patches smaller than a certain size (Whitcomb et al. 1981). Most species lost from small patches were insect-eating birds that migrate to tropical regions of North and Central America. Individual birds that inhabit small forest patches also may have difficulty finding mates (Villard et al. 1993) because fewer birds are present.

The size and arrangement of habitat fragments also affect how animals use the space around them. For example, red squirrels in forest fragments had reduced home ranges in small forest patches (Wauters et al. 1994); the squirrels' use of forest resources was influenced by the size and shape of patches and the presence of connecting corridors among patches. Negative effects of fragmentation have been recorded in midwestern forests (Gottfried 1979) and grasslands (Glenn and Collins 1992; Herkert 1994), the Rocky Mountains (Keller and Anderson 1992), and western forests (Harris 1984).

Loss of old-growth forest is another noteworthy case of habitat fragmentation. Little old-growth forest remains in the lower United States, and species that require the remaining rare old-growth forests will continue to be at risk as land use continues to change. There appear to be no species dependent on old-growth forests in the East today, but old-growth obligates probably disappeared long ago and may have included the ivory-billed woodpecker and Bachman's warbler. The apparent dependency of the northern spotted owl and marbled murrelet on the old-growth forests of the West Coast has ignited an intense controversy over timber harvesting in western forests (Simberloff 1987). The concern centers on both the absolute loss of old-growth habitat and how disconnected the remaining habitat patches have become. Because fragmentation of habitat makes dispersal more difficult and reduces population stability (Lande 1988; Doak 1989), the pattern of timber harvest activity has important consequences (Franklin and Forman 1987). A common practice on national forests in the Pacific Northwest had been to maximize spacing of clear-cuts, leading to a highly fragmented forest condition that persists for many years (Wallin et al. 1994). Consequently, species that require large areas of old-growth or interior forest are thought to be at risk because of these logging practices, particularly the widespread spacing of clear-cuts throughout the forest.

Land-use activities also introduce new human-dominated habitat types such as roads, which may disconnect natural habitats. Road length and area increase with land development, and roads can be effective barriers to the movements of animals, especially invertebrates and smaller vertebrates. Mader (1984) demonstrated the almost complete division of populations of a forest-dwelling ground beetle by a road and parking loops. Of 387 small rodents that were tagged and recaptured during an extensive study on the effects of a highway in the Mojave Desert, only one was found on the opposite side of the road (Garland and Bradley 1984). Large animals are also susceptible to road effects. Grizzly bears in the northern Rocky Mountains used areas within 100 meters of roads less frequently than areas away from roads; this resulted in a nearly 9% loss of prime bear habitat (McLellan and Shackleton 1988). Roads also increased the bears' vulnerability to poachers and legal hunters. In northern Wisconsin, wolves were much more likely to use portions of the landscape where road density was lowest (Mladenoff et al. 1995). In Florida, the highway system presents both a significant barrier to movement and a cause of death for the endangered Florida panther. Even when behavioral responses (such as avoidance) to roads have been observed, the long-term effects of roads on population size and population growth rates are not known and require further study.

Many questions remain about the effects of habitat fragmentation, especially because habitat fragmentation affects different species in different ways (Robinson et al. 1992). In a study of an arthropod (joint-legged animals such as crabs, spiders, and insects) community, an amphipod population declined severely in small habitat patches, but habitat size had no effect on a scorpion (Margules et al. 1994). Some authors (for example, Haila et al. 1993) have argued that the lower numbers of species observed in small habitat patches are simply due to chance. For example, McCoy and Mushinsky (1994) found more vertebrate species in large patches of Florida scrub habitat, but when the effect of patch area was removed from the data, the small patches did not have significantly fewer species.

The fragmentation—or connectivity—of a habitat depends on both its abundance and spatial arrangement. Land-use changes generally alter both the area and configuration of habitats. If habitats decrease in area, effects on plants and animals are aggravated if the habitat also becomes fragmented. Fragmentation can result in the loss of species in single habitat patches as well as loss from the regional landscape. Land-use planning can minimize the effects of habitat loss by maintaining large blocks of native habitat and protecting natural corridors—such as river forest corridors and ridgetops—that connect the remaining large habitat blocks.

Indirect Effects of Land-Use Change

Land-use patterns and habitat fragmentation can initiate a chain of events that leads to unexpected effects. In some instances, the relative abundances of different species change in response to land use, and this in turn causes other organisms to respond. These occurrences can be considered as indirect effects because the land-use activity starts a series of events in which the final result may be unexpected. For example, elevated densities of organisms that thrive in fragmented landscapes have triggered chain reactions that affect many other species. The large numbers of many herbivores (animals that eat plants) that presently occupy our landscapes are a consequence of past land use as well as the government-sponsored predator removals of the early 1900's. Declines of species that play important roles in the ecosystem can also start a chain reaction that affects other species. For example, land-use changes on the Coastal Plain have resulted in loss of habitat for gopher tortoises. Decline of this species may cause reductions or losses of many other species because nearly 400 species of invertebrates and vertebrates have been found in gopher tortoise burrows (Noss et al. 1995).

Densities of white-tailed deer have reached unprecedented levels in many parts of the Northeast (McCabe and McCabe 1984; Witmer and deCalesta 1992; Parker and Van Kley 1993; Correll 1994). These high levels are largely due to the widespread increases in early successional habitats, the added edge habitat between forested and nonforested lands, and the reduced predation and hunting since the 1930's. Land-use changes in the past century provided bonus habitat for deer, but their overabundance has led to deleterious consequences for many other species. The high numbers of deer first influence vegetation structure and composition because the larger deer population consumes more food. Browsing damage by deer can result in significant loss of species and abundance of woody and herbaceous plants (Kroll et al. 1986; Alverson et al. 1988; Tilghman 1989; Miller et al. 1992). Deer damage can become so severe in preserves where hunting is prohibited (for example, state parks and research forests) that seedlings of trees, shrubs, and woody vines are almost completely eliminated. In preserves with dense deer populations, wildflower and grassy cover may be less than 65% of that outside the preserves (Parker and Van Kley 1993; Correll 1994). Because the number of species and abundance of forest songbirds depend on woody vegetation (MacArthur and MacArthur 1961; Karr and Roth 1971), songbird populations are depressed by high deer numbers (Casey and Hein 1983; McShea and Rappole 1992; deCalesta 1994). Clearly, land-use patterns play an important role in this story. Reduction of forest edge to reduce deer densities has been proposed (Alverson et al. 1988), but any successful solution must likely include reduction of deer numbers by hunting (Alverson et al. 1988; deCalesta 1994).

When forests are fragmented, forest birds experience higher rates of parasitism by brown-headed cowbirds—another species that thrives and increases with forest clearing. Cowbirds lay their eggs in the nests of other bird species, and the young cowbirds effectively commandeer the food and attention of the host parents, usually at the expense of the host's own offspring. Cowbirds feed almost exclusively in open short-grass habitats, so the frequency of parasitism is primarily influenced by the amount and type of open land near the nest site (Brittingham and Temple 1983; Robinson 1992). Cowbird nest parasitism is generally limited to areas within 7 kilometers of feeding sites (Rothstein et al. 1984), although average commuting distances are usually much less (Robinson et al. 1993; Thompson 1994). Parasitism rates are generally higher near forest edges (Brittingham and Temple 1983; Yahner and Scott 1988). Nationwide, cowbirds became rarer away from the center of their range in the Great Plains and also declined as the proportion of a landscape in forest increased (Thompson et al. 1996). In the Midwest, cowbird abundance and parasitism were lower in areas with more total forest, more forest interior, and larger forest patches (Thompson et al. 1996).

Almost by definition, indirect effects of land-use change can be difficult to anticipate. These effects are passed along through the intricate web of interactions among species and may take many years to appear. It is important to recognize, though, that there may be significant and surprising long-term consequences from inducing large changes in the abundance of species.

Importance of Landscape Context

The animals and plants contained within habitat patches are affected by what is around them—that is, the context of the surrounding landscape (Askins and Philbrick 1987; Pearson 1993). Better understanding of this broad-scale influence is sorely needed, and it must be considered in land-use decisions. Landscape context is important because the biological diversity of parks, preserves, and wildlife corridors may be affected by changes in the regional landscape (Franklin 1993). For example, the ability of a species to disperse to a particular habitat patch will depend on whether the surrounding landscape makes movement easier or more

difficult (Taylor et al. 1993). Harsh and unsuitable habitats in the landscape may present barriers to species movements. River forests are often protected to maintain water quality and to provide wildlife habitat, but the effectiveness of river forest corridors is influenced by the surrounding upland landscape. For example, the species of birds found in river forest corridors are different depending on whether the surrounding landscape is forested or agricultural (Croonquist and Brooks 1993) or whether it is in the country or the city (Smith and Schaefer 1992). Urbanization of the surrounding landscape also affects other natural habitats, such as woodlots (Whitcomb et al. 1981; Tilghman 1987). The effect of cowbirds in forests, for example, depends on the presence of open feeding habitats in the broader landscape (for example, Gustafson and Crow 1994). Thus, interpretation or projection of trends in terrestrial species must consider the broader landscape.

The importance of the landscape for aquatic systems is paramount. Freshwater quality and biological diversity depend on riverine forests and floodplains that slow the transport of water, retain silt and nutrients, and provide spawning sites, food, and shelter for fishes and wildlife. Diverse, self-sustaining river and lake-edge vegetation is crucial to the quality of lakes and streams. Logging, cultivation, or residential development of river- or lake-edge forests accelerate water flow, increase soil erosion, and eliminate habitat. Such changes in these forests thereby result in significant costs in wildlife, fishes, and downstream water quality. Once the forests at the edges of rivers or lakes are significantly changed, restoration may be very difficult and extremely expensive. Thus, decisions about river- and lake-edge land use should consider costs to wildlife, fishes, water quality, and the potential permanent problems caused by development. Wetland, floodplain, and riparian restorations, which are sorely needed in many areas of the United States (National Research Council 1992), should be ranked by comparing the costs and benefits of each project. Benefits need to accumulate at the level of watersheds or even larger spatial units, and this scale must be considered in the accounting process.

Land-Use Practices

Actual land-use practices, of course, affect biological diversity. Forest-cutting methods and fire reduction serve here as examples that illustrate this occurrence. However, the ways developments are sited and built, how lands are used for grazing, and the ways in which agriculture is practiced are other ways in which land-use practices are important.

Several different logging methods are widely used in North America; these have fairly predictable consequences on the structure and pattern of habitats. Even-age methods result in stands composed of trees of a single age class, while uneven-age systems periodically remove trees to maintain a variety of different ages of trees within the stand (Thompson et al. 1993). The effects of these logging methods on forest birds have been studied in ecosystems throughout the country (Conner and Adkisson 1975; Crawford et al. 1981; Steffen 1985; Thompson and Fritzell 1990; Dickson et al. 1993; Hutto et al. 1993; Thompson 1993). The common finding of all these studies is that, in the short term, logging enhances habitat for some species and degrades habitat for others. Openings produced by even-age logging upset the continuity of closed canopy forest and may have negative effects on birds of the forest interior (Porneluzi et al. 1993). Some logging methods produce so many small, dispersed openings that interior forest conditions are very difficult to maintain (Gustafson and Crow 1994). The edges produced by even-age harvests and group selection may increase predation and brood parasitism rates so much that bird reproduction is seriously reduced (Paton 1994). Uneven-age methods do allow retention of mature forest bird communities, though at lower densities than in unmanaged forests. Nevertheless, uneven-age harvest methods do not produce the same level of landscape diversity of old and young forest patches that characterizes natural forests (Dickson et al. 1993; Thompson et al. 1993).

The short-term effects of logging on bird populations have been the subject of many studies, but long-term consequences are not as well known. For example, clear-cutting may cause profound short-term changes in forests, but these changes may be critical to a long-term approach for maintaining the kind of historical ecological conditions dependent on widespread, frequent disturbances such as fire (Hunter 1992; Hutto et al. 1993; Reice 1994). The long-term effects of excluding large-scale natural disturbances from ecosystems are not well known because such protection has been relatively recent.

Concern has recently been raised about the effects of logging on land-dwelling salamanders (Petranka et al. 1993) and nonwoody plants of the forest understory (Duffy and Meier 1992). There is no general agreement on the effects of land-use practices on plants and animals that have not been well-studied; these species deserve continued investigation (Elliott and Loftis 1993; Johnson et al. 1993).

Sometimes land-use practices alter the natural disturbance regimes that generate the

complex patterns of habitats required by native plants and animals. If land-use practices change the frequency, size, and intensity of natural disturbances, then altered sequences of vegetation development may lead to completely different plant communities (see chapter on Natural Processes for a complete discussion of disturbance regimes). For example, although eastern oak–hickory forests were traditionally thought of as a stable climax forest community (Weaver and Clements 1938; Braun 1950), they are now being succeeded by moist forests dominated by hard maples (Schmelz et al. 1975; Lorimer 1985; Schlesinger 1989). This trend has been attributed to the reduction in natural fire caused by fire control during the twentieth century (Curtis 1959; Lorimer 1985; Van Lear and Waldrop 1989). Periodic fires enable oaks to become dominant among competing species (Rouse 1986), and the oaks cannot replace themselves without disturbance (Kessler 1992).

Forest composition in the Southeast is also dominated by disturbance-initiated species and has been attributed to human activity over the last one or two thousand years (Buckner 1989). The exclusion of fire and major disturbance in many eastern forest systems is relatively recent and may now be producing completely new combinations of plant communities in certain regions. The abilities of animal species to adapt to these new plant communities are unknown. Clearly, the ways in which land is managed for particular uses will continue to influence the plants and animals that are present.

Land Use and Biological Diversity: Important Next Steps

Serious environmental problems often come as surprises. Some of the more obvious symptoms of environmental degradation in the United States are now being addressed through public or private management actions. But what is the likely origin of the next environmental surprise? When examined in retrospect, some surprises have come from incremental shifts that crossed a threshold to catastrophic change. Such big effects from small causes (Ricker 1963) are known from many natural and social systems (Holling 1978). We suggest that it is the accumulation of small local changes that poses the greatest long-term challenge to encouraging sustainable land-use patterns in the United States.

Individual changes in land use may appear to have only local significance. In total, however, the large number of local changes is transforming the landscape of the United States. Gradual but widespread change leads to significant effects on vegetative cover, wildlife habitat, soils, and water quality. If the current path of land use in the United States continues, we can expect continued loss of wildlife and vegetation, erosion of soils, and nonpoint pollution of groundwater and surface water. If we are willing to manage landscapes for the larger good, these losses can be prevented, and the resources can be restored. Progress will require adaptive change and planning, monitoring, and research. Most importantly, it requires the political will to maintain a landscape that supports the natural resources we expect and need.

Present trends in land use suggest that collisions between the desires of the human population and natural ecological processes will continue. Ongoing urban development in our landscapes—including suburban sprawl and development of vacation homes—locks a pattern onto the landscape that is hard to reverse. Many farms of the previous century have been returning to more natural vegetation, but urban and suburban areas are more permanent. The larger lot sizes and the more sprawling nature of subdivisions that extend well into the countryside are an increasingly important cause of habitat loss and fragmentation. Housing located near natural areas may be quite desirable for the views and the privacy afforded; however, as a result of this practice, encounters between humans and wild animals or conflicts over the management of natural fires intensify. Developments are often designed to transport water off the land as quickly as possible, so developed watersheds become more prone to flooding. The fragmentation of large blocks of habitat can be minimized by the clustering of similar land uses, which has important implications for cities and suburbs. In general, it is more beneficial for habitat connectivity if human activities are concentrated than if they are dispersed widely throughout the landscape.

Land managers must enlarge their perspective to encompass the landscape. Clearly, plants and animals respond to regional patterns and to changes in habitat availability and connectivity. Natural disturbances, which create patchiness and structure biotic communities, must also be considered. Managers of natural areas that do not consider the surrounding seminatural environments lose crucial opportunities for maintaining more extensive habitats that harbor richer arrays of native plants and animals (Franklin 1993). When land managers focus too closely and don't "see the forest for the trees," the benefits of biological diversity may be lost. Management of freshwater habitat, for example, is likely to fail if the important riparian animals and plants are neglected or if land use in the floodplains is ignored. Land management should become a more cooperative venture that

works within ecologically meaningful boundaries rather than political or jurisdictional boundaries.

Effective conservation of aquatic ecosystems and their biological diversity also requires a landscape perspective (National Research Council 1992). Unfortunately, most attempts to manage or restore aquatic systems address isolated components—for example, individual lakes, rivers, or wetlands. Agency responsibilities are oriented toward components rather than whole ecosystems (Leopold 1990), and the expertise needed for restoration is divided among various disciplines (National Research Council 1992). In practice, this division creates problems because uplands, wetlands, groundwater, rivers, lakes, and estuaries are interconnected by flows of water and nutrients and by migrations of organisms. These connections, though, must be considered. For example, wetlands are often essential to restoring lakes, but well-intentioned lake management (such as water level stabilization) could harm the wetlands. Pragmatic approaches to managing aquatic ecosystems require coordination at the watershed or landscape scale. At present, no organization or institution in the United States is responsible for the integrated view that makes watershed restoration practical (Cairns 1994). Addressing this challenge would benefit us all.

Species do not recognize political boundaries, suggesting the potential for considering some degree of integrated management of the natural and seminatural landscape. Of course, land-use regulation is a potentially explosive issue. A solution to balancing human needs and maintenance of biological diversity is not ecologically sustainable unless it is also politically sustainable. Forcing landowners to enhance biological diversity by regulation will probably produce a backlash that could lead to long-term loss of species. Research should proceed on the development of market-based incentives that encourage maintenance of species and habitats. Perhaps the greatest challenge for biological diversity protection is to preserve the structure and function of native ecosystems while protecting the rights and privileges of private property owners.

Many questions remain about the past and future effects of land use on animals and plants, and a few research needs stand out. Because the pattern of habitats across the landscape has such a strong influence on native animal and plant communities, improvements in methods for predicting future land-use patterns are sorely needed. Predicting land-use change requires linking knowledge and techniques from numerous disciplines, including economics, sociology, and ecology (Lee et al. 1992; Turner et al. 1996; Wear et al. 1996). Such interdisciplinary study is naturally complex, but there should be strong encouragement to develop the required integration. Better understanding is needed of what drives land-use change and how land-use patterns will respond to changing human population growth. Predictions of land-use change also should include not only the amount of change but also how the changes are arranged across the landscape. The effects of patch size and habitat fragmentation are sufficiently important that models should incorporate these factors (Turner et al. 1995). Models are a crucial component of research geared toward land use and biological diversity. Models permit us to project effects on plants and animals of the land-use experiments that society is presently conducting and to explore alternative future scenarios.

Greater explanation of what caused the pattern of plants and animals across today's landscapes is needed. The extent to which observed changes in present-day plant and animal communities are due to effects caused by changes in land-use practices decades ago or are directly related to recent practices is unclear. Some effects of past land use may persist for many decades, especially if long-lived organisms like trees are considered. In addition, the degree to which natural successional trajectories have been permanently altered by land use is not known. For example, the endpoints of the changing forest composition observed in the East and upper Midwest are not known. Many more empirical studies relating land-use change to biological diversity would be valuable, and more case studies would improve general understanding, as well as better explain local biotic patterns. These are important needs for relating land-use changes in the future to expected species' responses.

The most remarkable aspect of the landscape of the United States since European settlement is its continually changing face. Effects of these vast changes are long-lasting and crucial to our understanding of the present-day plants and animals that inhabit our landscapes (Foster 1992). In turn, conservation remains challenging in part because we seek to preserve areas that are changing (White and Bratton 1980). Ecological systems do not exhibit an undisturbed state that can be maintained indefinitely, but land use can alter both the rate and direction of natural trajectories. Because land-use patterns create the environment in which plants and animals must live, reproduce, and disperse, our understanding of the influence of land use on biological diversity is critical to the future of land management. The question is not whether we should or should not use land, but rather how we can best use the land. Open lands in the United States still abound in many areas. We are not predestined to continue past trends in land use. Rather,

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we have the opportunity to choose our destiny and plan for quality growth, balancing human needs while maintaining the integrity of our nation's primary resource—the land.

Acknowledgments

We especially thank J. Fraterrigo for her timely assistance with the library research required for this chapter. Comments from L. Iverson, J. Magnuson, and an anonymous reviewer improved the manuscript. This research was funded by the National Biological Service. The National Science Foundation also contributed to the ideas developed here through funding to the Coweeta and North Temperate Lakes Long-term Ecological Research Sites.

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Water Use

Fresh water is vital to life and to habitat preservation. It is a major component of climate and a determining influence on economic growth and human population patterns. Modern competition for freshwater resources directly relates to the complex history of land use as humans evolved from hunter-gatherers to farmers and to modern agriculturists, industrialists, and members of modern urban communities. Water developments that proliferated during the twentieth century have greatly benefited most aspects of modern life, including public health and safety, agriculture, recreation, and commerce, but at the same time, these water developments have caused many environmental changes (Schilling et al. 1987; McDonald and Kay 1988; Waterstone and Burt 1988; Johnson and Viessman 1989; Moore 1989). The need to balance water use and development with environmental change will continue to increase as the human population grows and associated changes in land use accelerate.

Trends in Freshwater Use

From 1950 to 1990, both the population and domestic water use in the United States increased steadily. Withdrawals of fresh and salt waters increased to a peak of 1.7 billion cubic meters per day in 1980, and by 1990 daily freshwater withdrawals were 1.5 billion cubic meters (Fig. 1). Rural use of water for households and livestock increased from 1960 to 1990 (Table 1). Irrigation increased from 1950 to 1980, to a maximum of 570 million cubic meters per day, while per capita water use in the United States decreased from 6.8 million cubic meters per day in 1970 to 5.9 million cubic meters per day in 1990. Commercial and industrial uses of water, including self-supplied industrial use and withdrawals of water for mining, increased to a plateau in 1975–1980 before declining by 14%. The estimated use of fresh groundwater—fresh water drawn from below the ground—was 130 million cubic meters per day in 1950. Use of groundwater increased to 310 million cubic meters per day by 1975, decreased during the 1980's to 280 million cubic meters per day, and then increased again to 300 million cubic meters per day in 1990 (Table 1). The use of fresh surface water peaked in 1980 at 1.1 billion cubic meters per day and declined to 980 million cubic meters per day by 1990 (Table 1). Consumptive use—water that is withdrawn from a water source and does not eventually return to the water source—of fresh water followed the same patterns as withdrawals (Table 1). The reduction of withdrawals during 1980–1985 reflected conservation but could also relate to climate or the economic slowdown (van der Leeden 1975; Solley and Pierce 1988; Solley et al. 1993).

Fresh water is now a limited ecological (physical and biological) and economical resource. The trend in the present use of water reflects its limited availability. Krusé (1969) estimated that by 1965, withdrawals of 1.3 billion cubic meters per day were exceeding the available dependable water supply by 13%. The deficit reflected the need for reusing water, the increased use of salt water, and the lack of new water development opportunities. How did we reach this point?

Courtesy Agricultural Service, USDA

Table 1. Water use in the United States, 1950–1990[a] (in million cubic meters per day; modified from Solley et al. 1993).

	1950	1955	1960	1965	1970	1975	1980	1985	1990
Offstream use									
Total withdrawals[b]	680	910	1,000	1,200	1,400	1,600	1,700	1,500	1,500
Public supply	53	64	79	91	100	110	130	140	150
Rural domestic livestock	14	14	14	15	17	19	21	29	30
Irrigation	340	420	420	450	490	530	570	520	520
Industrial									
Thermoelectric power	150	270	380	490	640	760	790	710	740
Other	140	150	140	170	180	170	170	120	110
Source of water									
Groundwater									
Fresh	130	180	190	230	260	310	310	280	300
Saline		2.3	1.5	1.9	3.8	3.8	3.4	2.5	4.6
Surface water									
Fresh	530	680	720	790	950	980	1,100	1,000	980
Saline	38	68	120	160	200	260	270	230	260
Reclaimed water		0.8	2.3	2.6	1.9	1.9	1.9	2.2	2.8
Consumptive use			230	290	330	360	380	350	360
Instream use									
Hydroelectric power	4,200	5,700	7,600	8,700	10,600	12,500	12,500	11,500	12,500

[a]For years before 1960, data include the contiguous United States; 1960–1965, the 50 states; 1970, the 50 states and Puerto Rico; and after 1970, the 50 states, Puerto Rico, and the Virgin Islands. For 1970 and after, consumptive use values are for fresh water only.

[b]The numbers in this column are not column totals because of rounding.

History of Water Use in the United States

The beginning of water development in North America can be traced to between A.D. 600 and A.D. 800, when the Hohokam Indians of southern Arizona dug irrigation canals for cornfields (Josephy 1968; Hurt 1987). Modern water development for irrigation began in Utah in 1847 (Lea 1985), and the first dam for municipal water was completed in 1916 (van der Leeden et al. 1990). Today, an estimated 75,000 dams and an untold number of canals, levees, locks, power plants, and pipelines exist (Parfit 1993). The U.S. Army Corps of Engineers reported that in 1982, each of 2,654 large dams stored more than 6 million cubic meters of water, 50,000 smaller dams stored 60,000 to 6 million cubic meters, and more than 2 million small dams and farm ponds stored an undisclosed amount of water (van der Leeden et al. 1990). By 1988, 91% of the river lengths in the lower United States had been developed (Hunt 1988). Water storage in reservoirs increased to 549 billion cubic meters in 1990 (Fig. 2).

The national emphasis of water development in the United States has shifted back and forth among flood control, water supply and quality, and conservation (Table 2). Likewise, the responsibility for water management in the United States has also shifted greatly over time (Josephy 1968; Hurt 1987; Hunt 1988; Johnson and Viessman 1989; van der Leeden et al. 1990; Tyler 1992; Wilkinson 1992). Until 1850 the responsibility for water use remained primarily with individuals or corporate entrepreneurs. During the next century, however, the management of the waters of the United States in public trust was the joint responsibility of the states and the federal government. Federal interest in interstate water-use conflicts on major rivers resulted in agreements such as the Pick-Sloan Plan for the Missouri River (Schmulbach et al. 1992) and the Colorado River Compact (Trelease 1967). The states have determined how water uses are administered and who has the right to use water primarily through two different approaches. The first approach is by the riparian common law doctrine in the humid eastern United States, where streamside owners are entitled to the natural flow of the streams

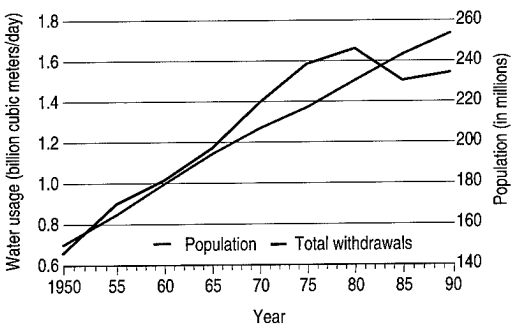


Fig. 1. Population and water use in the United States, 1950–1990 (Solley et al. 1993).

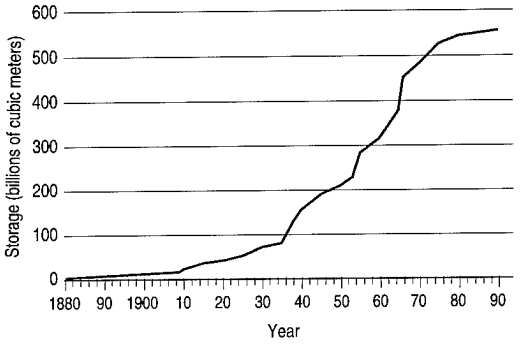


Fig. 2. Reservoir storage in the United States (© W. B. Solley, unpublished table of reservoir data, 1994).

past their land, substantially undiminished in quantity and unimpaired in quality (that is, a reasonable use of water consistent with like use by others). The second approach is by the prior appropriation doctrine in the arid western United States, where first in time is first in right, and beneficial use of water (not landownership) and priority of use (not equality of right) are the basis for division when there is not enough water for everyone (Trelease 1967). These legal approaches reflect the public interest in the availability of water for beneficial uses. Major federal projects that support national purposes and respond to national emergencies and regional needs also had a significant influence on the nature of water development during the nineteenth century (Table 2).

Table 2. Events that characterize water use in the United States.

Date	Event
A.D. 600–800	Diversion of water for irrigation by the Hohokam Indians
1824	General Survey Act: the U.S. Army Corps of Engineers given responsibility for navigation and flood control of the Mississippi River and other rivers
1847	First modern U.S. irrigation project, Salt Lake City, Utah
1848, 1850	Swamp Lands Acts: first federal activity in water resources management
1870	Irrigation in Greeley, Colorado
1899	Rivers and Harbors Act as amended through 1977
1902	Reclamation Act: established the Reclamation Service—responsible for irrigation of arid land
1916	Ashokan Dam on Esopus Creek near Olive Bridge, New York, completed. First high dam in United States (over 75 meters high and 1.9 million cubic meters in volume content)
1917, 1928, 1936, 1938	Flood Control Acts: emphasized flood control, not water resources management
1920	Federal Water Power Act: created Federal Power Commission to regulate water resources
1922	Colorado River Compact: divided the states' rights to use the Colorado River
1933	Bureau of Reclamation joined Public Works Administration
1933	Tennessee Valley Authority created, ultimately changing the lower Ohio and Tennessee River valleys
1935	Soil Conservation Service created
1936	Flood Control Act: had the first benefit–cost analysis for water development
1936	Hoover Dam–Lake Mead started operation: supplied power to the urban West
1938	Soil Conservation Service given responsibility for flood and soil erosion control
1938-1956	Colorado–Big Thompson Project: largest transfer across the Continental Divide
1948	Upper Colorado River Compact
1956	Federal Water Pollution Control Act (as amended P.L. 92-500, 1972)
1965	Water Resources Planning Act: mandated river basin planning
1968	Wild and Scenic Rivers Act: effort to protect the remaining undeveloped U.S. rivers
1969	National Environmental Policy Act
1970	Rivers and Harbors Act
1973	Endangered Species Act
1977	Safe Drinking Water Act
1977	Clean Water Act, with the Safe Drinking Water Act, provided safe, clean water to the general public

Effects of Water Use on Watersheds

The withdrawal of water or the alteration of water quality elicits responses in watersheds—the area drained by a stream or river. These alterations occur even in the most remote places, and responses include changes in biological diversity and ultimately in the entire landscape (Ward and Stanford 1979; Becker and Neitzel 1992; Pederson 1994). In fact, few wild rivers are completely wild, and few native populations are not affected by humans. Benke (1990) estimated that during the past century, 98% of the 5.2 million kilometers of streams in the contiguous 48 states were altered sufficiently by human activities so that they did not meet the more stringent requirements for protection under the Federal Wild and Scenic River provisions (Fig. 3). For example, as human population and water use increased, the species diversity of fish communities decreased (Moyle and Leidy 1992). Thus, by 1989, in spite of conservation and restoration, over 100 species of freshwater fishes were added to the threatened or endangered list and more than 250 freshwater fish species were in danger of disappearing (Deacon et al. 1979; Williams et al. 1989; Johnson 1995). The endangerment of freshwater fishes in several regions of the United States has been linked to dams, the straightening of channels of large rivers, the building of cities, the expansion of agriculture, the logging and clearing of headwaters, the erosion of river channels, the pollution of water, and the introduction of nonindigenous species. The total effect of these developments is the alteration of stream ecology as evidenced by changes in the migration patterns of fishes, in stream water temperature and nutrient levels, in water chemistry, and in biological diversity (Warren and Burr 1994).

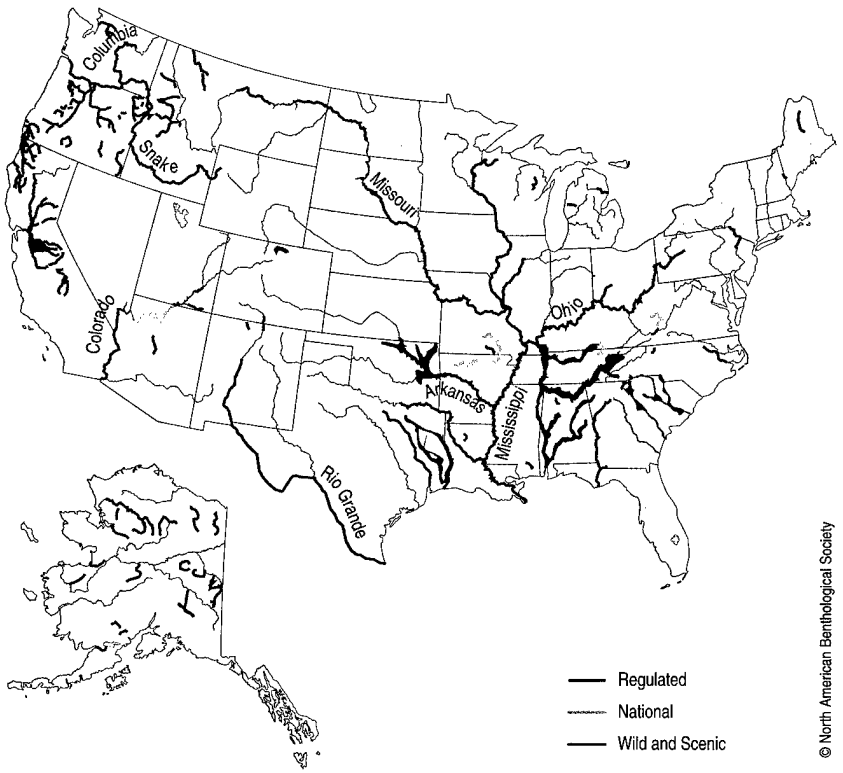


Fig. 3. Regulated, National, and Wild and Scenic Rivers in the United States (Benke 1990).

The terrestrial part of the watershed ecosystem is also threatened (Table 3). Before European settlement, the estimated amount of riparian land in the 100-year floodplains of the lower 48 states was 49 million hectares. By the 1980's it was reduced by 81%, to 9.3 million

Table 3. Endangered and threatened species in the contiguous United States (U.S. Fish and Wildlife Service 1994).

Species	Total species endangered	Aquatic and riparian species endangered	Total species threatened	Aquatic and riparian species threatened
Mammals[a]	53	18	10	4
Birds[b]	30	15	12	7
Reptiles[c]	8	3	18	6
Amphibians	6	6	3	3
Fishes	64	64	36	36
Clams	50	50	6	6
Snails	13	12	7	4
Insects	19	9	9	5
Arachnids	4	4	0	0
Crustaceans	11	11	2	2
Flowering plants[d]	187	55	74	29
Conifers and cycads	2	1	0	0
Ferns and allies	4	3	2	1
Lichens	1	0	0	0
Total	452	251 (56%)	179	103 (58%)

[a]Mammals that occur only in saline or marine environments; 12 endangered and 2 threatened species.
[b]Birds that occur only in saline or marine environments; 6 endangered and 2 threatened species.
[c]Reptiles that occur only in saline or marine environments; 4 endangered and 4 threatened species.
[d]Flowering plants that occur only in saline or marine environments; 2 endangered species.

hectares (Brinson et al. 1981); 22 states had lost more than 50% of their wetlands (Fig. 4). Although the rate of change in wetland areas slowed between the mid-1970's and mid-1980's, there was still a net loss (Table 4), which created a major shift and reduction in the variety of plants and animals in riparian lands (Johnson and McCormick 1979; Petts 1984; U.S. Office of Technology Assessment 1984; Mathias and Moyle 1992).

The total effects of human activities in aquatic and riparian lands are not nearly understood. The change in biological diversity, however, can be linked to habitat change and to the loss of species (Hunt 1988). From alpine and mountain streams to estuaries and deltas, anthropogenic changes have accumulated, and many of the nation's watershed ecosystems have been drastically altered by these changes.

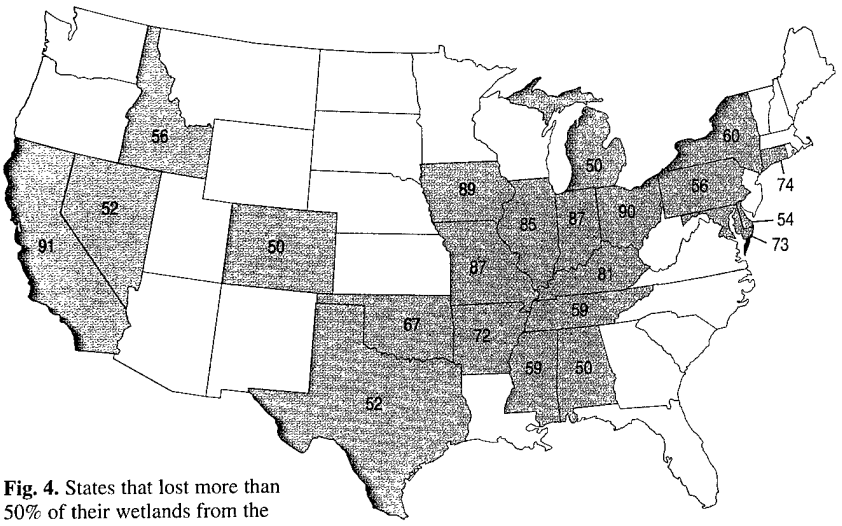


Fig. 4. States that lost more than 50% of their wetlands from the 1780's to the mid-1980's (Dahl and Johnson 1991).

Nature of Water Development and Use

The development of freshwater resources for human use has many consequences for aquatic biota and for riparian and terrestrial species that depend on aquatic ecosystems for food or habitat. Direct human effects include changes in stream and river flows and lake water levels from dams and irrigation (Mesa 1994), the introduction of pollutants (Crowder and Bristow 1988), both intentional and inadvertent introductions of nonindigenous species by providing access pathways (Kitchell 1990; Cloern and Alpine 1991; Mackie 1991), and the overexploitation of selected species, especially fishes and mussels (Hedgecock et al. 1994). Indirect effects on aquatic biota include introductions of extensive atmospheric contaminants (Schindler et al. 1985), widespread use of salts on roads (Likens 1985), change in aquatic species composition from UV-B radiation, change in water nutrient content and temperature from livestock grazing in the riparian zone (Armour et al. 1991), and change in water quality from human development in upstream watersheds (Byron and Goldman 1989; Fisher 1994; O'Dell 1994).

Water developments have single or multiple purposes. For example, stored water may be withdrawn for cooling of electrical power plants, or it may be released for the generation of electric power. A development may provide water for municipal, agricultural, and industrial withdrawals, as well as for recreational uses (boating, fishing, swimming). The American Rivers group (1995) attributed the most frequent threats to the 30 endangered and threatened rivers on their list to dams (13), agricultural (10) and urban (10) runoff, mining (6), and flood-control or navigation demands (6). Other problems include overgrazing, logging, overuse, and sewage. Water projects often must balance competitive uses that can have different direct or indirect effects on aspects of the biological, physical, or chemical environment.

Table 4. Estimated gains and losses of freshwater wetlands in the United States from the mid-1970's to the mid-1980's (in million hectares; modified from Dahl and Johnson 1991).

Wetland type	Mid-1970's	Mid-1980's	Change
Palustrine emergent	9.839	9.929	+0.090
Palustrine forest	22.320	20.942	-1.378
Palustrine scrub	6.275	6.210	-0.065
Palustrine nonvegetated[a]	2.165	2.485	+0.320
Lacustrine	23.327	23.409	+0.082
Riverine	2.073	2.101	+0.028
Total freshwater wetland	65.999	65.076	-0.923
Total intertidal estuarine	2.239	2.215	-0.024

[a]Palustrine nonvegetated wetlands include aquatic beds and unconsolidated bottoms and shores.

Flood Control

Flood-control structures (dams, levees, and diversions) may hold back excess runoff (upstream dams), speed runoff (channelization), confine runoff (levees), or do all three for large river basins such as the Missouri–Mississippi River basins. Flood-control structures do not consume water but remove water from rivers and aquatic ecosystems. When flood-control systems fail, the consequences are often catastrophic for the farmlands and cities for which the flood control was provided. The effects of flood control on ecosystems of the Red River, a tributary to the Mississippi River, include shifts from river to lacustrine aquatic habitats, change from river forests to open land from conversion to agriculture, and loss of species richness in habitats (Hardaway and Yakupzak 1981). For example, in the Yazoo Basin on the Mississippi River, flood control caused a significant decline in the quality of the aquatic ecosystem. Only 20% of the stream length now supports a fishery, and even fewer kilometers support a sport fishery (U.S. Fish and Wildlife Service 1979). Since 1870 in south-central Oklahoma, 87% of the riparian forests and 17% of the channel length have been eliminated by flood control (Barclay 1978).

Bank stabilization and navigation structures created erosion and deposition in the natural channel of the Missouri River. Structures reduced the channel from 120,000 to 50,000 hectares (U.S. Army Corps of Engineers 1980; Hunt 1988). Between 1879 and 1954, channelization decreased the total water-surface area of the Missouri River from 49,000 to 16,000 hectares. Modification of the river caused the disappearance of the river otter by 1935. Commercial fish catches declined by 80% between 1947 and 1963. Lake sturgeon, paddlefish, and blue catfish populations greatly declined (Funk and Robinson 1974; Hunt 1988).

Navigation and Transportation

Rivers are important to commerce (Fig. 5). For example, human manipulation of the Upper Mississippi River has a long history. The construction of a lock and dam system in the 1930's to aid commercial transportation not only created a diversity of lentic habitats in the upper basin but also changed the water level and the amount of transported sediment (Holland-Bartels 1992).

Alterations of the Ohio River for navigation since 1800 have been extensive, but the construction of navigation dams from 1900 to 1927 has had especially widespread effects. The biological effects of siltation after clearing of forests in the nineteenth century, combined with

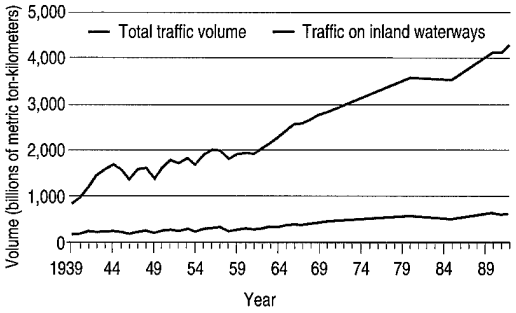


Fig. 5. Volume of domestic intercity freight carried in the United States (modified from U.S. Department of Commerce Bureau of the Census 1975 and 1994).

modern pollution in the upper third of the river, reduced biological diversity. For example, although 159 fish species were identified between 1819 and 1988, since 1970, 13 of these species have not been found (Pearson 1992).

In Florida, the Jim Woodruff Dam, which opened in 1957, now traps almost all silt and debris from the Chattahoochee and Flint rivers, reducing the flow of nutrients and sediments to the Apalachicola Bay. Dams on the Chattahoochee and Flint rivers eliminated the striped bass fishery and caused a shift to rough and forage fish species (Livingston 1984; Hunt 1988).

Similarly, in the major rivers of the Mobile Bay basin, dams eliminated many aquatic species that still occur in the smaller tributaries. Construction of the Tennessee–Tombigbee Waterway, for example, eliminated 17 aquatic species from the main channel. In the basin, 99 species of snails and 24 species of freshwater clams and mussels are now endangered or threatened, and 14 species of freshwater pearly-mussels were lost from the Tennessee River (Ward et al. 1992).

Hydroelectric Power, Irrigation, and Municipal Use

Diversions

When water is diverted to crops, air is humidified and cooled in irrigated areas. Reservoirs behind dams decrease daily air temperature variation over stored waters and increase evaporation. Little change in the local climate is noted unless the reservoir is located in arid lands (Budyko 1982). The ultimate effects of diversions and irrigation on the hydrological cycle are not fully understood and are presently impossible to completely separate from natural factors. Large-scale effects, however, are suggested (Pielke et al. 1992). The quantity and quality of available water, soil moisture, and frequency of extremes such as droughts are affected by precipitation and evaporation changes from whatever source. For example, climate change—the altering of the amount and timing of rainfall, carbon dioxide levels, and temperature—could limit available

water and therefore adversely affect agriculture. How soil temperature and moisture are affected by the combination of increased precipitation, carbon dioxide, and temperature is not clear. Therefore, the effects on water caused by anthropogenic change, such as water diversions, cannot be separated easily from processes such as climate change in any given location (MacCracken et al. 1990).

Fourteen major dams that were constructed on the Columbia River for hydroelectric production of power, transportation, and agriculture provide many economic benefits to the region but changed a rapid-flowing river ecosystem to a warmer water, slow-flowing series of impoundments (Strober and Nakatani 1992). The dams inhibit or block migrating fishes and, by flooding spawning grounds, cause changes in competition between species, changes in predator–prey relations, and a decline in the variety and numbers of native fish species. In 1911 the commercial fish harvest on the river was 24,400 metric tons, but by the early 1970's it had declined to 6,800 metric tons. In 1949 the Lower Columbia River Development Program was funded for fish restoration. By 1962, 50% of the harvested coho and chinook salmon were raised in hatcheries. Since then, other innovations, such as protection devices, fish passages, and timing of flows and construction, have been used (Trefethen 1972). Even so, hydrological regulation, especially by dams, is probably still the principal factor in placing 75% of the native Pacific salmon stocks at moderate to high risk of extinction (Nehlsen 1994).

The effects of hydrological regulation by dams have been well-studied. Findings from the Columbia River point out the ecological complexity of dam effects on the declining salmon populations, especially juveniles. Juvenile salmon incur multiple stresses from water agitation below dams and become lethargic and disoriented, which heightens their vulnerability to predation (Mesa 1994). Dams also reduce the biological diversity of aquatic primary producers and their immediate predators, which are prey for fishes. For example, the Columbia pebblesnail population experienced major declines because of the creation of inhospitable habitat along the Columbia River drainage (Neitzel and Frest 1992).

Water development in the Columbia River basin, not including the Snake River, has also been responsible for the loss of more than 108,000 hectares of fish and wildlife habitat (Hunt 1988; Fig 6). The flooding of backwaters, bays, canyons, riparian forests, and river banks eliminated habitat and reduced populations of many animals. Changing water levels also affected nest sites on islands and reduced the nesting success of birds in rookeries. Because of the loss of prey, the abundance of many predators is also declining.

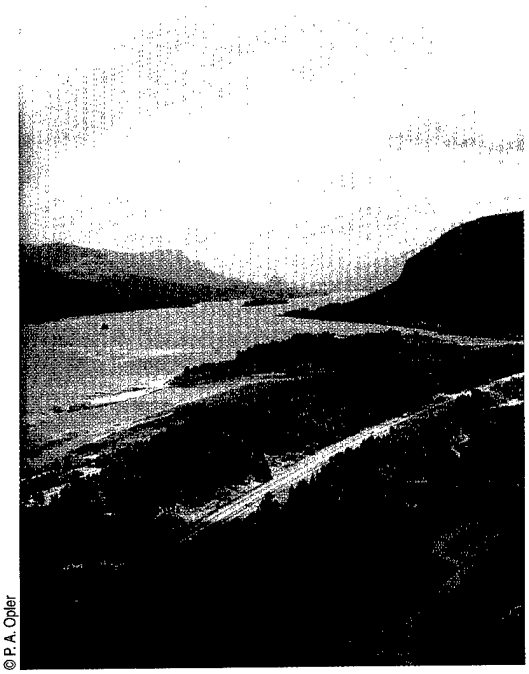


Fig. 6. The Columbia River in Oregon below the Bonneville Dam. Most of the Columbia River is now controlled by water-development projects.

The Sacramento River drainage has also been affected by human activities and water development. During the past 20 years, the size of the river's salmon population has declined 50% in the Sacramento–San Joaquin watershed because dams and upstream developments eliminated rearing and spawning habitat. The river was greatly modified during the last 200 years to provide more than half of the surface water used in California (Mongan and Miller 1992). More recent modification of diversion and irrigation processes demonstrated that changing the way water is used and treated is possible. For example, California rice farmers flood fields after harvest to get rid of stubble through natural decay instead of through burning; this flooding creates seasonal wetlands for migrating waterfowl. Later, a timed release of the water assists with the migration of salmon downstream to the open ocean (Hunt 1988; Conniff 1993). Such modifications—although they do not address the loss of natural habitats or biological diversity—require cooperation rather than competition in water use.

Irrigation

Irrigation is critical to modern life and to agriculture in the dry western United States. In addition, eastern farmers are beginning to use supplemental irrigation to increase crop yields

Impounded River Systems

River basin development projects, including the construction of dams and irrigation diversions, were led by state and federal government partnerships during the 1950's and 1960's. Human demands for flood protection, water for irrigation, hydroelectric power, navigation, and bank stabilization resulted in large public works undertaken by the U.S. Army Corps of Engineers and the U.S. Bureau of Reclamation. These projects pose pervasive threats to midcontinent aquatic ecosystems because they have significantly altered the physical characteristics of most of the region's major river systems, which has resulted in numerous adverse effects, including the loss or decline of many native plant and animal species, especially fishes.

In fact, The Nature Conservancy's *Troubled Waters: Aquatic Ecosystems at Risk* (Flack and Chipley 1996) states that nationally 67% of freshwater mussels, 64% of crayfish, 37% of freshwater fishes, and 29% of amphibians are at risk. Alterations of river habitats have been instrumental in causing the decline in abundance and diversity of many species (Figure).

Unimpounded River Corridors

The large-river systems of the midcontinent are characterized by native riverine species of fish, mussels, and crayfish. These systems course through an arid to semiarid environment where often the only forested habitat is the extensive riparian corridor that lines these streams. This riparian zone provides important habitat for wetland species and serves as a migratory corridor for waterfowl, shorebirds, mammals, and other animals. The native river fishes require flowing water habitats for either all of their life stages (for example, the darters) or for only a portion of their life history (such as paddlefish, sturgeons, and other migratory species).

Melting snowpack in the distant mountains and high-intensity summer rainstorms are the dominant forces that shape the river channels as they cut through alluvial materials. The rivers are composed of shallow, often braided channel habitats, with warm, turbid water interspersed with deep pools along the outside of meander bends. The annual scour and fill cycle deposits sediments on the floodplain and replenishes the bars with the fresh sand and soil necessary for cottonwood regeneration.

After Impoundment

The impacts of damming and flow regulation can be classified as immediate or delayed (Holden 1979) or as first-, second-, and third-order effects (Becker and Gorton 1995). The immediate or first-order effects are obvious blockage of upstream and downstream migration of fishes and alteration of the downstream habitat by dewatering and releasing cool (or cold) and clear (free of suspended fine sediments) water through the low-flow portion of the channel. Many kilometers of upstream river corridors are inundated and converted to lakelike habitats. The cold, clear water tends to pick up sediment from the riverbed or banks, which causes the bed to gradually lower or widen. Water releases from midcontinent reservoirs generally produce lower water temperatures in summer and higher water temperatures in winter. Native riverine fishes adapted to the natural temperature regime are displaced downstream and may be unsuccessful in reproduction because of changes in timing of physiological processes keyed to temperature cues. Consequently, these native riverine species may be (and often are) gradually replaced by generalist species, which are often nonindigenous species introduced by humans and adapted to cool or cold water. Basses, sunfish, and northern pike often escape from reservoir stocking programs into the river below, where these predatory nonindigenous fishes not only compete for habitat but also prey on the young native fishes.

The longer-term effects of dams include a degraded and widened channel that can carry a higher volume of flow. This, along with a decrease in the magnitude of peak flows and the trapping of sediments by reservoirs, results in a much lower frequency of overbank flooding. The lack of overbank floods, which deposit sediments, and the erosion of the bed and banks by the sediment-starved reservoir releases result in the loss of sandbars and cause bankwater habitats to be replaced by steep, raw banks along the channel.

Over a period of decades, the cessation of the annual scour and fill cycle that replenishes the bars with fresh sand and soil causes riparian cottonwood stands to gradually become open; these stands are eventually replaced by nonindigenous plant species. Thus, biological productivity is reduced as the number and diversity of wetland and riparian communities along the river corridors decline. In addition, the reproductive success of the native riverine fishes is greatly reduced due to temperature changes and loss of spawning areas. Those fish that do spawn have fewer of the remaining backwater habitats they need to feed and grow. As previously noted, after nonindigenous species such as pike and centrarchids invade, they compete with native species for habitat and they prey on the young native fishes.

Rehabilitation, Monitoring, and Research

Restoration of these declining large-river ecosystems is being discussed widely among resource agencies, conservation groups, and the public. Restoration of these areas to their natural predevelopment condition is almost impossible, however; most restoration efforts are simply attempts to rehabilitate selected segments of river to some predetermined structure and function (Gore and Shields 1995). Dramatic examples include the Kissimmee River in Florida, which biologists are trying to reroute to its original channel, and the March 1996 "test flooding" by the Department of Interior in the Grand Canyon, Arizona. Federal listing of several native large-river species as threatened or endangered and declining biodiversity of aquatic and riparian communities throughout the midcontinent have prompted a reevaluation of how the U.S. Army Corps of Engineers and the U.S. Bureau of Reclamation operate many large federal reservoirs.

Two major studies are ongoing in the Colorado River basin: the Recovery Implementation Program for Endangered Fish Species in the Upper Colorado River basin and the Grand Canyon studies. Extensive monitoring studies have recently begun in the Missouri and Yellowstone rivers. The U.S. Army Corps of Engineers has funded wetland, riparian, and fisheries studies as part of the Missouri River Master Manual Review and Update Study, and the U.S. Bureau of Reclamation is funding fisheries and geomorphological studies in the upper Missouri and Yellowstone rivers. The objective of these studies is to build an analysis and decision support system to allow water managers to better understand the trade-offs associated with various operating scenarios. Biological monitoring is being designed and coordinated through the Missouri River Natural Resources Committee, a group of scientists from each

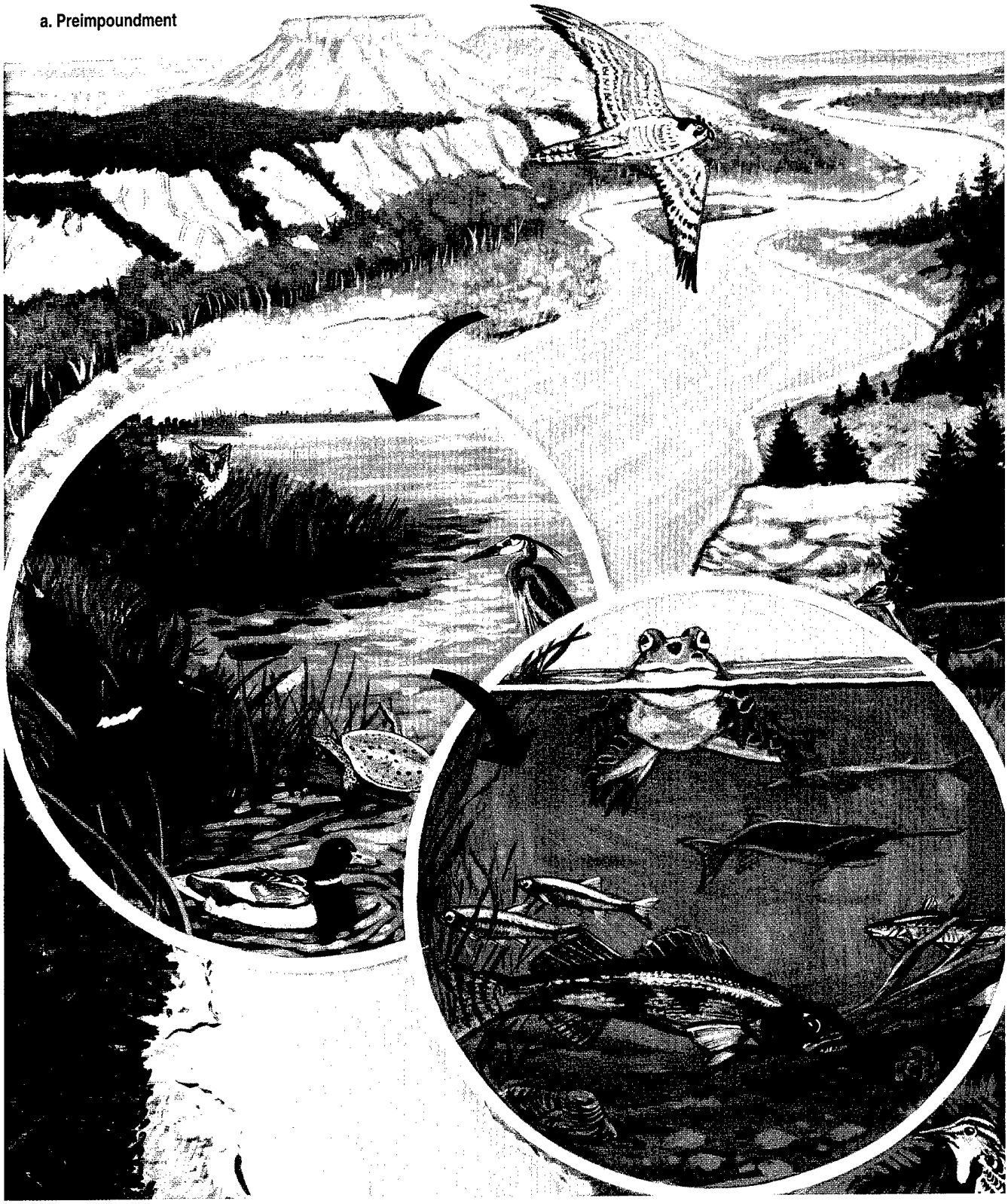
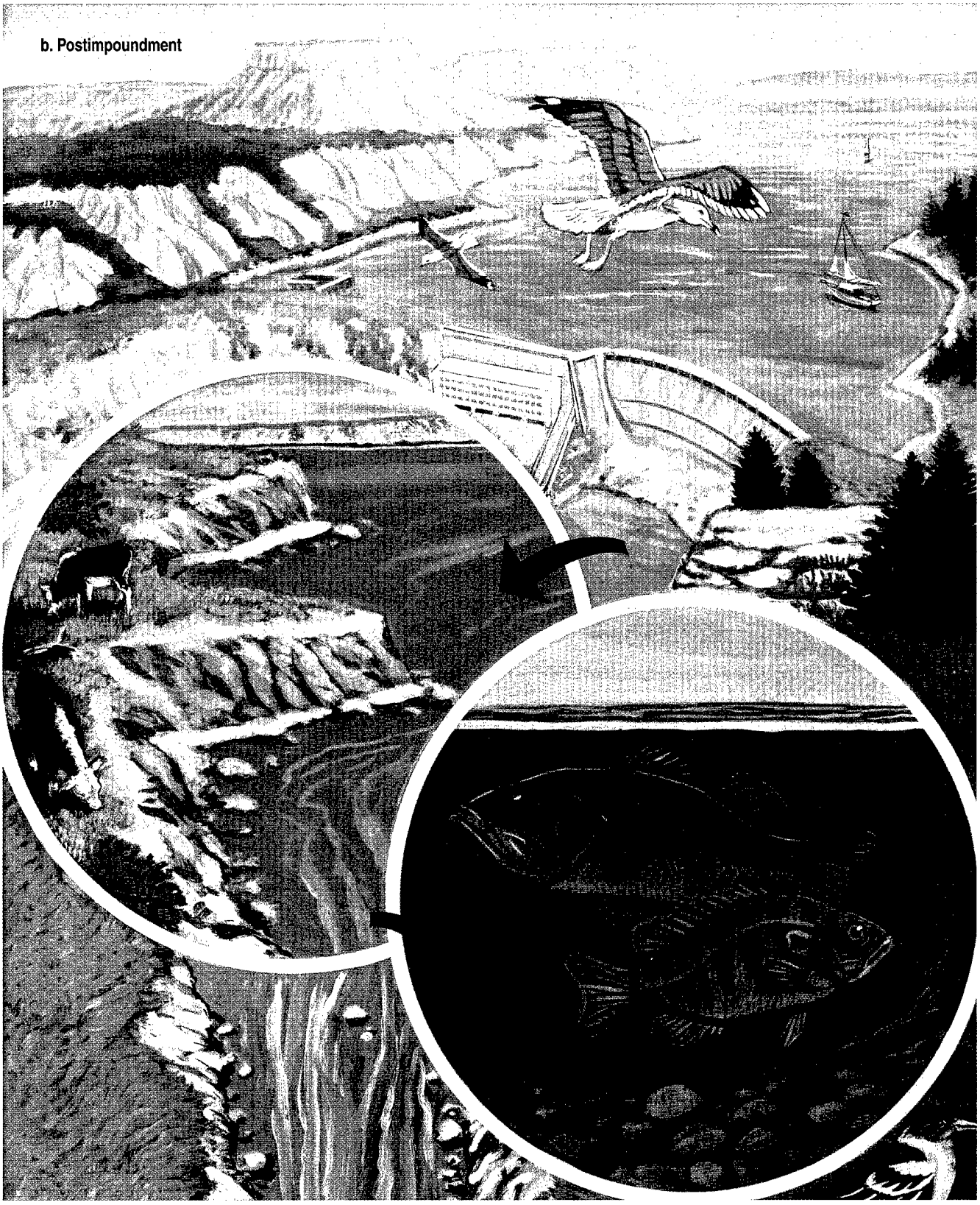


Figure. Depiction of a segment of the Missouri River with a) pre- and b) postimpoundment views of the river channel and biota, including close-up views (see circles) of a benthic (bottom) habitat and a marsh habitat before and after impoundment. The preimpoundment river corridor provides for a rich and complex array of habitats, including a thriving riparian and wetland community and a diverse instream fauna of benthic (bottom-dwelling) insects, mollusks, and native riverine fishes such as paddlefish, pallid sturgeon, and sauger (see bottom circle in a). In contrast, the postimpoundment river channel, though it may appear



visually attractive at first glance, has eroded banks, is devoid of the native riparian habitats that are so invaluable in this region, and has an impoverished instream benthic fauna, including a fish fauna that is now dominated by nonindigenous centrarchid species (basses and sunfish; see bottom circle in b), which gradually replace native species.

of the basin states, the U.S. Army Corps of Engineers, U.S. Fish and Wildlife Service, U.S. Geological Survey, U.S. Bureau of Reclamation, and the Western Area Power Authority.

Much remains to be learned about the ecology and life-history requirements of the biological communities of the midcontinent river corridor before rehabilitation schemes can be designed by ecologists and natural resource scientists. The opportunities for designing and carrying out scientific studies on the physical and biological processes of large warmwater environments appear good for the next decade. By perfecting large-river sampling techniques and intensive monitoring in large-scale experiments (such as the Grand Canyon), we will have more science-based information about how to manage these systems, which in turn will allow us to more accurately assess the status of these biological communities.

See end of chapter for references

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and as crop insurance to guard against drought. About 86% of the irrigated land in the United States is in the West, where irrigation waters are delivered by furrows or ditches, flooding, sprinkler systems, or underground systems. Future growth in irrigated agriculture is limited by water supply and cost, high energy and operating costs, water laws, water pollution from agricultural salts and chemicals in runoff, and competition for land and water from urban areas. Because urban growth competes for water supplies (Lea 1985), it is important to agricultural water users. In 1990, 517 million cubic meters of water per day were withdrawn for irrigation, and 288 million cubic meters per day were consumed. During that year, water use for governments, businesses, and households was 148 million cubic meters per day and consumption was 25.6 million cubic meters per day (Solley et al. 1993).

Interbasin Transfer

Ten major interbasin transfers, which move water from one river basin into another by canal, aqueduct, or pipeline, occur in the western United States (van der Leeden et al. 1990). The movement of water across river divides is not unique to the West, however. Since 1967, New York City has met about 50% (2.83 million cubic meters per day) of its daily demand for water by transferring water from the Delaware River (Major 1992). Another example of interbasin transfer was the construction of the Colorado–Big Thompson diversion, which began in 1938 and was completed in 1956; this diversion, which transfers water through the Alva D. Adams Tunnel (Fig. 7), was supported by the federal government under the 1902 Reclamation Act. Recent growth of cities and suburbs has placed additional demand on this water. Although the Colorado–Big Thompson diversion transfers the greatest volume of water in Colorado, 37 other large and small transmountain diversions contribute to the annual transfer of more than 802 million cubic meters of water from the basins of the Gunnison, San Juan, and Colorado rivers on the Western Slope across the Continental Divide to the Eastern Slope of Colorado, where 80% of the state's human population resides (Tyler 1992). These diversions changed the ecological character of both slopes by elevating salinity (chemical salts) in Colorado River waters and by reducing the amount of water in the basin and in the river that, according to treaty obligation, should flow to Mexico. The projects limit future growth and development on the Western Slope and encourage continued urban growth on the Eastern Slope.

Point and Nonpoint Pollution

Public concern about the quality of the nation's waters was demonstrated by the passage of the Water Pollution Control Act of 1956 and its amendments in 1972 and by the passage of the Clean Water and Safe Drinking Water acts of 1977. These acts developed a clear statement of the national goal to restore and maintain the chemical, physical, and biological integrity of the nation's waters (Federal Water Pollution Control Act 1972). In spite of substantial cleanup, however, harmful substances are still discharged into the nation's natural waters, and their effects are often not obvious. The following few examples demonstrate the physical and biological nature and effects of these pollutants (also see chapter on Environmental Contaminants).

Pollutant Sources

Many studies have been conducted on the effects of specific water or airborne pollutants on aquatic biota. Many of these studies, though, have been narrowly focused; assessments of the magnitude of effects on ecosystems are incomplete or nonexistent. Research on the effects of atmospheric contaminants, such as hydrogen, nitrogen, and sulfur, on small lake or stream ecosystems is an exception and is considered in a separate chapter.

Irrigation runoff is a major source of nonpoint pollution, which occurs over broad land

areas often at low levels. Contaminants in such runoff include sediments, salts, fertilizers, pesticides, and bacteria (Lea 1985). Airborne contaminants are another widespread source of nonpoint pollution. Whenever contaminants such as oxides are released into the atmosphere—for example, by burning fossil fuels—they can be transported considerable distances before falling to the ground. Not only can such contaminants cause changes in surface-water quality, but animals and plants can also be harmed by such pollution. One airborne pollutant, nitrate, is of particular concern to the environment because elevated nitrate levels in lakes, rivers, marshes, and other water bodies can contribute to increased plant productivity or potentially to increased acid levels. Nitrate in rain or snow can lead to acidification of the upper parts of some watersheds.

Release of Atmospheric Contaminants into Lakes and Streams

Beginning in the 1970's, national attention focused on the release of atmospheric hydrogen, sulfur, and nitrogen into small, sensitive lakes and streams. During this period, many studies of aquatic ecosystems began, and the results of these studies improved our understanding of the structure and function of these systems.

One of the better long-term studies on small lakes was conducted in the Experimental Lakes Area in southwestern Ontario (Schindler et al. 1985; Schindler 1987). This study showed that the earliest response to stress from experimental acidification was a change in species composition of phytoplankton. Other research revealed morphological change in benthic invertebrates such as crustaceans, which are sensitive early indicators of stress from pollution. It is important to note that aquatic ecosystem processes such as productivity, respiration, and nutrient cycling are relatively less sensitive to stress.

Effects of Multiple Pollutants on Lakes and Streams

Point sources of pollutants in surface waters affect local areas but often can be eliminated more easily than more widespread nonpoint source pollutants. Examples of point-source pollutants include nitrogen and phosphorus, which increase algal growth in surface waters and estuaries.

Many studies have revealed ecosystem-level responses to air- and waterborne pollutants in the Great Lakes. The addition of limiting nutrients such as nitrogen and phosphorus to the lakes by nonpoint drainage waters from developed and agricultural areas creates eutrophication and locally high levels of algal biomass (Conley et al. 1993; Schindler et al. 1993). This rapid increase of biomass limits other nutrients such as silica, essential for exoskeleton development of primary producers such as microscopic diatoms. The subsequent fluctuation in species composition of producers alters the cycling of nutrients and changes populations of zooplankton and their predators. Rapid increases in aquatic plant biomass can then drastically change water nutrient levels and lower oxygen concentrations.

This, in part, is what happened during the 1960's and 1970's in Lake Erie (Nalepa et al. 1991) and is what initiated the cleaning of the lake. Such chemical change can directly affect benthic species such as mussels, which are especially sensitive to increased turbidity and low dissolved oxygen levels. Manufacturing in the Great Lakes region historically released high levels of contaminants into the lakes. Organic pollutants in particular may concentrate in benthic macroinvertebrates, reducing the size of their populations and promoting the incorporation of contaminants into the food chain (Nalepa 1991). Increased organic

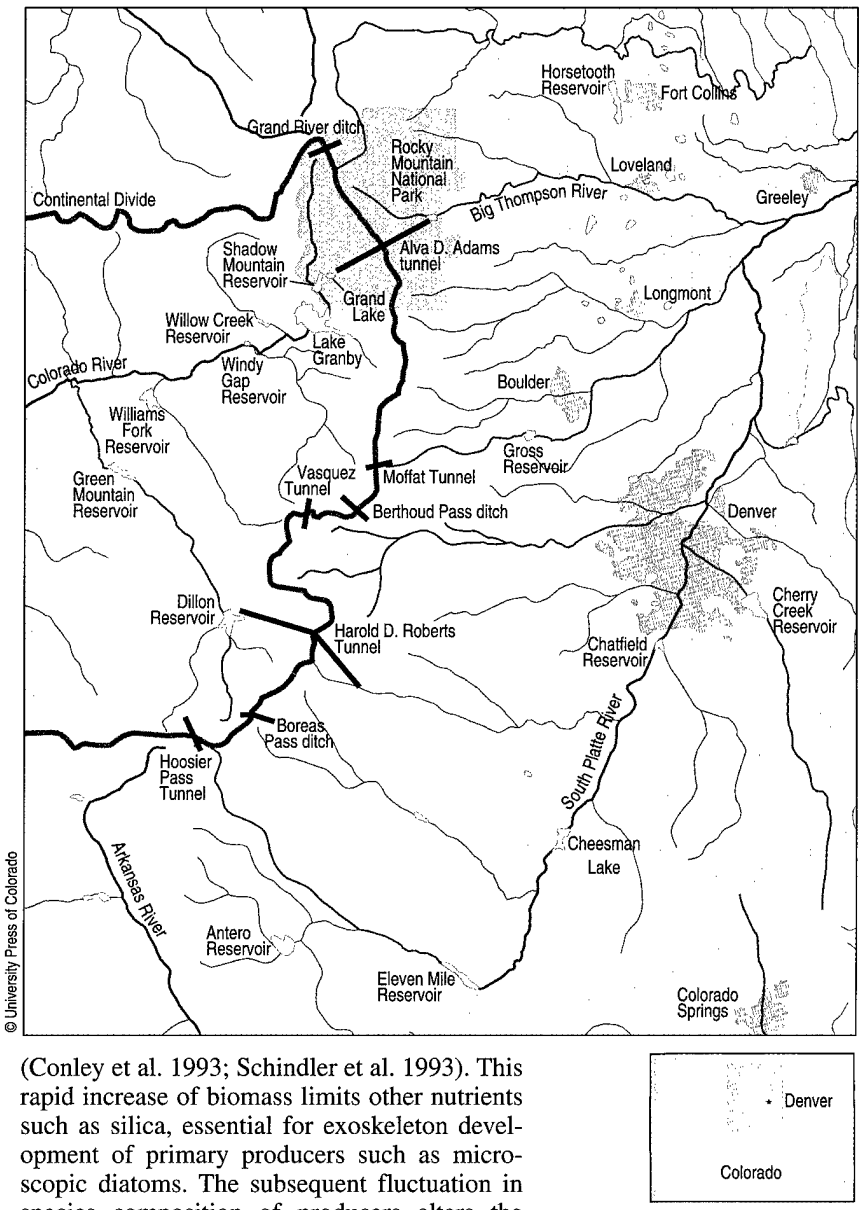

Fig. 7. Major trans-mountain diversions in Colorado (Tyler 1992).

contaminant concentrations in predatory fishes limited human consumption of those fishes, greatly reduced the value of a historically important fishery, and reduced fish population sizes and community composition by limiting reproduction.

Long-term studies of point and nonpoint pollutants have been conducted in the Great Lakes and their tributaries (Smith et al. 1992). Concentrations of toxic materials such as arsenic, chlordane, dieldrin, dichlorodiphenyltrichloroethane (DDT) and related compounds, and polychlorinated biphenyls (PCB's) recently declined, but mercury levels remained constant. These data represent the success of major efforts to clean up point-source discharges.

Other regions have not improved. Streams in agricultural areas of the Midwest have high herbicide concentrations. In the Mississippi River and its major tributaries, alachlor and atrazine occasionally exceed the maximum contaminant levels set by the U.S. Environmental Protection Agency (Smith et al. 1992). These contaminants adhere to the high loads of suspended sediments and are carried long distances, which increases their potential harm to aquatic organisms and humans (Ellis 1993).

Most aquatic ecosystems suffer from multiple anthropogenic stresses (Karr et al. 1985). The Illinois River in the Midwest exemplifies a river in which increased city populations and agricultural uses in its watershed, hydrological regulation, discharge of oxygen-demanding wastes, overuse of water, and introduced nonindigenous species have interacted to drastically alter the aquatic ecosystems. The river, with a drainage area of 73,000 square kilometers, starts southwest of Chicago and flows to the Mississippi River. Lands surrounding the river were cleared, and bottomlands, including lakes, were drained for agriculture. Sediment, fertilizer, and pesticide runoff from agriculture now enter the river, adding to urban runoff. Elevated and rising nitrate levels were noticed from 1975 to 1994 by Schideman and Blanchard (1994). The number of phytoplankton is high in reaches with nutrient enrichment from farmland runoff and low in reaches with turbidity and toxic metals. The poor water quality of the Illinois River is exemplified by high turbidity and low dissolved oxygen levels (Anderson et al. 1991), which have resulted in an increase in abundance of aquatic species that favor cloudy water (bottom-feeding fish). More recent studies (Lerczak and Sparks 1995) have indicated that water-quality improvements on the Illinois River have resulted in a return of a more diverse fish community.

Sedimentation is a factor in the loss of aquatic plants in the Illinois River; sedimentation and the loss of aquatic plants contributed to the disappearance of 20 fish species and the loss of the commercial fishery. Loss of aquatic plants also adversely affects the waterfowl that feed on the plants. In addition, the draining of bottomland lakes and marshes further decreased the abundance of fishes and the habitat of migratory waterfowl along the river (Starrett 1972; Holland-Bartels 1992). In sum, contaminants that are released into the nation's waters greatly restrict the usefulness of receiving waters for human water supply, fish habitat, other wildlife habitat, and water-contact activities.

Sediment

Sediment that erodes from the land into streams and rivers is transported to reservoirs and deposited behind dams, where flow velocity decreases. Data compiled by Crowder (1987) indicate that this process has decreased the storage volumes of large reservoirs in the United States by 0.22% annually (van der Leeden et al. 1990; Table 5). Hunt (1988) cited losses as high as 73% over 30 years (1942–1972) from the Ocoee Dam Number 3 in North Carolina.

Trapped sediment alters river channel characteristics, which, in turn, affect water-table elevation and adjacent riparian vegetation. With a reduced downstream sediment load, rivers below dams erode their beds and banks. This decreases floodplain width, reduces riparian habitat area, and alters river channel character and level. In response to these changes, people often line and stabilize the banks of the main

Table 5. Water storage capacity that is lost annually (in million cubic meters) from reservoirs because of sedimentation; data are for reservoirs in the contiguous United States with total capacities of 6.17 million cubic meters (modified from Crowder 1987).

Farm region	Total water storage capacity	Usable water storage capacity	Water storage capacity lost (est.)	Percent water storage capacity lost (est.)	Reservoir sedimentation from cropland (est.)	Percent stream sediment originating on cropland (est.)[a]
Northeast	45,000	31,100	34.7	0.08	10.1	29
Appalachian	73,400	37,800	93.2	0.13	27.0	29
Southeast	90,800	58,700	157.1	0.17	51.8	33
Lake states	36,200	24,100	97.6	0.27	62.4	64
Corn Belt	49,000	18,800	129.3	0.26	81.4	63
Delta states	52,700	24,800	108.0	0.20	44.3	41
Northern plains	97,400	67,100	227.8	0.23	82.1	36
Southern plains	136,100	57,500	255.9	0.19	48.6	19
Mountain	206,200	170,400	373.3	0.18	29.9	8
Pacific	111,900	92,200	544.9	0.49	49.0	9
Total	898,700	582,500	2,021.8	0.22	486.6	24

[a] The percentage of the sediment in the stream that originated on cropland was calculated by dividing the estimated sedimentation from cropland in the reservoir by the estimated lost water storage capacity.

channel and affected tributaries to protect riparian land and adjacent developments. Such bank stabilization, though, further alters the natural channels (Simons 1979; Hunt 1988). An example of such processes can be seen downstream of the Gavins Point Dam on the Missouri River upstream of Yankton, South Dakota. Between the Gavins Point Dam and Ponca State Park, 0.88 hectares of land per kilometer of river have been lost each year since the dam was built in 1956. Similar data from four Missouri River dams show erosion losses below the dams of 53 hectares per year (Fort Peck), 30 hectares per year (Garrison), 121 hectares per year (Fort Randall), and 81 hectares per year (Gavins Point; Hunt 1988). This combination of erosion and siltation from river development and stabilization has caused the loss of 40,600 hectares of aquatic habitat, 26,400 hectares of island and sandbar habitat, and 125,000 hectares of associated riparian habitat along the Missouri River (Hunt 1988).

Habitat modification by sedimentation and siltation has caused extensive separation of fish populations in the Southeast. The most imperiled aquatic species live in creeks and small rivers, where they depend on clean streambottom substrates, especially for reproduction. Poor land-use patterns, though, have eliminated much suitable habitat for bottom-dwelling species (Walsh et al. 1995). In addition, removal of riparian vegetation has increased soil erosion and siltation because water cuts into banks that are no longer protected by plant roots. Loss of riparian vegetation also has increased soil temperature and soil water evaporation and has elevated stream water temperatures, which have increased algal growth and water stagnation. The end result is a great loss of plants and animals (Campbell 1970; Hunt 1988).

Effects of Grazing on Aquatic Ecosystems

The deterioration of riparian zones is a major factor in the loss of the integrity of aquatic ecosystems (Cummins et al. 1989; Armour et al. 1991; Gregory et al. 1991). Cattle grazing, especially in the West, has caused major effects on riparian zones (Fig. 8). Because riparian aquatic zones are often the most productive, they are grazed more heavily (Rinne and Medina 1988; Armour et al. 1991), which increases siltation. This increased siltation can cause the loss of fish-spawning areas and can reduce food for fishes by lowering the number of invertebrates, destroying streamside and instream cover, increasing water temperatures and velocities, decreasing organic matter, and reducing the number of species that prefer to inhabit cold, clear water (Behnke and Raleigh 1978).

Fig. 8. Cattle grazing causes deterioration of riparian vegetation, soil erosion, and siltation of streams.

Grazing also degrades aquatic ecosystems by adding nitrogen and reducing leaf litter necessary for stream benthic invertebrates such as shredders. Although the riparian zone contains ecologically important plant communities, wildlife, and fisheries, it has too often been considered strictly a component of the terrestrial-aquatic boundary instead of a zone with significant influence on both terrestrial and aquatic ecosystems.

Mining

Stream siltation from mining is significant in some regions of the nation. Mining of coal, oil shale, oil sands, sand, and gravel is a particularly important source of elevated stream sediment loads. Mining degrades water quality and channel integrity and withdraws large quantities of water for processing. Runoff from mines may also contain elevated concentrations of heavy and trace metals (Boyles et al. 1974; Hardie et al. 1974) or suspended sediments with metals. The direct effect of mining on surface waters is significant. By 1965, 9,300 kilometers of streams (about 23,000 hectares) and 12,000 surface hectares of impoundments and reservoirs in the United States were affected by surface coal mining, including acid drainage from mines (U.S. Department of the Interior 1973).

Acid mine drainage has been well publicized historically and remains a common, seasonal problem in much of the eastern and southeastern United States. A National Stream Survey by the U.S. Environmental Protection Agency revealed that 10% of the streams in the northern Appalachians were acidic because of receiving mine drainage during spring baseflow. Throughout the survey area, almost 5,000 kilometers of stream, or 2% of the total survey stream length, were acidic because of acid

drainage from mines; another 6,000 kilometers were severely affected (Herlihy et al. 1990).

Although the effects of gravel mining on aquatic ecosystems have been little publicized, the removal of gravel from one area of a channel affects areas upstream and downstream as bedload materials move to establish a new equilibrium in the stream bottom (Kondolf 1994). Following mining, gravel necessary for spawning by fishes is lost, and suspended sediments can travel far downstream, eliminating even more spawning area and altering the environment for benthic invertebrates. Stream instability from such mining also eliminates sandbars where migratory shorebirds often nest. For example, colonial waterbirds, such as the endangered least tern and the threatened piping plover, must use areas such as sand pits in place of lost sandbar habitat along the Platte River in Nebraska (Sidle and Kirsch 1993).

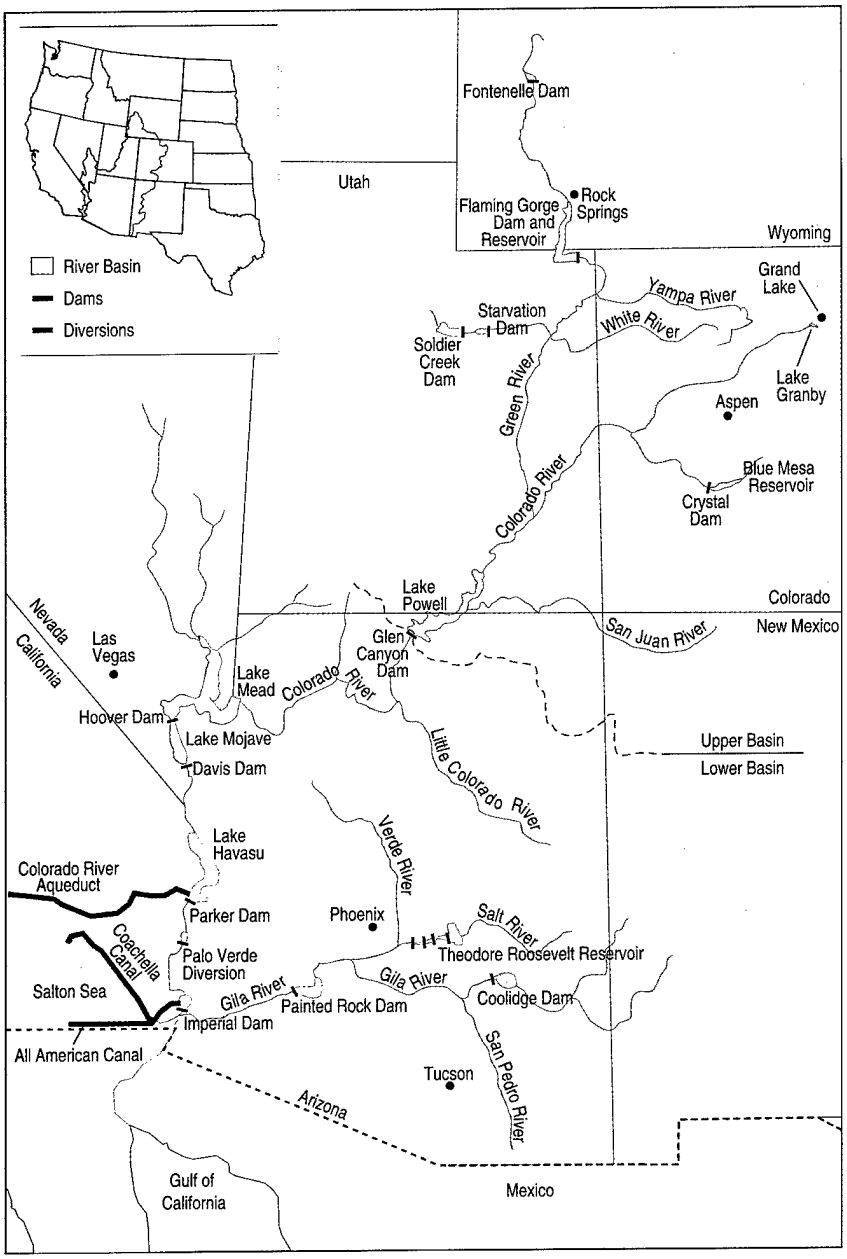

Fig. 9. The Colorado River basin (Tyler 1992).

Ecological Ramifications of Water Use

Colorado River

Water regulation has greatly altered the aquatic and riparian ecosystems in the Colorado River basin (Johnson 1977; Carothers and Brown 1991; Fig. 9). A century ago, few Americans knew much about the vast 632,000 square kilometers that make up the basin of the Colorado River, which originates as the Green River in the Wind River Range of Wyoming and as the Colorado River at Grand Lake, Colorado. After the scientific explorations of the river by Joseph Ives in 1857 and by John Wesley Powell after the Civil War, a period of mining began late in the nineteenth century. But the real effect on the drainage of the Colorado River did not occur until 1922, when the Colorado River Compact was signed. This agreement among the states in the river basin not only inadvertently divided too much river water among the basin states but, more importantly, also created the basis for major construction to put the basin's water to what was perceived as beneficial use. Thus, major alteration of the river to the benefit of the lower basin began with the completion of the Hoover Dam (Lake Mead) in 1935. In the upper basin, the most significant projects are the Glen Canyon Dam (Lake Powell), completed in 1963 (Figs. 9 and 10), and the Flaming Gorge Dam (Fig. 9) and reservoir on the Green River, completed in 1964.

The effects of water regulation through dams and through regulated water use on aquatic and riparian ecosystems were not understood at the time of the 1922 compact. Some initial studies were made before the construction of dams, but a systematic study of the affected ecosystems did not begin until 1971 (Johnson 1977); this systematic study was mostly confined to the river inside Grand Canyon National Park. By then, the drainage had significantly altered the river and had affected federal lands, numerous national parks and equivalent reserves, and Native American lands. The effects on the environment were profound and complex.

Control of the river eliminated naturally silt-laden floodwaters. Before construction of the dams, floods were much greater than today and brought much-needed sediments that provided nutrients, supplied new substrates for shorter-lived native riparian vegetation, and replenished the eroding shoreline (Fig. 11). With the downstream sediment loss, water clarity and light

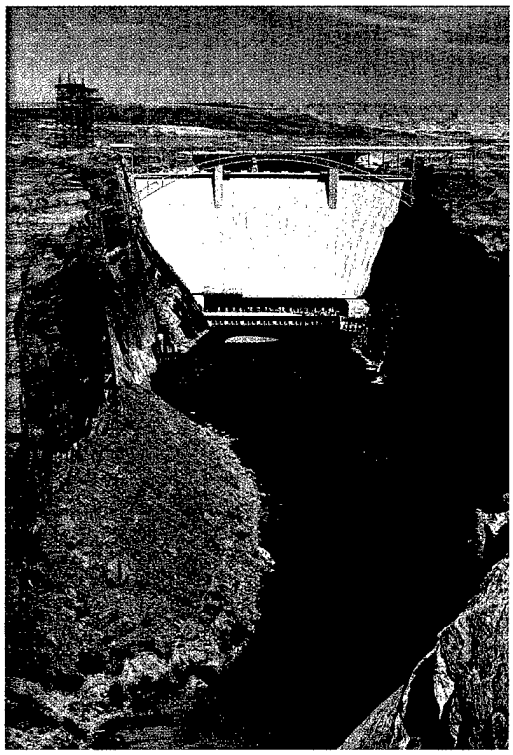

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Fig. 10. Glen Canyon Dam, near the Arizona–Utah border.

penetration increased and the environment for plankton and benthic algal growth improved, but phosphorus in stream waters—a limiting nutrient for freshwater algae—declined because of sediment loss (Carothers and Brown 1991; Fig. 12).

The reduction of water temperature and the variation in temperature in the rivers are other significant effects of hydrological regulation. Behind larger dams, water is released from considerable depths where temperatures are colder. In the Grand Canyon, for example, the average water temperature typically was about 28°C before the construction of the dams, but has been 11°C since the construction of the dams (Carothers and Brown 1991). Temperature reduction stresses native aquatic organisms and confines them to small, unregulated, and warmer tributaries. Conversely, improved water clarity, light, sustained flow, and reduced water temperature provide suitable conditions for the invasion of nonindigenous fishes such as trout and salmon, and their invertebrate prey. Such a change in important species has altered the entire aquatic community.

Flow regulation altered the natural predator–prey relations by benefiting nonindigenous predators of fishes. A well-studied example of this process is the effect of such species on native fish species below Glen Canyon Dam and above Lake Mead (Johnson 1977; Carothers and Brown 1991). Historically, the fish community in the Colorado River was dominated by Colorado squawfish, a native chub

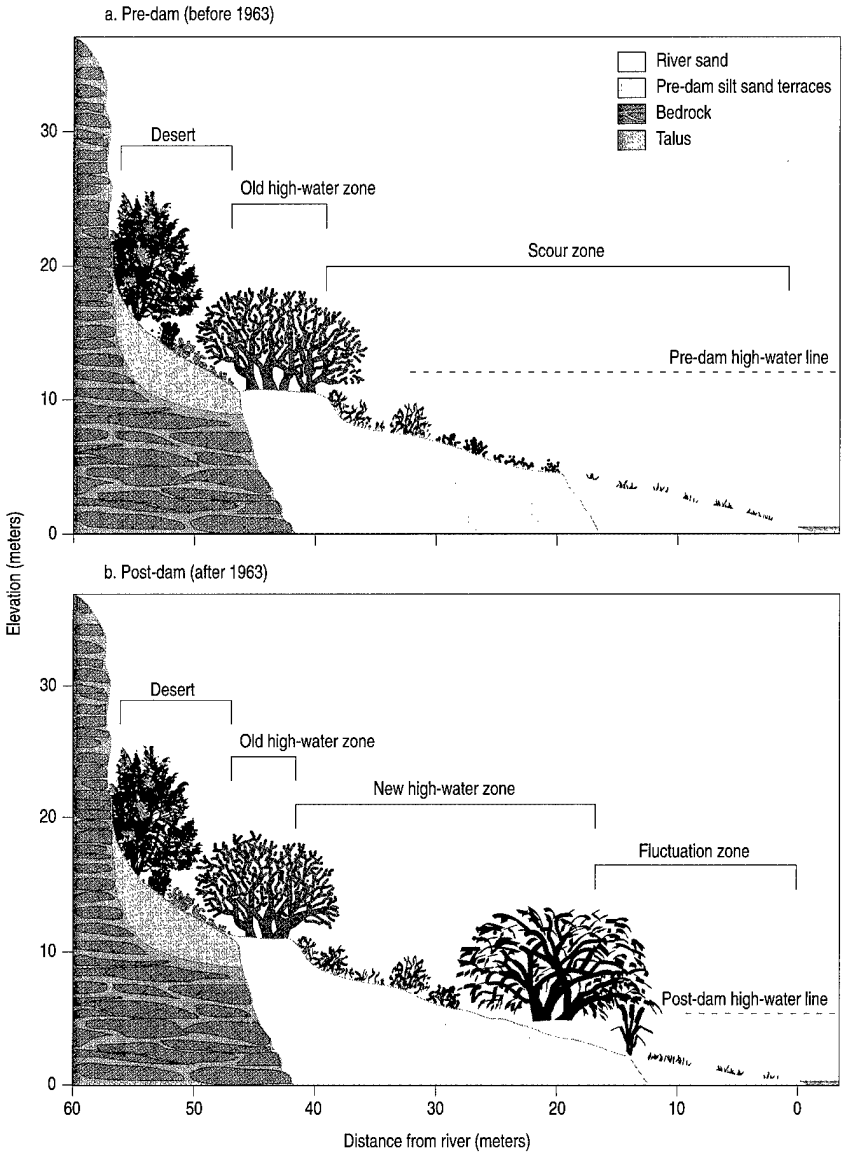

Fig. 11. Changes in downstream riparian zones caused by the construction of the Glen Canyon Dam.

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species, and flannelmouth and razorback suckers. Common carp and catfishes were introduced in the late nineteenth century and dominated much of the river before the major dams were completed in the twentieth century. After damming, flooding and the river's sediment load were greatly reduced; also, the water cleared and averaged 14°C cooler. These physical changes forced most of the remaining native fish species into the small but warmer tributaries and completely altered or eliminated their food sources on the river bottom. The lakes behind the dams became reservoirs that support additional nonindigenous fishes such as rainbow trout. In the clearer and cooler river, rainbow trout moved freely upstream and became significant predators on the remaining native fish species. Thus, the prognosis is poor for native fishes in much of the Colorado River today, as it is for native fishes throughout the Southwest. Razorback suckers no longer

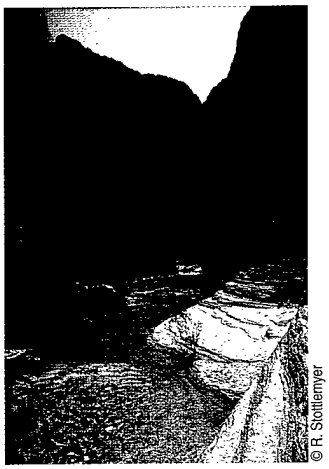

Fig. 12. Control of the Colorado River by dams upstream eliminated naturally silt-laden floodwaters, increasing water clarity and light penetration in the river in the Grand Canyon, thereby reducing habitat for native fishes.

reproduce in the Grand Canyon below the Glen Canyon Dam, and their reproductive success is poor in Colorado River reservoirs; the species will probably be eradicated by early in the twenty-first century. The Colorado squawfish is considered extirpated from the Colorado River below Glen Canyon Dam. The humpback chub is the only remaining chub species, but for spawning it requires water temperatures warmer than those now found in this stretch of the Colorado River. In addition, native fish species were deliberately eradicated by poisoning because nonindigenous trout provide a more economical sport fishery (Carothers and Brown 1991). As with so many studies of species that were lost during major human alteration of an aquatic ecosystem, the nearly complete absence of biological and ecological research on the Colorado River before 1960 means the role of the human effect in the decline and extinction of these species cannot be fully quantified. In addition to the effect from hydrological regulation of the Colorado River, major portions of the riparian habitat were destroyed by grazing, land-use practices, and polluted surface water.

Reservoirs created by damming can also create their own set of internal problems, such as the effect of fluctuating water levels on shoreline erosion and developments (Lorang et al. 1993), high fecal coliform levels (Doyle et al. 1992), invasions of nonindigenous plants such as hydrilla (Bain 1989), and high nonpoint contaminant levels in reservoir sediments (Novotny and Chesters 1989).

Before the construction of Glen Canyon Dam, annual flood flows near the Grand Canyon exceeded 2,400 cubic meters per second (Carothers and Brown 1991), and frequent flooding subjected the riparian community to unpredictable change. Such natural flooding created a roughly 9-meter-wide zone along the river where only short-lived native species, such as grasses, could exist in small numbers (Figs. 11, 12, and 13). Longer-lived vegetation, such as mesquite and cat-claw acacia, occur farther than 4.5 meters above river level where larger, periodic floods do not reach but from where the plants' roots can still reach water. Adjacent to this upper zone is desert vegetation. Overall, the riparian zone is one of the most productive vegetation associations and is especially important in drier regions. This zone represents a transition between different ecosystems, and it is a major pathway for plant and animal migration. Hydrological regulation, though, has caused the invasion of the riparian zone by nonindigenous vascular plants, particularly saltcedar or tamarisk (Fig. 14). Some native vegetation, especially coyote willow, also became established in what once was the flood zone. Overall, hydrological regulation increased the riparian

Fig. 13. Lack of beach replenishment by silt-laden floodwaters means natural erosion in the Grand Canyon significantly erodes beaches and changes the riparian zone.

biomass by allowing longer-lived shrubs and trees and animal species to exist in that zone—biological diversity increased in part through species substitution. After hydrological regulation, restoration of equilibrium in the new riparian community takes more than 10 years, and the number, frequency, and balance among native and nonindigenous species are not well understood.

More than 12 million hectares of riparian and associated habitat were flooded in the Colorado River basin by water development projects. This represents a gain of narrow riparian corridors in steep-walled canyons but a large loss of broad riparian flats in other stretches. Although the lost flats made up only a small percentage of the landscape, they included the important cottonwood and cottonwood–willow forests along the river; the loss of these forests is attributed to inundation and to dehydration caused by the interruption of seasonal streamflow or reduction of streamflow in unflooded areas. This, in turn, has caused many bird populations to decline (Hunt 1988). Farming and ranching communities that moved into the basin do not support bird populations as large as those in native riparian communities (Conine et al. 1978).

Fig. 14. Tamarisk (the taller, darker green shrubs) is a nonindigenous plant that has invaded the riparian zone of the Colorado River in the Grand Canyon since hydrological regulation of the river.

After three decades, the hydrological regulation of the Colorado River in the Grand Canyon has fundamentally changed the structure and function of the aquatic and riparian ecosystems. Changes in aquatic chemical and physical properties do not favor native species of plants and animals but do support some nonindigenous species, which is most apparent in the few native fish species that must now compete with 20 nonindigenous fish species. In addition, the invasion of what used to be the riparian scour zone (area of the riverbank that is swept clean of vegetation by fast-flowing water) has not yet stabilized, and the eventual biological diversity, biomass, and relative mix of native and nonindigenous species is not yet known. New species, especially invertebrates, continue to invade. The insect community in particular is dynamic (Carothers and Brown 1991).

The Everglades of South Florida

In southern Florida, flood-control structures, canals, and conservation areas drain lands for agriculture, flood natural habitat, and rapidly remove floodwaters. These projects reduce flooding in the greater Miami urban area and protect the Biscayne Aquifer, a subsurface water-bearing layer and the source of Miami's fresh water. A history of use, overuse, and conservation, beginning in 1896 and continuing to the present, has ensured sufficient fresh water to the metropolitan area and lowered water levels for agriculture (Fig. 15). But the cost has been massive, and the change of the Everglades ecosystem is long term (Davis and Ogden 1994).

Factors that regulate the amount and diversity of living and dead biomass in time and space include moisture, temperature, high wind, fire, and nutrient availability (Gunderson and Snyder 1994). Long-term cycles, such as shifts in sea level and climate, episodic events such as hurricanes and fire, and annual variation such as wet and dry seasons must be understood to measure potential effects of human use on an ecosystem like the Everglades. In this diverse ecosystem, species adapt to change by being mobile or, as is true for most plants, by having a wide tolerance for change. Taken together, these physical forces drive the biological diversity in the Everglades.

The 5,000-year-old Everglades are an ecosystem with rich biological diversity that is dominated by sawgrass, wet prairie, tree islands, sloughs, ponds and creeks, and the highly productive mangroves (Fig. 16). The ecosystem's diversity and productivity result from the complex interaction of seasonally high and low water levels that bring in needed inorganic nutrients and promote the decomposition

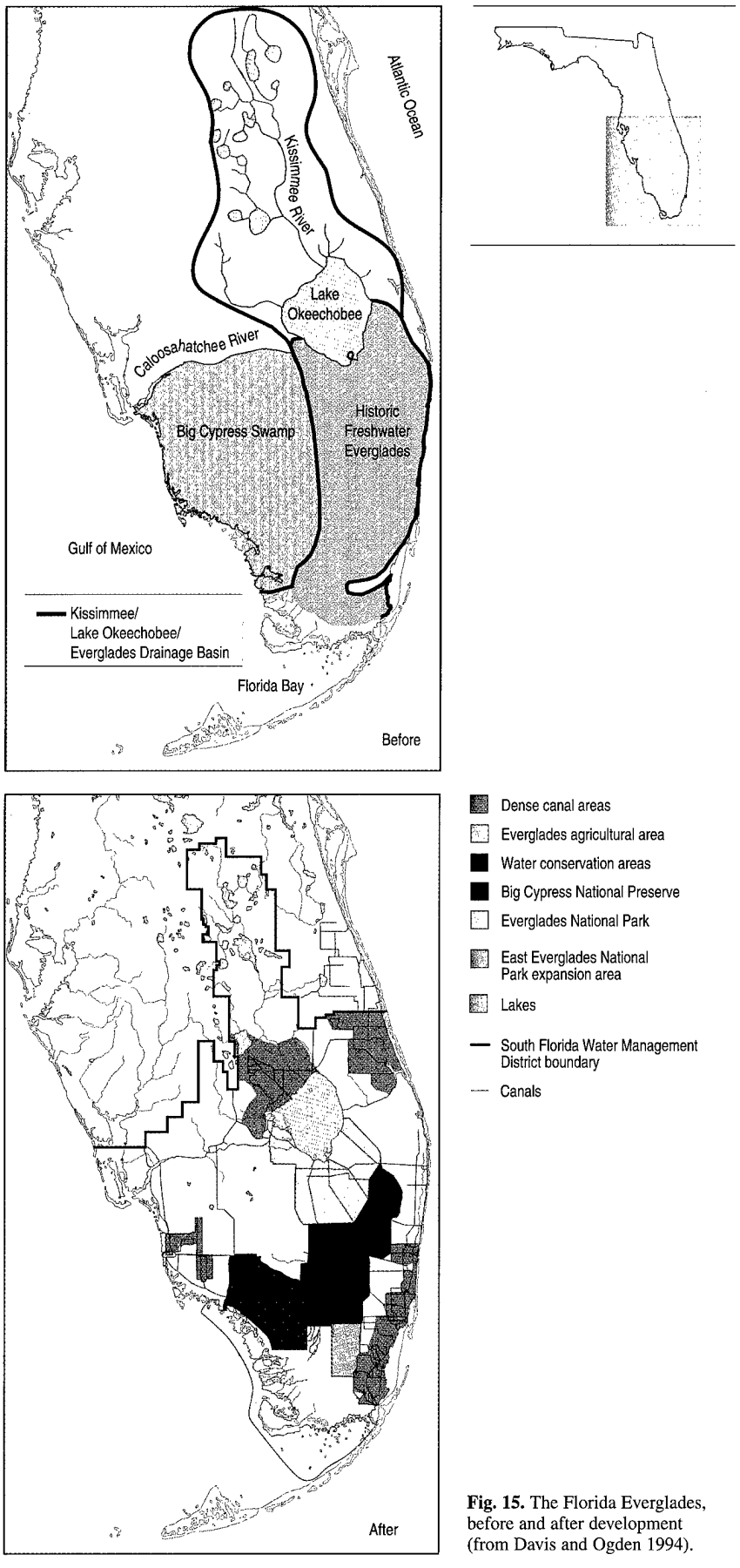

Fig. 15. The Florida Everglades, before and after development (from Davis and Ogden 1994).

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of accumulated organic matter. The local change in topographic relief permits tree islands to flourish, and the frequent and widespread fires during the dry season rapidly reduce accumulated dead organic matter and release much-needed nutrients. Historically, hurricanes have also been important for maintaining the biological diversity of the Everglades, especially of the tree islands and perhaps of the mangroves.

Much of the present controversy and research focus on Everglades National Park, a World Heritage Site, and on adjacent reserves. These protected areas encompass only about 20% of what was originally an ecosystem of more than a million hectares. Half the original area was drained for development and agriculture. Much of what remains has been diked for water conservation areas where water levels and flows are controlled to balance environmental concerns and the rapidly expanding human population in south Florida. The control of water to the Everglades is one example of a change in quantity, quality, and seasonal availability of water that exceeds natural variation, to the detriment of native species (Robertson and Frederick 1994; White 1994).

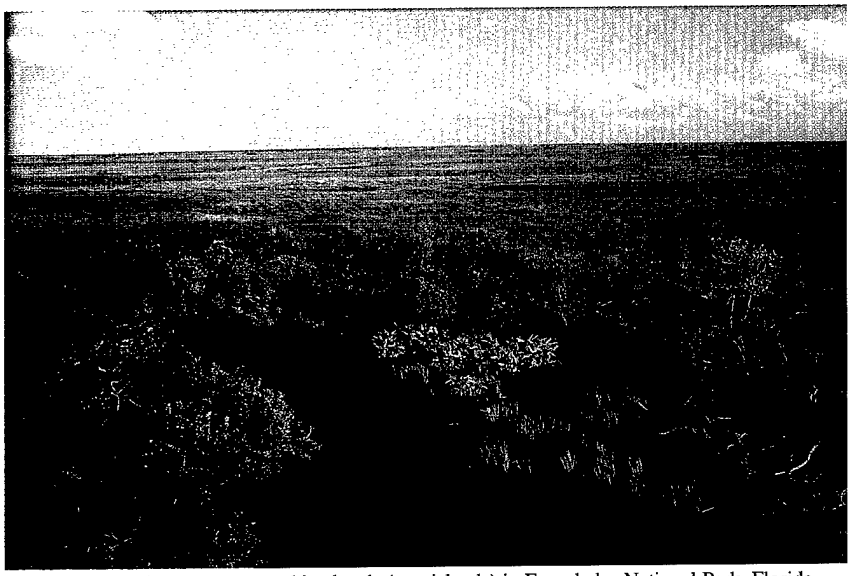
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Fig. 16. A sea of sawgrass around bayheads (tree islands) in Everglades National Park, Florida.

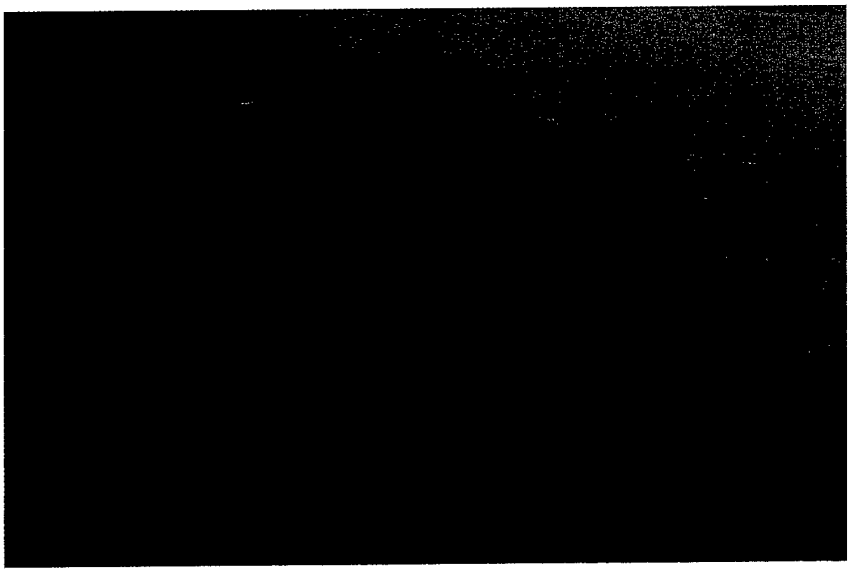
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Fig. 17. Sawgrass glades in Everglades National Park, Florida, under artificially lowered water table conditions in winter.

Research conducted largely since 1970 has revealed that most of the ecosystem is denied sufficient water at the proper time (Fig. 17). This lack of water has permitted the invasion of sawgrass into wet prairies and sloughs. American alligators moved from former wetlands, which are now too dry, to the sloughs, and the estuarine salinity is now too high for mangroves, thereby reducing the productivity of those trees (Lodge 1994). Breeding populations of birds have sharply declined since 1930. The abundance of wood storks decreased by 90%, white ibises by 95%, great egrets by 35%, and small herons by 90% (Fig. 18). Much of the decline of these birds is attributed to poorly timed water releases, which reduce aquatic prey concentrations for nesting birds. Furthermore, hydrological control structures often redistribute the water far from suitable nesting areas (Ogden 1994). Agriculture in the Everglades also began early in this century and intensified with the control of water. Agricultural practices were not compatible with the high water table and wet season and, directly or indirectly, are the major source of nutrient enrichment of water that enters the Everglades (Davis 1994).

Change in water quality promoted the expansion of cattails, which are not suitable aquatic habitat for wading birds. Water concentrations of phosphorus, a limiting nutrient in this aquatic ecosystem, increased considerably in water that enters the park, thereby profoundly changing the primary production and diversity of the aquatic plants and animals on which birds and other animals feed (Frederick and Powell 1994). Today, the remnants of this disrupted ecosystem are not self-sustaining.

In the Everglades, the introductions of nonindigenous biota and their spread in the human-modified environment are becoming a major source of stress on native aquatic species. For example, the introduction of Cuban treefrogs and marine toads in the Miami area eliminated other native amphibians such as the squirrel treefrog, green treefrog, and southern toad. These amphibians have been poorly studied, but because of their seasonal abundance, they are certainly important food sources for wading birds and reptiles (Lodge 1994).

Nonindigenous fishes are the most common introduced species, and their complex effects are exemplified by the nonindigenous blue

tilapia and its close relatives. Locally, this species eliminated the growth of naiads, important aquatic plants that provide cover for smaller native fishes and food for larger fishes such as shiners, which, in turn, are important prey for many native waterbirds. The greatest threat that an introduced species poses to the integrity of the Everglades, though, seems to be from the Australian melaleuca. After humans drain marsh and swamp, melaleuca invades the stressed sawgrass marsh and cypress swamps (Fig. 19). The tree is fire-tolerant and transpires large amounts of water, thereby further drying out areas it invades.

The water cycle also links the Everglades to the adjacent estuary of Florida Bay. Altered amounts and timing of freshwater flows to and through the Everglades have sharply increased the salt levels in Florida Bay. The increased salinity has caused reduced reproduction and distribution of the aquatic and terrestrial species once typical of the bay (McIvor et al. 1994).

As shown by these examples of widespread decline in aquatic ecosystem function and biological diversity, the absence of baseline research before a region has experienced major alteration by humans makes understanding the exact causes of ecosystem decline difficult, if not impossible. Without a baseline, recent research during and after human manipulation is hampered and may seem only to document ecosystem decline. Even with the limitation of a lack of baseline research, however, the synthesis of recent studies provides a good understanding of how the ecosystem now functions. By using this research as the basis for modeling the future of ecosystems, some attempts at restoration are feasible.

Small Lakes

The conditions of endangered, commercial, and recreationally important aquatic species generally represent long-term changes in habitat quality (Schindler et al. 1985; Schindler 1987; Rinne and Medina 1988). Comprehensive experimental studies of entire lake ecosystems reveal extensive alteration and loss of macro- and microinvertebrate biota before the effect may be seen in species higher in the food chain, such as fishes (Likens 1985; Schindler et al. 1985; Edmondson 1988; Byron and Goldman 1989). The results from such studies strongly suggest that the detection of the early effects of anthropogenic stress on aquatic ecosystems requires an overall knowledge of species composition that is rarely available. Without such information, the restoration of aquatic ecosystems is difficult because of the substantial time it takes a system to recover from such stresses (Kondolf 1993).

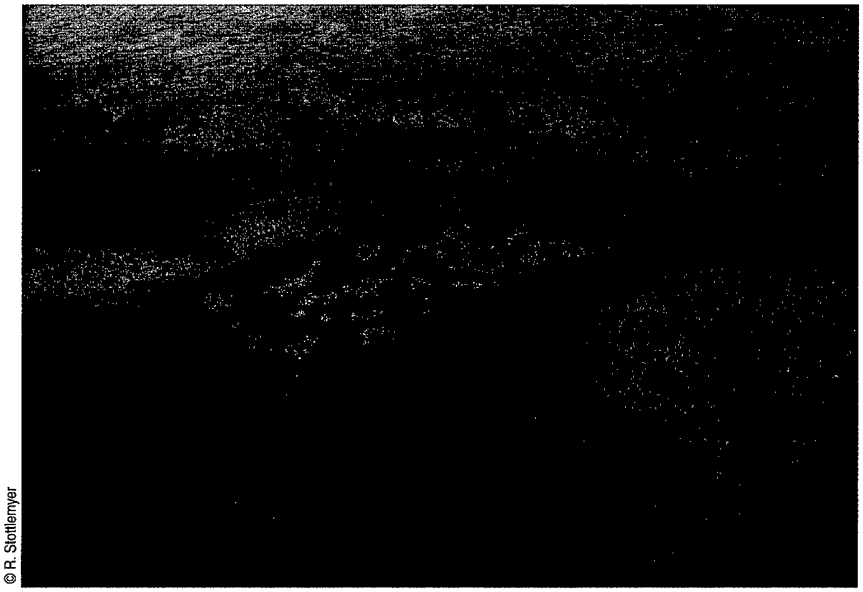

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Fig. 18. Egrets on islands and a wilderness waterway in Everglades National Park, Florida. Many breeding bird populations are threatened by human-altered distribution and timing of water in the ecosystem.

Lake Washington in Seattle went through a typical case of eutrophication caused by sewage effluent, experiencing sharp increases in plant biomass and reductions in light transmission. The public took corrective action before the deterioration became serious—in part because ongoing research revealed the early phases of lake eutrophication (Edmondson 1991). This early and unusual corrective action was taken after an unprecedented campaign of public education and the formation of an organization that could issue bonds to finance a cleanup.

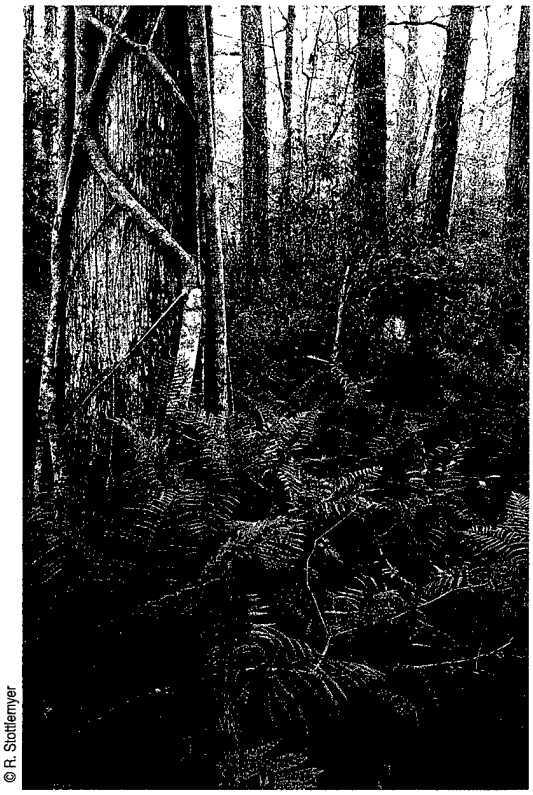

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Fig. 19. A baldcypress tree supports a strangler fig in Corkscrew Swamp, Florida. Baldcypress swamps are threatened by the invasion of melaleuca, a tree introduced from Australia.

In sum, aquatic ecosystems, possibly more than any others, have taken the brunt of human activities that are incompatible with the structure and functions of these ecosystems. Humans have derived tremendous short- and occasionally long-term economic benefits from changing aquatic ecosystems but have caused instability, massive losses of integrity that preclude the natural functioning of the systems, and large reductions in species composition. None of these are short-term effects. Restorations have not returned some of these ecosystems to the degree of self-sufficiency and sustainability they possessed before human perturbation.

Conclusions

For most of the last century and at least until the 1950's, the people of the United States largely ignored the true environmental and long-term economic costs of water development and use. Since 1970 a rapid expansion of the human population and per capita consumption of natural resources has revealed limits to past water-use and development practices and to the ecological, societal, and ultimately economic costs of such practices.

The cumulative effects of human activities in aquatic and riparian ecosystems have been dramatic but remain poorly understood. We can link changes in biological diversity to habitat alteration or species loss; the importance of long-term shifts in habitat are also being assessed. There are enough scientifically documented declines of species abundances and extinctions of aquatic species that are direct results of human activity to indicate that present water-use and development practices cannot continue. Although much research is still needed, much better use can be made of existing information in aquatic resource management decisions.

Future Research Needs

The future of water resource management in the United States will be influenced by an increasingly complex set of issues because of expanding human populations and an uncertainty about the United States economy. These forces accelerate the rate of present nonpoint pollution and the problems arising from incompatible land and water uses. We must improve our understanding and ability to deal with these complex problems of land and water interactions, including agricultural runoff, landfill management, urban industrial waste treatment, sludge disposal, and radioactive or hazardous wastes, while balancing strategic needs to retain the wetlands and natural rivers that influence how water is conserved, recycled, and reused (Patrick 1989; Whipple 1989). We must protect our water sources, including groundwater, from contamination and overuse, and commit to maintaining or continuing to restore degraded aquatic systems, riparian forests, and natural rivers.

Continuing emphasis on water quality and pollution control will draw more attention to the importance of instream flow issues, and will increase attention to widespread repercussions of global changes such as the greenhouse effect (Caulfield 1989). Managers of water resources must recognize the benefits of having sufficient pure fresh water for humans and for ecosystems (Fig. 20).

Limited availability of water for withdrawal and use by urban areas will continue to require innovative planning for water use. Traditional expansions of capacity no longer solve the problems of supply and demand for public water. Satisfying uncontrolled future requirements for water is too expensive. Current solutions include increasing the supply from existing storage facilities, managing water demand, reducing loss from distribution systems, providing lower-quality supplies for nondrinking purposes, encouraging reuse, and conservation through pricing (a large increase in costs for exceeding an established level of use) (Rees 1976; Billing and Day 1989). But all competing uses, including the needs of natural ecosystems,

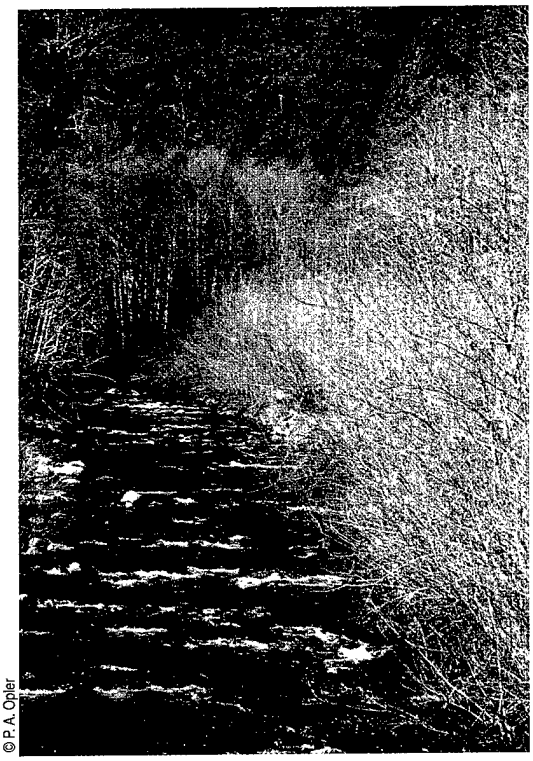

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Fig. 20. Fresh water for humans and for natural ecosystems: an undammed stream in the Pacific Northwest.

must be considered to suitably manage watersheds and river basins.

Research, especially at the ecosystem level, should be a top priority (Likens 1985) so that we can better understand watershed ecosystems. Sustained ecological research is essential for developing good water-use policy and for developing a more comprehensive basis to effectively manage or restore aquatic ecosystems. An understanding of processes over time and of their range of natural variation provides a strong tool for an early assessment of when human activities may force these processes beyond their natural variation. In aquatic ecosystems, we must continue to take a special interest in monitoring changes in species and in community composition.

In addition, we need more replication of long-term watershed studies. Such studies should be initiated primarily in a series of representative systems, not just in systems that are known to be affected or which are only representative of what is defined as sensitive. Too often, past studies that focused on sensitive systems greatly limited broad application of their results.

Most hypothesis testing today is short term, although the importance of long-term monitoring and research to provide a context for developing more meaningful hypotheses cannot be overstated. Paleoecological techniques, when calibrated with ecosystem-level experiments, may help resolve deficiencies of past monitoring. More effort should also be made to use results from current long-term studies for the development and calibration of complex models of aquatic and watershed ecosystems.

Future Management of Watersheds

Human effects on watershed ecosystems are long term. Water-resource management may be limited by past actions, legal or political considerations, conflicting user needs, lack of new water sources, environmental or economic concerns, or global events. For these reasons, we must learn to understand the complex social, ecological, and environmental problems of water management in the United States and acquire more information about the relations of watersheds with climate, the hydrological cycle, chemical processes, and the biota. Demand for existing water supplies continues to increase even though unallocated supplies are rarely available. In the past, humans looked toward engineering for increasing supplies. In many cases, humans may continue to use construction to meet their water needs, but environmental concerns may be leading us away from many large water project choices and toward new models of sustainable uses and watershed management.

To improve the management of watersheds, researchers are striving for a greater understanding of ecological processes in minimally disturbed watersheds and the responses of watersheds to various anthropogenic influences. Management depends on an ability to predict the consequences of human interference. Society's choices are limited by changes—many are known, but many are not yet understood. Decisions about water use must take into account resource alterations that directly and indirectly influence the hydrological cycle and associated lands and biota. Our ability to manage and to sustain water resources is constrained by current limits to our understanding of these cause-and-effect relations.

Water is the most limiting factor to life. For now, the human species has the capacity to alter the amount and quality of water for most of the planet's animals and plants. In the United States and worldwide, however, trends clearly show that our present water-development and use practices cannot continue. We must plan water use as part of a sustainable relation between the environment and society.

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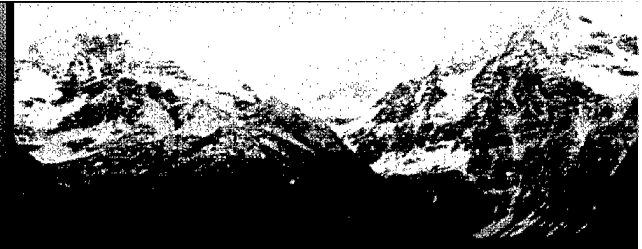
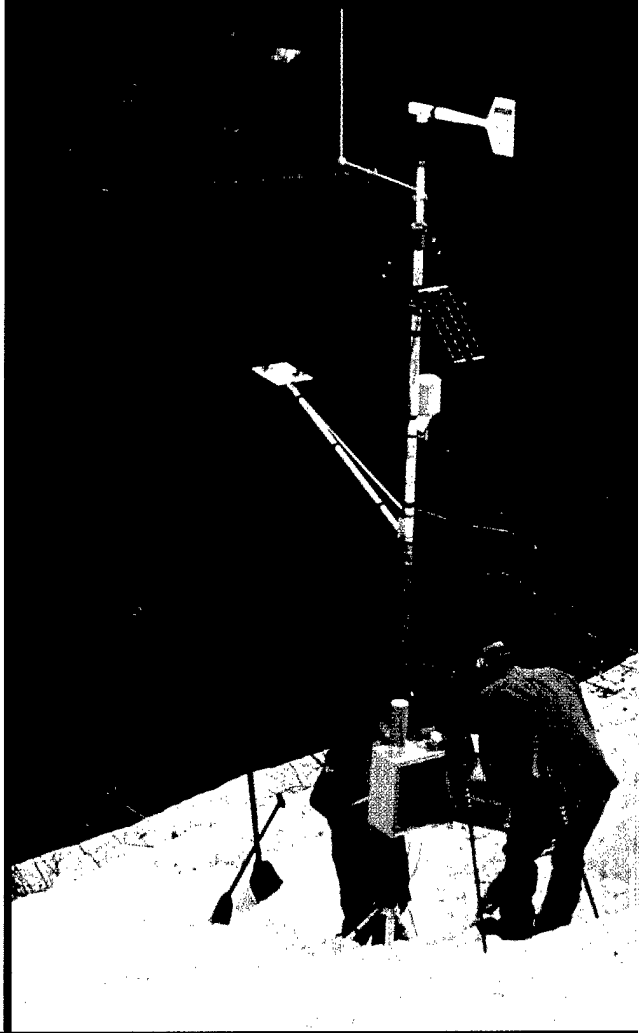
Climate Change



The Earth's climate is vastly different now from what it was 100 million years ago when dinosaurs roamed the planet and tropical plants thrived closer to the poles. It is different from what it was 20,000 years ago when ice sheets covered much of the Northern Hemisphere. Although the Earth's climate will surely continue to change, climatic changes in the distant past were driven by natural causes, such as variations in the Earth's orbit or the carbon dioxide (CO_2) content of the atmosphere. Future climatic changes, however, will probably have another source as well—human activities. Humans cannot directly rival the power of natural forces driving the climate—for example, the immense energy input to the Earth from the sun that powers the climate. We can, however, indirectly alter the natural flows of energy enough to create significant climatic changes. The best-known way people could inadvertently modify climate is by enhancing the natural capacity of the atmosphere to trap radiant heat near the Earth's surface—the so-called greenhouse effect. This natural phenomenon allows solar energy to reach the Earth's surface and warm the climate. Gases such as water vapor and CO_2, however, trap a much larger fraction of long wavelength radiant energy called terrestrial infrared radiation near the Earth's surface. This causes the natural greenhouse effect to be responsible for some 33°C (60°F) of surface warming. Thus, seemingly small human-induced changes to the natural greenhouse effect are typically projected to result in a global warming of 1°C to 5°C in the next century (Intergovernmental Panel on Climate Change 1990, 1996a). This could result in an ecologically significant change, which is why climatic considerations are fundamental in the discussion of the status and trends of ecological conditions.

We may already be feeling the climatic effects of having polluted the atmosphere with gases such as CO_2. Many activities associated with human economic development have changed our physical and chemical environment in ways that modify natural resources. When these changes—such as burning fossil fuels that release CO_2 or using land for agriculture or urbanization that cause deforestation—become large enough, significant global (worldwide) changes are expected. Such modifications can disturb the natural flows of energy in Earth systems and thus can force climatic changes. These disturbances are also known as global change forcings. Quantitative evaluations of the potential effect of human activities in creating global change are needed. Such evaluations are also central to potential policy responses to mitigate global changes (Schneider 1990; Intergovernmental Panel on Climate Change 1996b,c).

How can human societies prepare for so uncertain a climatic future? The ability to predict that future with a known degree of confidence would help. The processes that make up a planet's climate, however, are too large and complex to be reproduced physically in a laboratory. Fortunately, they can be simulated mathematically with the help of computers. In other words, one can devise mathematical expressions for the observed behavior and the physical principles that govern the system—laws of thermodynamics and Newton's laws of motion. The computer can then calculate how the climate would change (Trenberth 1992). For reasons detailed in this chapter, mathematical climate models cannot simulate the full complexity of reality, but they can, in combination with field



Courtesy Glacier National Park archives

and laboratory studies, reveal important aspects of how the climatic system operates. The critical scientific tasks are to formulate, build, and verify the models to produce ecologically useful forecasts. Verifying these forecasts requires knowledge of how the actual climate has changed.

What Has Happened

About 2.5 million years ago, continents moved into roughly their present positions. Antarctica was, by then, completely covered with an ice sheet, and year-round sea ice developed in the Arctic Ocean. Although permanent polar ice has been present since then, the polar ice caps and other ice masses have expanded and contracted on a 40,000-year cycle. About 750,000 years ago, this cycle was joined by a much longer (100,000-year) and more intense cycle of ice ages and relatively ice-free periods (interglacials). For example, an ice age occurred about 150,000 years ago and an interglacial from about 140,000 to 120,000 years ago; the last major glacial ice age peaked about 20,000 years ago, and the current 10,000-year-long interglacial period (Holocene) began (Lorius et al. 1990; Fig. 1). Scientists can reconstruct these events because when snow falls on high, cold glaciers two notable aspects are preserved: the air trapped between snow grains is eventually transformed into air bubbles as the snow is compressed into ice from the weight of subsequent accumulations, and the ratio of two oxygen molecules with different molecular weights (O^{16} and O^{18} isotopes) is a proxy record for the temperature conditions that existed when the snow was deposited. Cores taken from holes drilled into some 2,000 meters of ice on Greenland and Antarctica show similar gross patterns, but the Greenland core exhibits larger, shorter-term fluctuations. The ice buildup from 90,000 years ago to 20,000 years ago was quite variable and was followed by a (geologically speaking) fairly rapid 10,000-year transition, known as a termination, to the climatically very stable Holocene period. The Holocene is the 10,000-year interglacial period in which human civilization developed and modern plant and animal distributions evolved to their current states (Eddy and Oeschger 1993).

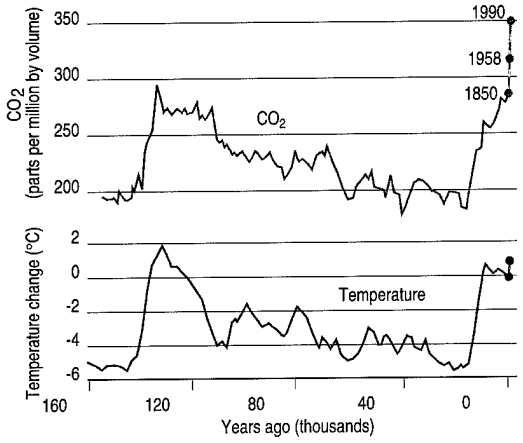


Fig. 1. Long-term temperature and CO_2 records from Antarctic ice cores and recent atmospheric measurements. Data show that CO_2 changed in the atmosphere in association with climatic changes over the past 160,000 years, with less of this greenhouse gas occurring in colder periods and more in warmer times (Lorius et al. 1990). For CO_2, the vertical line between the circles represents changes attributable to human activities in the industrial era. For temperature, the line between the circles represents instrumental records of global changes since the Industrial Revolution.

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These ice cores also provide information on the presence of CO_2, an important greenhouse-effect gas (Fig. 1). Carbon dioxide was in much lower concentrations during cold periods than in interglacials (which is similar for the greenhouse gas methane, CH_4). This implies an amplifying effect, or a positive feedback, because less of these gases during glacials means less trapped infrared radiative heat amplifying the cooling—and means the reverse during interglacials. The ice cores also show that concentrations of CO_2 and CH_4 and temperature were remarkably constant for about the past 10,000 years (before A.D. 1700), particularly when compared with the longer record. That relative constancy in chemical composition of the greenhouse gases held until the last two centuries—the industrial era.

The transition from Ice Age to the Holocene took from 5,000 to 10,000 years, during which time the average global temperature increased 5°C and the sea level rose 100 meters. Thus, it took nature about 5,000–10,000 years to transform the ice landscape for much of North America and Europe and to transform subpolar seas to their more current conditions in which their permanent ice is restricted to polar seas, high-latitude lands, or high mountains. Because this 5,000- to 10,000-year transition coincides with about a 5°C global warming, we estimate that natural rates of warming on a sustained global basis are about 0.5°C to 1°C per thousand years. Such changes were large enough to have radically influenced where species live and to have potentially contributed to the well-known extinctions of woolly mammoths, saber-tooth cats, and enormous salamanders.

To illustrate the dramatic ecological changes accompanying the Ice Age to the recent interglacial transition, we will briefly describe the findings of a large interdisciplinary team of scientists. The team included ecologists, palynologists (scientists who study pollen), paleontologists (scientists who study prehistoric life, especially fossils), climatologists, and geologists who formed a research consortium known as the Cooperative Holocene Mapping Project (1988; Wright et al. 1993). One group of these researchers used a variety of proxy indicators to reconstruct vegetation patterns over the past 18,000 years for a significant fraction of the Earth's land areas. In particular, cores of fossil pollen from dozens of sites around North America clearly showed how boreal tree pollen, now the dominant pollen type in the boreal zone

in central Canada, was a prime pollen type during the last Ice Age (15,000–20,000 years ago) in what are now the mixed hardwood and Corn Belt regions of the United States. During the last Ice Age, most of Canada was under ice; pollen cores indicate that as the ice receded, boreal trees moved northward chasing the ice cap. One interpretation of this information was that biological communities moved intact with a changing climate. In fact, Darwin (1859) asserted as much:

> As the arctic forms moved first southward and afterward backward to the north, in unison with the changing climate, they will not have been exposed during their long migrations to any great diversity of temperature; and as they all migrated in a body together, their mutual relations will not have been much disturbed. Hence, in accordance with the principles inculcated in this volume, these forms will not have been liable to much modification.

If this were true, the principal ecological concern over the prospect of future climate change would be that human land-use patterns might block what had previously been the free-ranging movement of natural communities in response to climate change. The Cooperative Holocene Mapping Project, however, incorporated multiple pollen types into its analyses, including not only boreal species but also herbs and more arid (xeric) species, as well as oaks and other mesic species. What they discovered was that during the transition from the last Ice Age to the present interglacial, nearly all species moved north, as expected. During a significant portion of the transition period, however, the distribution of pollen types provided no analog associations to today's vegetation communities (Overpeck et al. 1992). That is, whereas all species moved, they did so individual by individual, not as groups. Consequently, the groupings of species during the transition period were often dissimilar to those present today (Fig. 2). The relevance of this is that in the future ecotypes will not necessarily move as a unit as climate changes (assuming there is time and space enough for such a migration). Past vegetation response to climatic change at an average rate of 1°C per millennium indicates that credible predictions of vegetation changes from comparable or even more rapid climatic changes projected from human activities cannot neglect time-evolving (that is, transient) dynamics of the ecological system.

What is known about the response of various animal taxa to the ice age-interglacial transition? Mammals responded to the last deglaciation in North America by shifting their ranges (Graham 1992; Fig. 3) relatively quickly (Graham and Mead 1987). Graham and Grimm (1990), however, cautioned against relying too much on past conditions in forecasting future patterns resulting from global change forcings, because the forecasted global average rate of temperature increase exceeds those rates typical of the last 120,000 years, a conclusion consistent with the results of the Cooperative Holocene Mapping Project researchers studying vegetation communities (Davis 1990).

Future climates may not only be quite different from more recent previous climates but may also be different from those inferred from paleoclimatic data and from those to which some existing species are evolutionarily adapted. Therefore, possible future changes inferred from past changes can be taken only as a guide or a means to verify aspects of the forecasts of models of climate or ecosystem dynamics (Crowley 1993; Schneider 1993a). Such verification exercises may provide more credible forecasts of the effects of climatic change on animals.

Why Climate Changed

The two basic categories of causes of climatic change are external and internal. External causes mean that the climate change arises outside of the system and it is not influenced much by the system, although external processes do not have to be physically external to the Earth (such as the sun). If our focus is on atmospheric change on a 1-week time scale (that is, the weather), the oceans, land surfaces, biota, and human activities that produce CO_2 are all external (that is, they are not influenced much by the atmosphere in such a short time). If our focus is on 100,000-year ice age interglacial cycles, however, the oceans, ice sheets, and biota are part of the internal climatic system and vary as an integral part of the Earth's environmental systems. On this longer scale we must also include as part of our internal system the "solid" Earth, which really is not solid but viscous and elastic. Therefore, stating which components are external or internal to the climatic system depends on the time period and spatial scale being examined, as well as on the phenomena being considered.

Fluctuations in heat radiated by the sun—perhaps related to varying sun spots—are external to the climate system. Influences of the gravitational tugs of other planets on the Earth's orbit are also external. Many researchers think that such tugs gave rise to the 40,000-year ice cycle in the past 2.5 million years and possibly contributed to the 100,000-year ice age and interglacial cycles as well (Imbrie et al. 1993). Human-caused

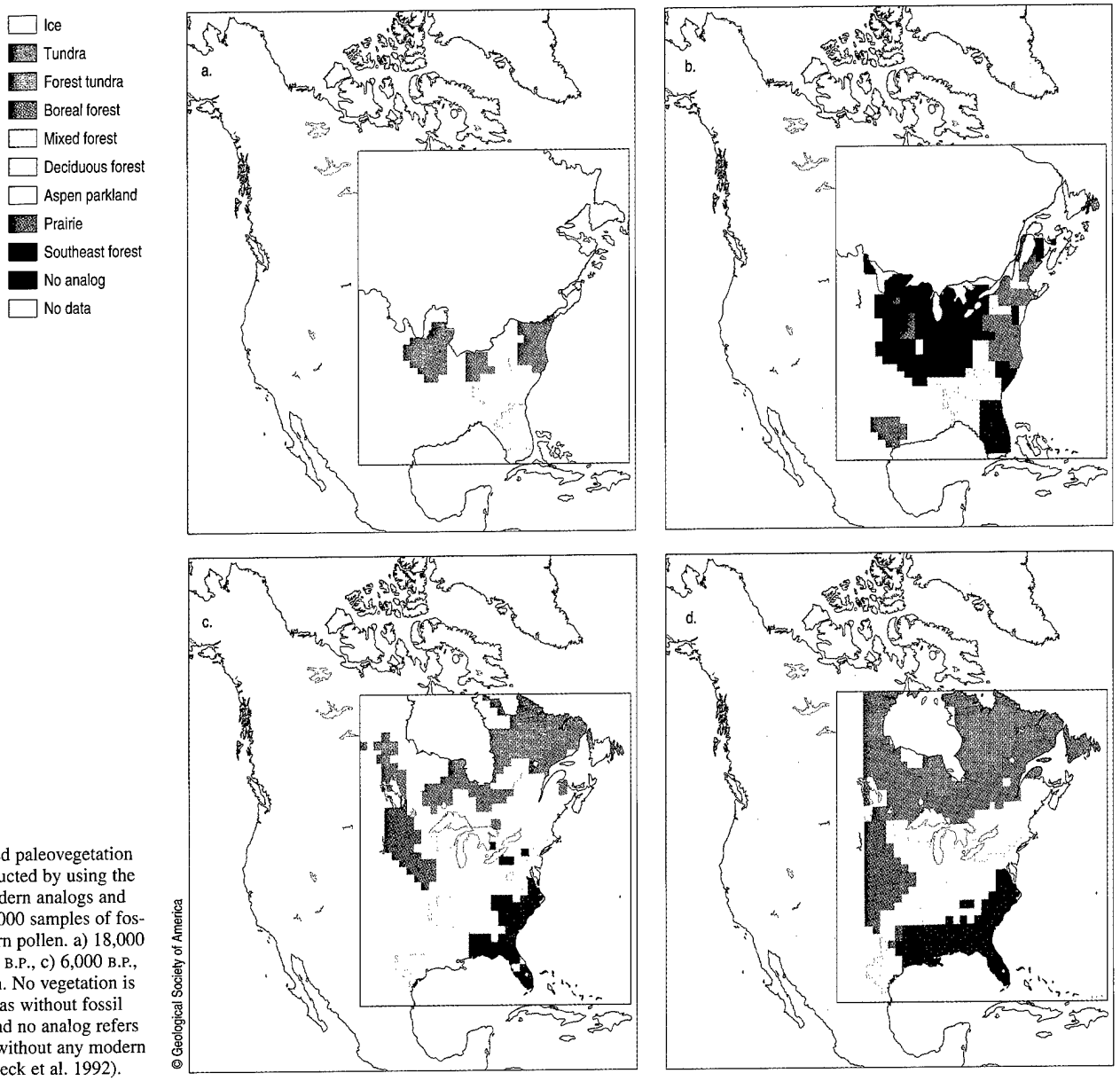

Fig. 2. Selected paleovegetation maps reconstructed by using the method of modern analogs and more than 13,000 samples of fossils and modern pollen. a) 18,000 B.P., b) 12,000 B.P., c) 6,000 B.P., and d) modern. No vegetation is mapped in areas without fossil pollen data, and no analog refers to vegetation without any modern analog (Overpeck et al. 1992).

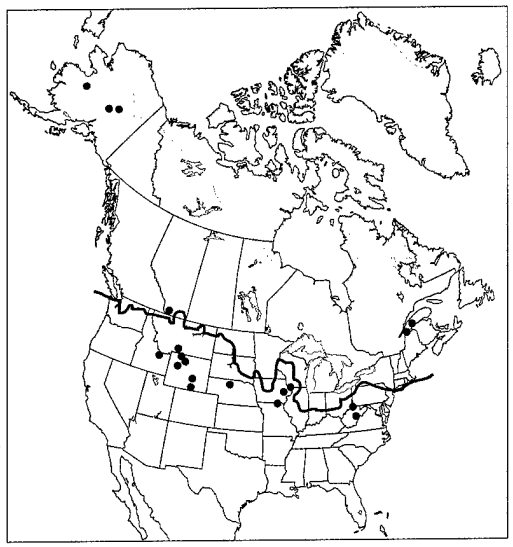

Fig. 3. Modern distribution (orange area) of Greenland collared lemmings and fossil localities (red dots) that illustrate the southern extension of their distribution during the late Wisconsinan. Purple line marks Wisconsinan glacial maximum (Graham 1992).

changes in the Earth's climate could not perceptibly alter either one of these cycles.

Changes in volcanic dust or CO_2 in the atmosphere also influence climate; volcanic dust can cool the climate by scattering some sunlight back to space, and CO_2 can warm the climate through the greenhouse effect. On short time scales, these factors are largely external because the state of the climatic system presumably does not have much influence on them. This may not be true, though, in the long term. For example, the tendency for volcanoes to erupt might change when the Earth's crust is distorted by the weight of ice sheets. Likewise, if the climate changes in such a way that an area previously covered with plants becomes drier, dust can be raised more easily. Thus, on the long-term scale, dust generation falls into the internal category.

Carbon dioxide and methane levels rise and fall with ice age cycles (Fig. 1), which are clearly internal on a 10,000-year time scale. But on a 20-year scale these greenhouse gases become largely an external cause of climatic change, because small changes in climate have little feedback effect on, for example, humans burning fossil fuel.

Changes in the character of the land surface, if caused by human activities, are largely external. If vegetation cover changes because of climatic change, however, land surface change then becomes internal because changes in plant cover can influence the climate by changing albedo (reflectivity to sunlight), evapotranspiration, surface roughness, and relative humidity (Henderson-Sellers et al. 1993).

Snow and ice are important factors in climatic change because they have higher albedo (reflectivity) than warmer surfaces and, in the instance of sea ice, can inhibit transfer of heat and moisture between air and wet surfaces. Salinity, which affects changes in sea ice and in the density of seawater (which helps control where ocean waters sink), may also be an internal cause of climatic variation. The sinking and upwelling of ocean waters are biologically significant because the upwelling waters are often nutrient-rich.

Unusual patterns of ocean surface temperature—such as the El Niño—demonstrate the importance of internally caused climatic fluctuations because the atmospheric circulation can change simultaneously with ocean surface temperatures. The atmosphere rubs on the ocean, however, so the ocean responds with a modification in its motions and temperature pattern, which forces the atmosphere to adjust, which changes the winds, which changes the way the atmosphere rubs on the ocean, and so forth (Trenberth 1993). As a result, air and water interact internally in this coupled system like blobs of gelatin of different size and stiffness, connected by elastic bands or springs, all interacting with one another while also being pushed from the outside (by solar, volcanic, or human-caused change).

Credibility of Climate Change Forecasts

To predict the ecologically significant ways the climate might change, one must specify what people do that modifies how energy is exchanged among the atmosphere, land surface, and space because such energy flows are the driving forces behind climate. Making the atmosphere window dirtier through air pollution is an example of such a so-called societal forcing of the climate system. Estimating societal forcing involves forecasting a plausible set of human (or societal) activities affecting pollution over the next century. The next step is to estimate the response of the various components of the Earth system to such societal forcings. The Earth system itself consists of the following interacting subcomponents: atmosphere, oceans, cryosphere (snow, seasonal ice, and glaciers) and land-surface (biota and soils) systems.

Research in the field and in laboratories provides an understanding about various processes affecting the subcomponents of the Earth system. This understanding can be put into mathematical expressions, which, when combined, form a model of the behavior of particular components of the Earth system. In practice, models of the atmosphere are connected to models of the oceans, ice, biota, and land surfaces to simulate the consequences of some scenario of societal forcing on climate and ecosystems. Controversy arises because both the societal forcing that will actually occur and the scientific knowledge of each subsystem are still incomplete. Because models cannot be perfect replicas of the actual natural system, scientists must expend considerable efforts to test their models against the expanding base of field and laboratory data. This not only allows them to assess the credibility of current simulations, but it also reveals improvements for the next generation of models.

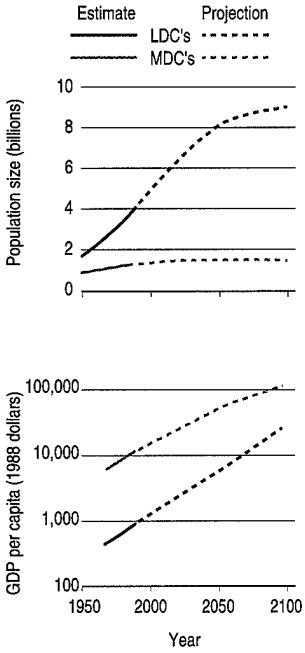

Fig. 4. Estimates and projections of population size and gross domestic product (GDP) per capita for less highly developed countries (LDC's) and more highly developed countries (MDC's) for 1950–2100 (Bongaarts 1992).

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Elements of Global Warming Forecasts

The societal driving forces behind global-warming scenarios are projections of population, consumption, land use, and technology. Typical twenty-first century projections for human population size and affluence for less highly developed countries and more highly developed countries show drastic increases in population and wealth (Fig. 4). When these factors are multiplied by the amount of energy used to produce a unit of economic product (the so-called energy intensity) and the amount of CO_2 emitted per unit of energy (the technology factor called carbon intensity), the result is a forecast for carbon emissions in the twenty-first century. For the particular projections shown in Figures 4 and 5 (from Bongaarts 1992), CO_2 emissions rise severalfold over the next 100 years. Such specific scenarios are plausible but debatable because the amount of carbon emitted through human activities will significantly depend on what kinds of energy systems will be developed and deployed globally and on what the standards of living will be over the next several decades. It is very difficult to make such projections credibly; therefore analysts disagree by as much as a factor of 10 about how much CO_2 will be emitted by 2100 (Johansson

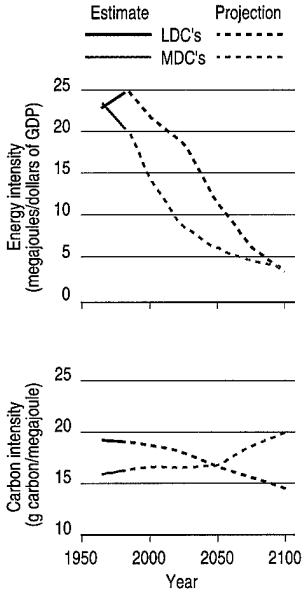

Fig. 5. Estimates and projections of energy and carbon intensities for less highly developed countries (LDC's) and more highly developed countries (MDC's) for 1965–2100 (Bongaarts 1992).

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et al. 1993; Intergovernmental Panel on Climate Change 1996a,c).

To turn estimates of CO_2 emissions into estimates of CO_2 concentrations in the atmosphere—the variable needed to calculate potential climate changes—one must estimate what fraction of CO_2 emitted will remain in the atmosphere. This airborne fraction is most simply estimated at 50%, because the amount of CO_2 buildup in the atmosphere each year (about 3 billion tons of carbon as CO_2) is about half the fossil fuel-injected CO_2. The atmospheric concentration of CO_2 should, however, be computed by using carbon cycle models, which account for the time-evolving amounts of carbon in vegetation, soils, oceanic, and atmospheric subcomponents (Intergovernmental Panel on Climate Change 1996a,b). The estimated CO_2 concentration can then be fed into computerized climatic models to estimate its effects on climate.

Climate prediction, like most other forecasts involving complex systems, generally involves educated guesses. Those attempting to determine the future behavior of the climate system from knowledge of its past behavior and present state basically can take two approaches. One approach, the empirical–statistical, uses statistical methods such as regression equations that connect past and present observations statistically to obtain the most probable extrapolation. The second approach, usually called climate modeling, focuses on first principles, which are equations representing laws believed to describe the physical, chemical, and biological processes governing climate. Because the statistical approach depends on historical data, it is obviously limited to predicting climates that have been observed or are caused by processes appropriately represented in the past conditions. The statistical method cannot reliably answer questions such as what would happen if atmospheric CO_2 increased at rates much faster than in the known past. Thus, the more promising approach to climate prediction for conditions or forcings different from the historic or ancient past is climate modeling. A significant component of empirical–statistical information, though, is often embedded into these models (Washington and Parkinson 1986; Root and Schneider 1995). This often makes modelers uncomfortable about the validity of predictions of such models on unusual or unprecedented situations unless a great deal of effort is expended to test the models against present and paleoclimatic baseline data.

Climate models vary in their spatial resolution, that is, the number of dimensions they simulate and the spatial detail they include. The simplest model calculates only the average temperature of the Earth, independent of the average greenhouse properties of the atmosphere. Such a model is zero-dimensional—it reduces the real temperature distribution on the Earth to a single point, a global average. In contrast, three-dimensional climate models produce the variation of temperature with latitude, longitude, and altitude. The most complex atmospheric models, the general circulation models, predict the time evolution of temperature plus humidity, wind, soil moisture, sea ice, and other variables through three dimensions in space (Washington and Parkinson 1986).

Relevance to Ecosystem Studies

Scientists who estimate the future climatic changes that are relevant to ecosystems have focused on the general circulation models that attempt to represent mathematically the complex physical and chemical interactions among the atmosphere, oceans, ice, biota, and land. As these models have evolved, more and more information has become available, and more comprehensive simulations have been performed. Nevertheless, the complexities of the real climate system still vastly exceed the general circulation models and the capabilities of even the most advanced computers (Intergovernmental Panel on Climate Change 1990, 1996a,b). Simulating one year of weather in 30-minute time steps with the crude resolution of 40 latitudinal lines x 48 longitudinal lines and 10 vertical layers—nearly 20,000 grid cells around the globe—takes about 10 hours on a supercomputer (the Cray Y-MP, for example). This level of resolution, however (Fig. 6), cannot resolve the Sierra Nevada of California and the Rocky Mountains as separate mountain chains. Refining the resolution to 50-square-kilometer grid squares would so dramatically increase the number of computations that it would take roughly one year of computer time to simulate weather statistics for one year.

What is most needed to evaluate potential biological effects of temperature change is a regional projection of climatic changes that can be applied to ecosystems at a regional or local scale. Analyses of large, prehistoric climatic changes (Barron and Hecht 1985; Budyko et al. 1987; Schneider 1987; Cooperative Holocene Mapping Project 1988) and historical weather analogs (Pittock and Salinger 1982; Jager and Kellogg 1983; Lough et al. 1983; Shabalova and Können 1995) provide some insights into such changes. Historical weather analogs, however, since they are empirically and statistically based, rely on climatic cause-and-effect processes that probably differ from those that will be driven by future greenhouse gas radiative effects (Schneider 1984; Mearns et al. 1990; Crowley 1993). Consequently, ecologists turn to climatic models to produce forecasts of

regional climatic changes for the decades ahead. How credible are such forecasts?

Regional Changes

Although the consensus among researchers about the plausibility of significant human-induced global climatic change is growing, no assessment (Intergovernmental Panel on Climate Change 1996a) has suggested the existence of a strong consensus about how that global climatic change might be distributed regionally. For example, the world is not actually undergoing a dramatic and instantaneous doubling of CO_2, which is the hypothesis used in most standard computer model experiments applied to ecological assessments. Instead, the world is undergoing a steady increase in greenhouse gas forcing. Because that increase is heating the Earth in a reasonably uniform way, one might expect a uniform global response, though this is far from likely. For example, the centers of continents have relatively low heat-retaining capacity, and the temperatures there would move relatively rapidly toward whatever their new equilibrium climate would be compared with the centers of oceans, which have high heat-retaining capacity. Tropical oceans, though, have a thin (about 50 meters) mixed layer that interacts primarily with the atmosphere. It takes about 10 years for that mixed layer to substantially change its temperature, which is still much slower than the response time of the middle of the continents, but is much faster than that of the oceans closer to the poles. At high latitudes, in places like the Weddell or Norwegian seas, waters can mix down to the bottom of the ocean, thereby continuously bringing up cold water and creating a deepwater column that takes a century or more to substantially change its temperature.

During the transient phase of climate change over the next century, therefore, one would expect the middle of continents, the middle of oceans, and the polar and subpolar oceans all to change toward their new equilibrium temperatures at different rates. Thus, the temperature differences from land to sea and equator to pole will evolve over time, which, in turn, implies that the transient character of regional climatic changes could be very different from the expected long-term equilibrium (Schneider and Thompson 1981; Stouffer et al. 1989; Washington and Meehl 1989). This does not imply that transient regional changes are inherently unpredictable, only that at present they are very difficult to predict credibly.

Even more uncertain than regional averages, but perhaps more important to long-term ecosystem responses, are estimates of climatic variability during the transition to a new equilibrium, particularly at the regional scale. These include estimates of such events as the frequency and magnitude of severe storms, enhanced heat waves, temperature extremes, sea-level rises (Titus and Narayanan 1995), and reduced frost probabilities (Mearns et al. 1984, 1990; Parry and Carter 1985; Wigley 1985; Rind et al. 1989). For example, there is a physical principle that evaporation increases dramatically as surface-water temperature increases. Because hurricanes are powered by evaporation and condensation of water, if all other factors are unchanged, the intensity of hurricanes and the length of the hurricane season could increase with warming of the oceans (Emanuel 1987). Such changes would significantly affect susceptible terrestrial and marine ecosystems (Doyle 1981; O'Brien et al. 1992).

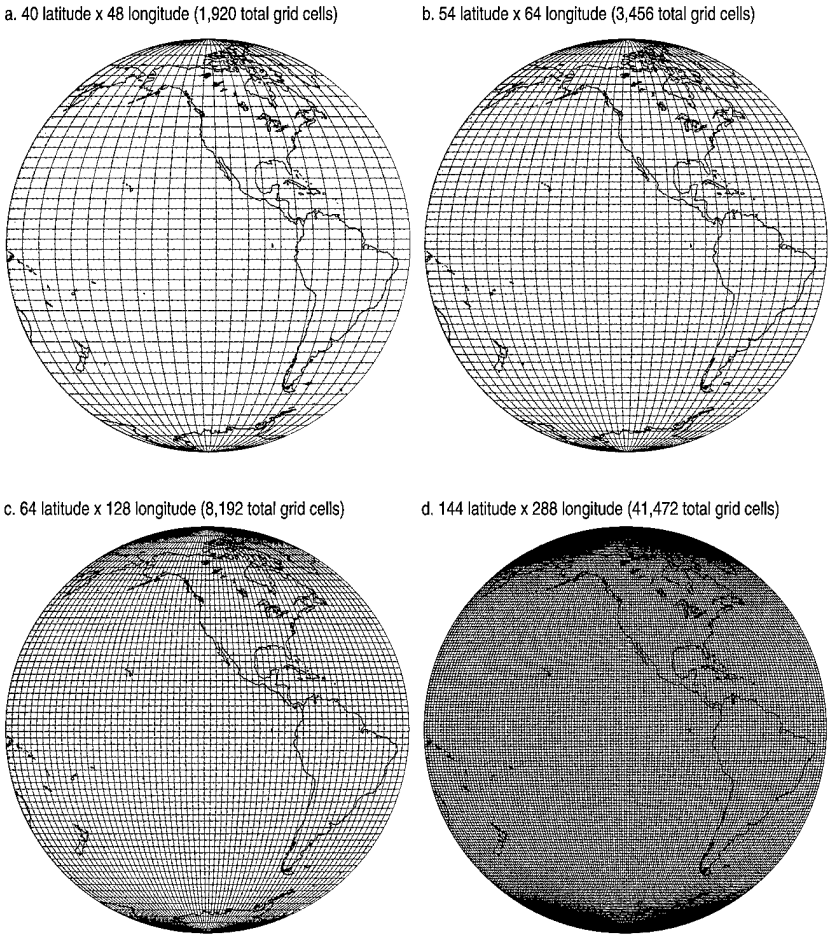

Fig. 6. The fineness of a climate model's grid size affects the accuracy of the simulations as well as the level of detail in the climate simulation that can be used for ecological applications. The information above each model shows the number of latitude and longitude lines for each grid-cell size and how many such cells cover the Earth's surface at the specified resolution. Most climate models use resolutions a, b, or c because computational resources increase by more than a factor of ten each time the length of a grid cell's side is halved. a) Grid R15, b) grid R21, c) grid T42, and d) grid T95.

Verifying Climate Forecasts

The most perplexing question about climate models is whether they can be trusted as a reliable basis for altering social policies, such as those governing CO_2 emissions or the shape and location of wildlife reserves. Even though these models are fraught with uncertainties, several methods are available for verification tests. Although no method is

sufficient by itself, several methods together can provide significant, albeit circumstantial, evidence of a forecast's credibility.

The first validation testing method involves checking the model's ability to simulate the present climate. The seasonal cycle is one good test because temperature changes in a seasonal cycle are larger on a hemispheric average than the change from an ice age to an interglacial period (that is, 15°C seasonal range in the Northern Hemisphere versus 5°C glacial-interglacial cycle). General circulation models map the seasonal cycle well (Fig. 7), which suggests that their mid- to high-latitude surface-temperature sensitivity to large-scale radiative forcing is not in error by more than a factor of three. This helps explain the scientific consensus about the plausibility of global warming of several degrees in the twenty-first century. The seasonal test, however, does not indicate how well a model simulates slow processes such as changes in deep ocean circulation, ice cover, forests, or soil carbon storage, which may have important effects on the decade- to century-long time scales over which atmospheric CO_2 is expected to double.

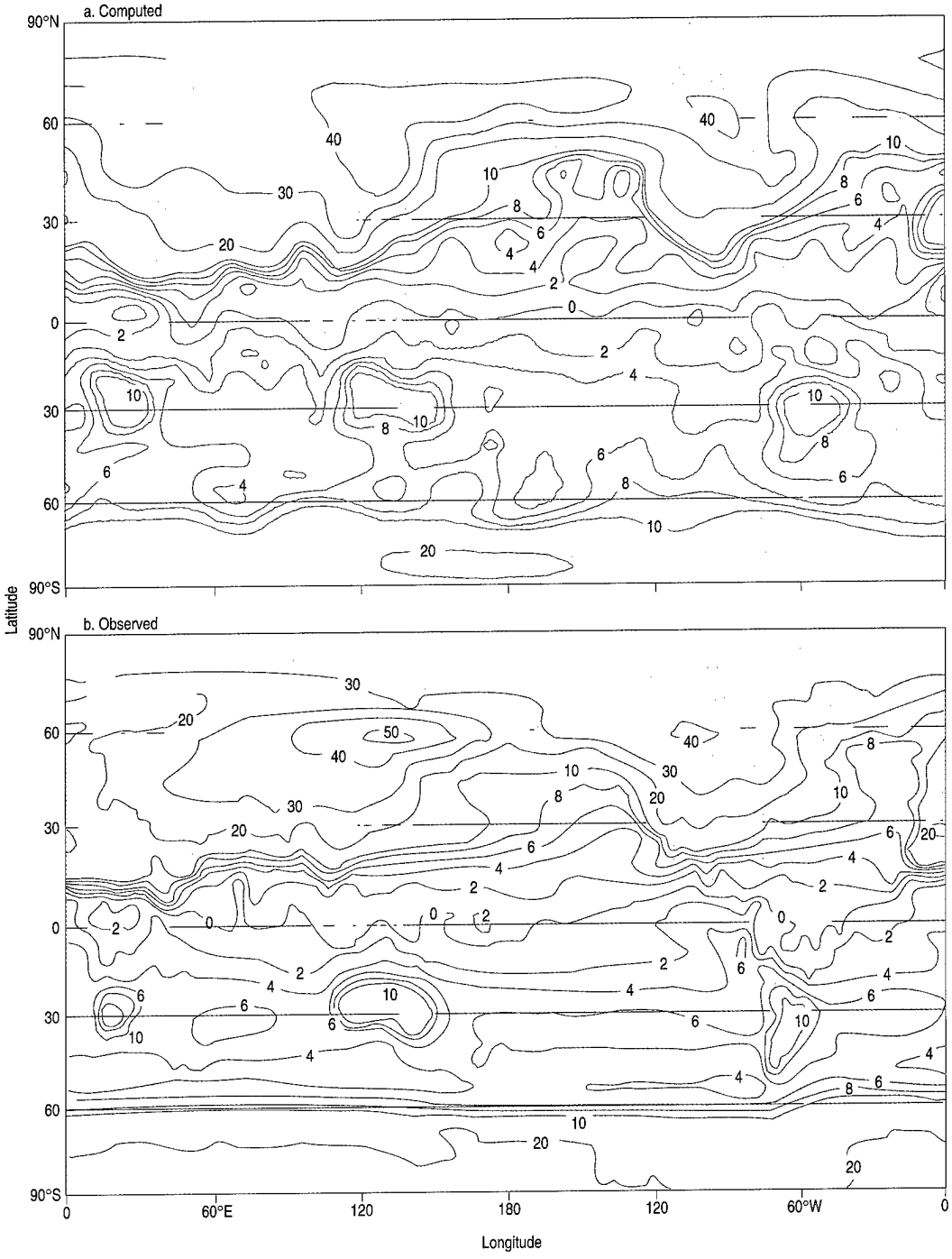

Fig. 7. A three-dimensional climate model was used to compute the absolute temperature difference between January and July over the globe. The a) computed model reproduces many of the features of the b) observed seasonal cycle shown here (Manabe and Stouffer 1980).

A second verification technique involves isolating individual physical components of the model and testing them against actual data. For example, one can check whether the model's cloudiness statistics match the observed cloudiness statistics of a particular area and season. This technique, though, cannot guarantee that the complex interactions of individual model components are properly treated. For example, the model may be reliable at predicting average cloudiness but unreliable at representing how cloudiness might change with a change in climate (the so-called *cloud feedback problem*). In this instance, simulation of overall global climatic response to some parameter like increased CO_2 is likely to be inaccurate. A model should reproduce the flow of thermal energy among the atmosphere, the surface, and space with no more than about a 10% error. Together, these energy flows make up the well-established natural greenhouse effect on Earth and constitute a formidable and necessary test for all models. A model's performance in simulating these energy flows is an example of physical validation of model components. In one encouraging example, Raval and Ramanathan (1989) used satellite observations to compute the infrared heat-trapping capacity of the atmosphere (that is, the natural greenhouse effect) with increased surface temperature. Next, they made a similar calculation between the heat-trapping-effect calculations in the general circulation model and compared this with satellite observations, finding that the models performed very well in this test.

A third validation method involves the model's ability to reproduce the diverse climates of the past. This method is aided by recording instrumental observations made during the past few centuries and paleo-records that serve as a proxy for climatic conditions of the ancient Earth, or even include testing models' ability to simulate climates of other planets (Kasting et al. 1988). Paleoclimatic simulations of the Mesozoic (Age of the Dinosaurs), glacial-interglacial cycles, or other extreme past climates help scientists understand the coevolution of the Earth's climate and living things (Schneider and Londer 1984). As verification tests of climate models, they are also crucial to predicting future climates and changes in biological systems.

Much has been learned from examining the global climatic trends of the past century. The years 1990 and 1995 were the warmest years on record for the lower atmosphere in the past century (Fig. 8); at the same time the stratosphere was at its coldest (Intergovernmental Panel on Climate Change 1996a). These data are consistent with an enhanced greenhouse effect signal that might be anticipated from the greenhouse gas injections over the past 150 years, which saw a 25% increase in CO_2, a 150% increase in CH_4, and the introduction of human-generated heat-trapping chemicals such as chlorofluorocarbons and halons. Most scientists still argue that, although the 0.5°C ± 0.2°C surface warming in the twentieth century is consistent with the human-induced greenhouse gas buildup, it is not possible to state with 99% confidence that the observed warming was caused by that greenhouse gas forcing (Intergovernmental Panel on Climate Change 1996a). It is possible—although at a relatively low probability of 10%–20% (Schneider 1994)—that the 0.5°C warming trend was wholly natural and that there was little or no contribution from the buildup of greenhouse gases (for estimates of the probability of global warming amounts, see Morgan and Keith 1995).

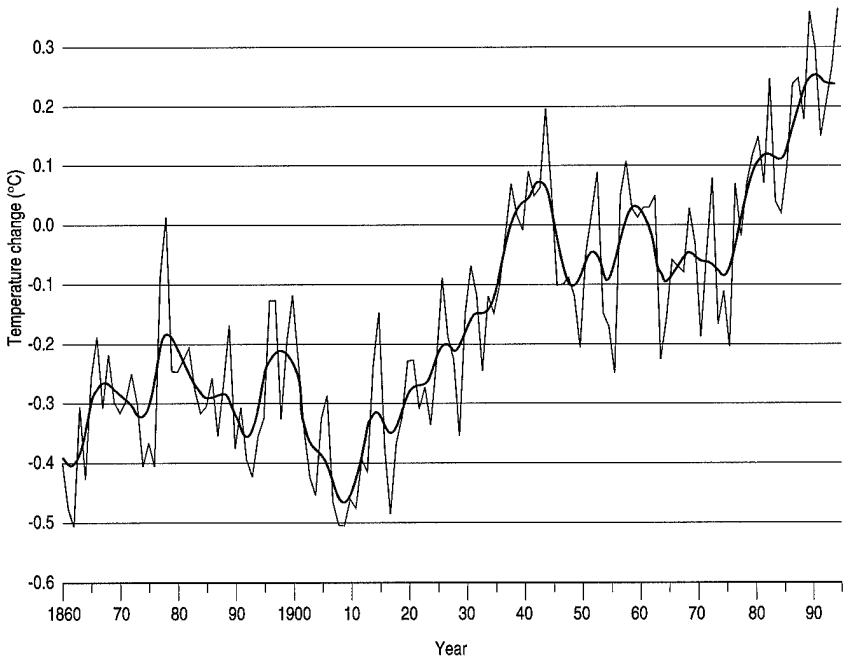

Fig. 8. The record of past global warming in observed global mean temperature changes, 1860–1995 (Intergovernmental Panel on Climate Change 1996a data). The purple line is the 5-year running mean; the blue line represents the annual values.

Of course, if one cannot tell whether an unforecastable natural fluctuation in climate in the twentieth century could have created the bulk of the observed warming, then one equally cannot tell whether there was a natural cooling fluctuation taking place during the twentieth century. If so, the world would then have warmed up much more than observed had we not had a fortuitous natural cooling trend. One could even speculate that the dramatic temperature rise in the 1970's and all of the associated new warm global temperature records reflect the termination of a natural cooling trend combined with the rapid establishment of the expected enhanced greenhouse effect.

One important possibility that could have helped create the twentieth-century temperature record seen in Figure 8 is the generation of aerosol particles (for example, human-made or

induced by natural sulfur dioxide) floating in the atmosphere that could either directly or indirectly reflect sunlight to space. The aerosol particles, through incorporation into clouds, could increase the number of water droplets, making some clouds brighter. Measurements and theory are not yet adequate to describe the latter mechanism quantitatively, although some attempts are under way (Kaufman et al. 1993). Charlson et al. (1992) suggested that industrial activities since the 1950's offset some of the greenhouse surface heating by countering it with some atmospheric cooling from haziness around and downwind of sulfur-burning areas in the Northern Hemisphere. Although such sulfur dioxide-induced cooling may have opposed any global warming by several tenths of a degree, the hazes occur regionally and could be producing ecologically significant, unexpected regional changes in climate patterns (Schneider 1994).

Recent studies (Santer et al. 1996) suggest that when aerosols and greenhouse gas forcings are combined, climatic change patterns in models over the past 30 years of observations match much more closely. Nevertheless, all these possibilities render current observations consistent with a CO_2 doubling effect of anywhere from as low as a 0.5°C warming to as high as a 5.0°C warming (Wigley and Raper 1991). Several reasons exist for such a wide range of uncertainty: difficulty in knowing how to model delays in global warming because of the large heat capacity of the oceans; not knowing what other global change forcings may have opposed warming—for example, sulfate aerosols from burning high-sulfur coal and oil or undetectable changes in the sun's light output before 1980; and large, unknown, internal natural climatic fluctuations.

In summary, no clear physical objection or direct empirical evidence has contradicted the consensus of scientists (Intergovernmental Panel on Climate Change 1990, 1996a) that the world is warming, nor has evidence emerged to contradict the substantial probability that temperatures will rise because of increases in greenhouse gases (Morgan and Keith 1995). The evidence for current global warming forecasts is circumstantial, but is sufficient enough that many researchers believe that recently observed climatic variations and human activities are probably connected (Karl et al. 1995). The Intergovernmental Panel on Climate Change 1996a:5 carefully weighed the uncertainties and concluded that "Nevertheless, the balance of evidence suggests that there is a discernable human influence on global climate."

The consensus remains widespread that a global temperature increase of anywhere from 1°C to 5°C is reasonably probable in the next century. The Intergovernmental Panel on Climate Change (1990), which reflects the consensus of hundreds of scientists in the United States and elsewhere, used a five-star rating system to describe various possibilities for global warming, one star being least likely and five stars most likely. The scientists gave global average temperature changes (from CO_2 doubling) ranging from 1.5°C to 4.5°C three stars, equivalent presumably to a 60% subjective chance. The Intergovernmental Panel on Climate Change (1996a) saw no reason to alter that assessment. As mentioned previously, though, the ecologically important forecasts of time-evolving regional climatic changes are much less credible and require that ecologists use many alternative scenarios of possible climatic changes.

Estimating the Effects of Climate Change on Ecosystems

Even the highest-resolution, three-dimensional general circulation model will not have a grid with nodes much less than 100 kilometers apart within the foreseeable future; individual clouds and most ecological research (to say nothing of cloud droplets) occur on scales far smaller than that. Therefore, general circulation models will not be able to resolve the local or regional details of weather affecting most local biological communities or the importance of regional effects of hills, coastlines, lakes, vegetation boundaries, and heterogeneous soil (Root and Schneider 1993). It is, nonetheless, important to have climatic forecasts and ecological response analyses on the same physical scales.

Shrinking Climate Forecasts to Regional Scales

Empirical Mapping Techniques

Techniques exist that can translate the output of climate models so that it is closer to most ecological scales. One method that uses actual climatic data at both large and small scales can help provide maps that may allow small-scale analysis of large-scale climate change scenarios. For example, the Sierra Nevada of California or the Cascades in the northwestern United States are north-south mountain chains whose east-west dimensions are smaller than the grid size of a typical general circulation model. In the actual climate system, onshore winds on the Pacific coast would produce cool upslope and rainy conditions on the western slope and a high probability of warmer and drier conditions associated with that flow pattern on the downslope or eastern slope.

One regional map has been generated for Oregon (Gates 1985), in which a high-resolution network of meteorological stations was used to plot temperature and precipitation

isopleths based on observed climatic fluctuations at large (for example, state-sized) scales. These maps show that the dominant mode of variation for this area is warm and dry on one side of the mountains, cold and wet on the other. Although this empirical mapping technique seems appropriate for translating low-resolution, grid-scale climate model forecasts to local applications, a strong caveat must be offered. That is, the processes in the climate system that give rise to internal variability or natural fluctuations are not necessarily the same processes that would give rise to local deviations from large-scale patterns if the climate change were driven by external forces rather than an internal variation of the system. For example, the Oregon maps would indicate that if the grid-box average temperature were warmer on the eastern slope, then it should be cooler and wetter on the western slope. That condition is the most probable regional situation for today's naturally fluctuating climate. However, if 50 years from now the warming on the eastern slope were, say, a result of doubled atmospheric CO_2 causing an enhanced downward infrared radiative heating, then both eastern and western slopes would probably experience warming. Although the degree of warming and associated precipitation changes would not necessarily be uniform, an entirely different climatic change pattern would probably occur as opposed to that obtained from the empirical mapping technique if one used the naturally varying weather conditions existing today rather than the anthropogenically forced conditions of the twenty-first century (Schneider 1993b).

Therefore, techniques to shrink climate forecasts that use current distributions of environmental variables at local scales and correlate them with current large-scale regional patterns will not necessarily provide a good guideline about how large-scale patterns would be distributed locally. The reason is that the causes of the future change may be physically or biologically different from the causes of the historical fluctuations that led to the empirical maps in the first place. This caveat is so important that it requires scientists to use extreme caution before adopting such empirical techniques for global change applications.

Driving Regional-Scale Models with Large-Scale Forecasts

Other techniques can still translate large-scale patterns to smaller scales, but these techniques are based on known processes rather than empirical maps for today's conditions. One such technique is to drive a high-resolution, process-based model for a limited region with the large-scale patterns produced by a general circulation model. In essence, this approach uses a mesoscale model (that is, 10–50 square-kilometer grid cells) based on physical laws to solve the problem of translating general circulation model grid-scale averages into a finer scale mesh much closer to the dimensions of most ecological applications. Of course, even this mesoscale grid will still be too coarse to assess many impacts, necessitating further down-scaling techniques. Neither are the problems of general circulation models entirely eliminated by mesoscale grids, because they too are bigger than individual clouds or trees. But such methods do bring climate model scales and ecological-response scales much closer.

Giorgi (1990) and colleagues at the National Center for Atmospheric Research have worked many years with this embedding technique. They have noted, for example, that a general circulation model with a very coarse grid that is unable to resolve the separate topographies of the Sierra Nevada and the Rocky Mountains (and therefore is unable to produce the rain shadow of the Great Basin) may still produce reasonably accurate simulations of large-scale wind and moisture patterns. By using the large-scale wind and moisture fields of the general circulation model to drive a mesoscale model with a factor of 10 higher resolution (capable of resolving much of these mountain and desert topographies), these researchers were able to reproduce much more realistically the regional distribution of current climatic conditions. Therefore, such a process-based technique could be used to translate general circulation model grid-box scenarios into at least watershed-scale changes that would be closer to the scale of ecological studies than current general circulation model grids.

Unfortunately, even this process-based technique has several serious problems yet to be solved. First, these models use about as much computer time to simulate several days of weather at regional scales as the general circulation model needs for simulating one year of weather globally. Second, the mesoscale model results depend on validity of the overall flow patterns from the large-scale models. If the latter exhibit roughly the right direction for prevailing wind and moisture flow, the smaller-scale model will more faithfully translate that large-scale pattern down to regional detail.

A new technique combining empirical and process-based approaches to translate general circulation model grid predictions of doubling CO_2 climate changes to 10-square-kilometer grid cells was developed by Stamm and Gettelman (1995) and is called a local climate model. Although they obtained encouraging results for local climate deviations in the highly varying topography of the western United States, Stamm and Gettelman found that their

technique has difficulty estimating ecologically important extreme (high or low) temperatures or extreme precipitation events. Resolving these difficulties with current techniques is critical to the utility of the local climate model for ecological impact assessment. Other downscaling techniques are summarized in Mearns (1997).

Examples of Ecological Responses to Climate Changes

Bringing climatic forecasts down to ecological applications at local and regional scales is one way to bridge the scale gap across ecological and climatological studies. Ecologists, however, have also analyzed data and constructed models that apply over large scales, including the size of climatic model grids. A long tradition in ecology has associated the occurrence of vegetation types or the range limits of different species with physical factors such as temperature, soil moisture, land–sea boundaries, or elevation. Biogeography is the field that deals with such associations, and its results have been applied to estimate the large-scale ecological response to climate change.

Predicting Vegetation Responses to Climate Change

The Holdridge (1967) life-zone classification assigns biomes (for example, tundra, grassland, desert, or tropical moist forest) according to two measurable variables, temperature and precipitation (Fig. 9). Other more complicated large-scale formulas have been developed to predict vegetation patterns from a combination of large-scale predictors (for example, temperature, soil moisture, or solar radiation); vegetation modeled includes individual species (Davis and Zabinski 1992), limited groups of vegetation types (Box 1981), or biomes (Prentice 1992; Melillo et al. 1993; Neilson 1993). These kinds of models predict vegetation patterns that represent the gross features of actual vegetation patterns, which is an incentive to use them to predict vegetation change with changing climate. Smith et al. (1992) show an example of a vegetation model's prediction of changes given the forecast of doubled CO_2 from a climate model (Fig. 10).

As we explore in more detail later, such models have limitations. One criticism of such

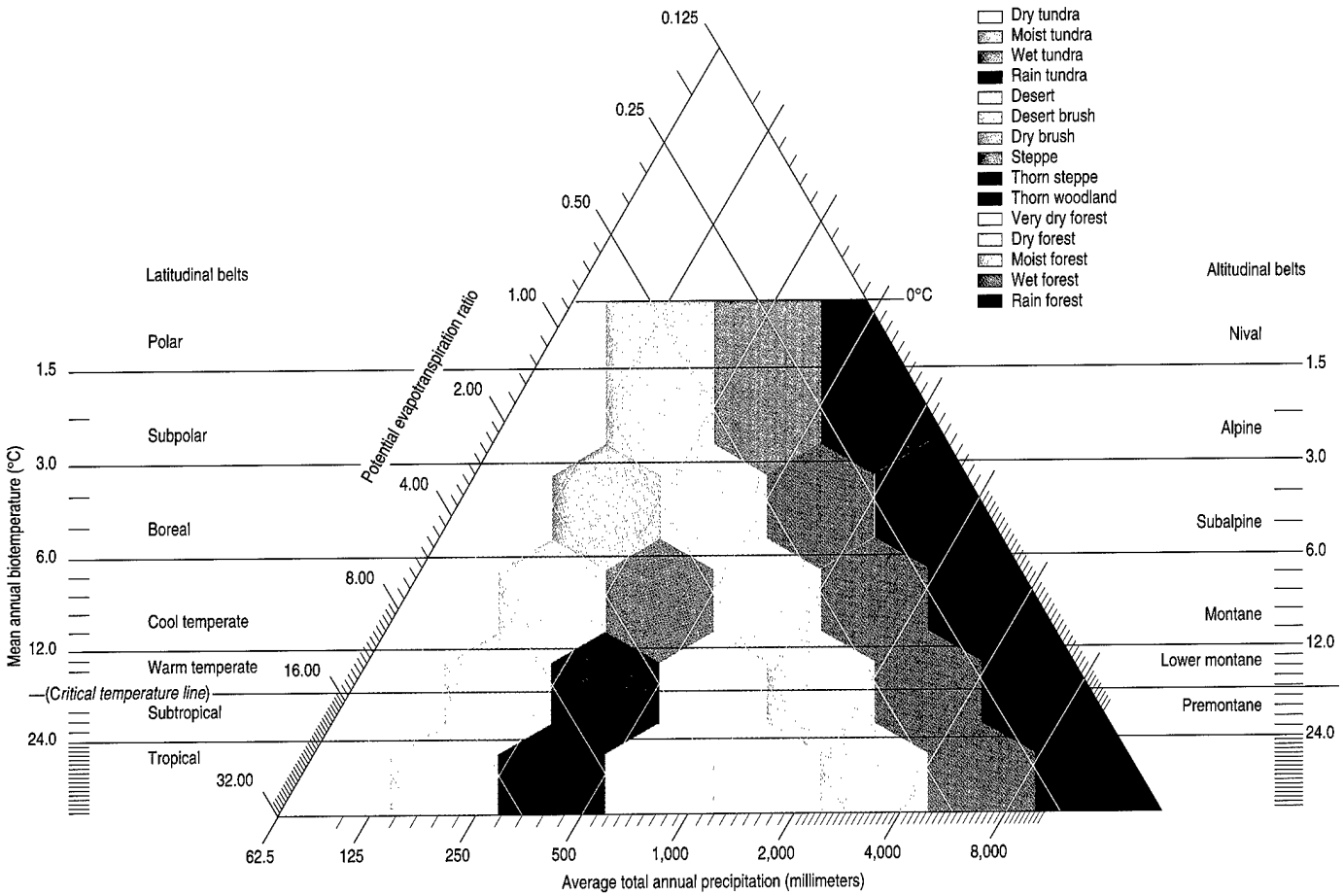

Fig. 9. Holdridge's (1967) climate–vegetation classification scheme.

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large-scale approaches is that, although the climate or other large-scale environmental factors are favorable to some biome that is actually present, these approaches also often predict vegetation to occur where it is absent. Other criticisms are aimed at the static nature of such models, which often predict vegetation changes to appear instantaneously at the moment the climate changes, neglecting transient dynamics that often cause a sequence or succession of vegetation types to emerge over decades to centuries following some disturbance (for example, fire), even in an unchanging climate.

Predicting Animal Responses to Climate Change

Scientists of the U.S. Geological Survey, in cooperation with Canadian scientists, conduct the annual North American Breeding Bird Survey, which provides distribution and abundance information for birds across the United States and Canada. From these data, collected by volunteers under strict guidance from the U.S. Geological Survey, shifts in bird ranges and abundances can be examined. Because these censuses were begun in the 1960's, these data can provide a wealth of baseline information. Price (1995) has used these data to examine the birds that breed in the Great Plains. By using the present-day ranges and abundances for each of the species (Fig. 11a), Price derived large-scale, empirical–statistical models based on various climate variables (for example, maximum temperature in the hottest month and total precipitation in the wettest month) that provided estimates of the current bird ranges and abundances (Fig. 11b). Then, by using a general circulation model to forecast how doubling of CO_2 would affect the climate variables in the models, he applied the statistical models to predict the possible shape and location of the birds' ranges and abundances (Fig. 11c).

Significant changes were found for nearly all birds examined. The ranges of most species moved north, up mountain slopes, or both. The empirical models assume that these species are capable of moving into these more northerly areas, that is, if habitat is available and no major barriers exist. Such shifting of ranges and abundances could cause local extinctions in the more southern portions of the birds' ranges, and, if movement to the north is impossible, extinctions of entire species could occur. We must bear in mind, however, that this empirical–statistical technique, which associates large-scale patterns of bird ranges with large-scale patterns of climate, does not explicitly represent the physical and biological mechanisms that could lead to changes in birds' ranges. Therefore, the detailed maps should be viewed only as illustrative of the potential for very significant shifts with different possible doubled CO_2 climate change scenarios. More refined techniques that also attempt to include actual mechanisms for ecological changes are discussed later.

Reptiles and amphibians, which together are called herptiles, are different from birds in many ways that are important to our discussion. First, because herptiles are ectotherms—meaning their body temperatures adjust to the ambient temperature and radiation of the environment—they must avoid environments where temperatures are too cold or too hot. Second, amphibians must live near water, not only because the reproductive part of their life cycle is dependent on water, but also because they must keep their skin moist because they breathe through their skin as well as their lungs. Third, herptiles are not able to disperse as easily as birds because they must crawl rather than fly, and the habitat through which they crawl must not be too dry or otherwise impassible (for example, high mountains or superhighways).

As the climate changes, the character of extreme weather events, such as cold snaps and droughts, will also change (Karl et al. 1995), necessitating relatively rapid habitat changes for most animals. Rapid movements by birds are possible since they can fly, but for herptiles such movements are much more difficult. For example, R. L. Burke (University of Michigan, Ann Arbor, personal communication) noted that during the 1988 drought in Michigan, many more turtles than usual were found dead on the roads. He assumed they were trying to move from their usual water holes to others that had not yet dried up or that were cooler (for example, deeper). For such species, moving across roads usually means high mortality. In the long term, most birds can readily colonize new habitat as climatic regimes shift, but herptile dispersal (colonization) rates are slow. Indeed, some reptile and amphibian species may still be expanding their ranges north even now, thousands of years after the last glacial retreat.

R. L. Burke and T. Root (personal communication) have begun analyzing North American herptile ranges in an attempt to determine which, if any, are associated with climatic factors such as temperature, vegetation-greening duration, solar radiation, and so forth. Their preliminary evidence indicates that northern boundaries of some species ranges are associated with these factors (Fig. 12), implying that climatic change could have a dramatic impact on the occurrence of herptile species. It could also alter the population genetics within species since there can be genetic differences among populations with respect to climate tolerance. Many more extinctions are possible in herptiles than in birds because the forecasted

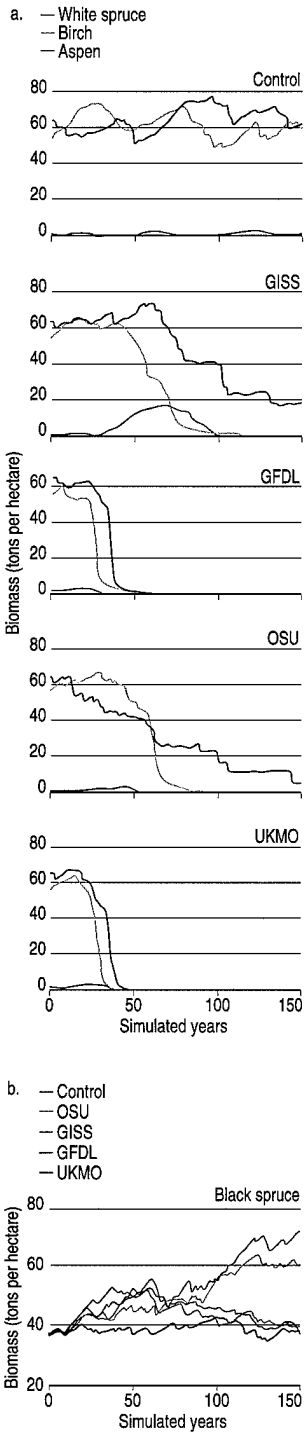

Fig. 10. Changes in biomass from gap model simulations for central Alaska sites with a) south-facing slopes and b) north-facing slopes for present climate (control) and for different climate model simulations with doubled CO_2 (Smith et al. 1992). GISS = Goddard Institute for Space Studies, GFDL = Geophysical Fluid Dynamics Laboratory, OSU = Oregon State University, UKMO = United Kingdom Meterological Office.

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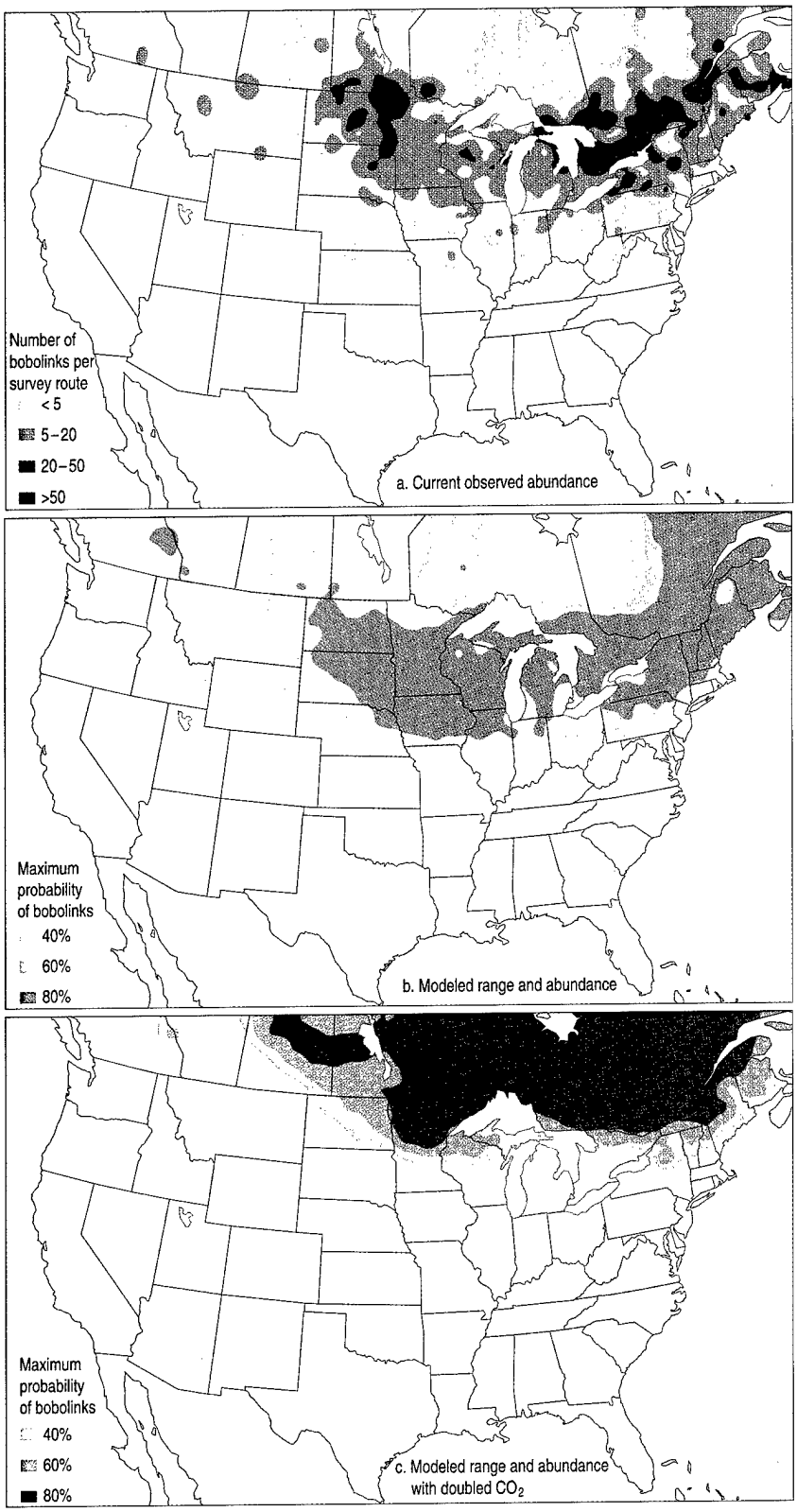

Fig. 11. a) Map of current range and abundance of the bobolink as determined from actual observations during the U.S. Geological Survey Breeding Bird Survey and b) map of current range and abundance of the bobolink as estimated from the empirical–statistical model. The high correspondence in patterns between maps a and b suggests that this model reliably captures many of the features of the actual observed range and abundance of this species as depicted in map a. c) Map of the forecasted range and abundance of the bobolink for climate change response of a model with doubled CO_2. This map illustrates the potential for very significant shifts that doubled CO_2 could cause (Price 1995).

human-induced climatic changes could occur rapidly when compared with the rate of natural climatic changes, and because the dispersal ability of most herptiles is painfully slow, even without considering the additional difficulties associated with human land-use changes disturbing their migration paths.

Several reptile species could exhibit vulnerability to climatic change because of an unusual characteristic: their sex is determined by the temperature experienced as they develop inside the egg. Such temperature-dependent sex determination makes these animals uniquely sensitive to temperature change, meaning that climatic change could potentially cause dramatic range contractions. For example, the European pond turtle, a species whose sex is determined by temperature, colonized England (Stuart 1979) and Denmark (Degerbol and Krog 1951) during a warm period in the late Ice Age. With the return of colder temperatures, these populations rapidly disappeared. Holman (1990; University Museum, Michigan State University, East Lansing, personal communication) suggested that a combination of shorter summers, which reduced available incubation time, and biased sex ratios, which were due to cooler summers, could easily have caused the swift retreat of this turtle to a more southern range.

Most North American turtles are subject to temperature-dependent sex determination (Ewert and Nelson 1991; Ewert et al. 1994); their populations can vary over the years from 100% males to 100% females (Mrosovsky and Provancha 1992; Janzen 1994). Janzen found that sex ratios were closely linked to mean July temperature, and he demonstrated that under conditions predicted by climate change models, populations of turtles will regularly produce only females within 50 years.

In general, animals most likely to be affected earliest by climatic change are those in which populations are fairly small and limited to isolated habitat islands. As a result of human-generated landscape changes, many reptiles now fall into this category, as do many other animals. Indeed, temperature-dependent sex-determined species are especially likely to suffer from extreme sex ratio biases, and therefore their sensitivity to rapid climate change appears potentially more severe than most other animals.

There are estimates that a number of small mammals living near isolated mountaintops (which are essentially habitat islands) in the Great Basin would become extinct given typical global change scenarios (MacDonald and Brown 1992; Fig. 13). Recent studies of small mammals in Yellowstone National Park show that statistically significant changes in both abundances and physical sizes of some species

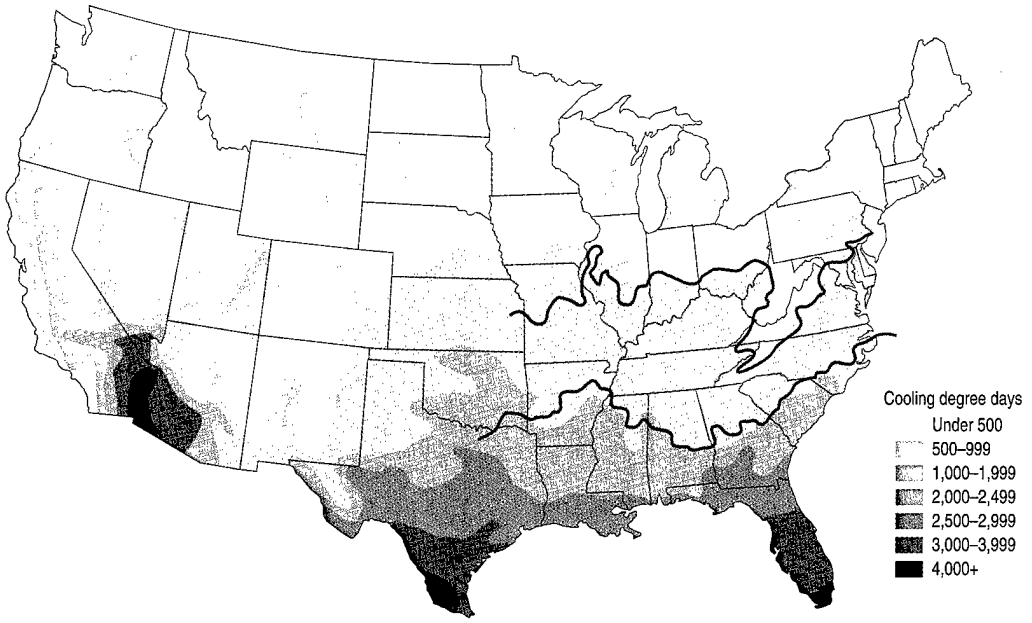

Fig. 12. Strong associations are evident between the northern range limit of the broad-headed skink (upper purple line) and 1,000 cooling degree-days, and between the northern range limit of the American alligator (lower purple line) and 2,000 cooling degree-days, suggesting the importance of climate on the large-scale biogeographic patterns of both species. Cooling degree-days indicate the accumulated number of degrees Fahrenheit over a year above a threshold of 65° F (R. L. Burke and T. Root, University of Michigan, Ann Arbor, personal communication).

occurred with historical climate variations (which were much smaller than most projected climate changes for the next century), but there appear to have been no simultaneous genetic changes (Hadley et al. 1997; E. A. Hadley, Montana State University, Bozeman, unpublished manuscript). Therefore, it is likely that climate change in the twenty-first century could cause substantial alteration to biotic communities, even in protected habitats such as Yellowstone National Park. In addition, the biomass of macrozooplankton in waters off southern California has decreased dramatically as surface waters warmed (Roemmich and McGowan 1995; Fig. 14). Similarly, a study suggests that statistically the range of the Edith's checkerspot butterfly in western North America has shifted northward and upward in association with long-term regional warming trends (Parmesan 1996).

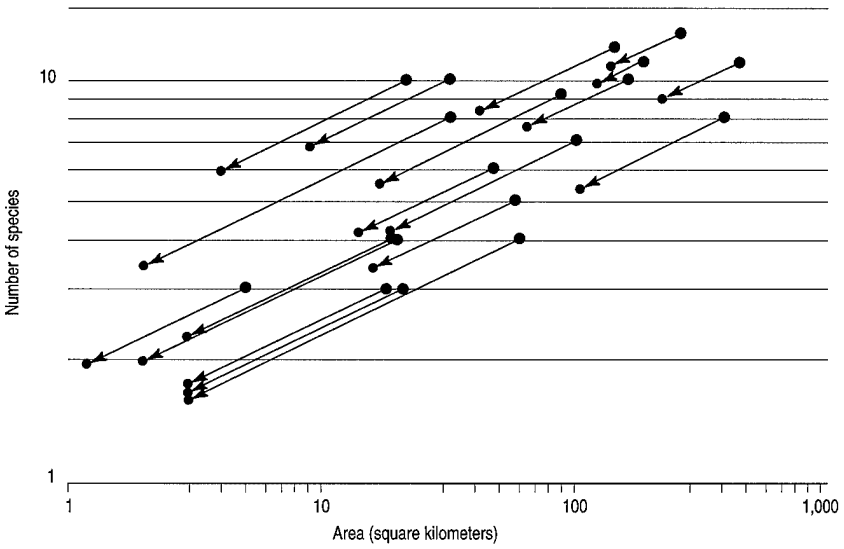

Fig. 13. Predicted changes in the number of species of small mammals inhabiting 19 isolated mountain ranges in the Great Basin after extinctions caused by (the assumed scenario of) climate and subsequent vegetation change. Such climate change would decrease the amount of suitable habitat for these species that live in island-type regions, eventually leading to a number of extinctions. For each mountain range, the purple dot represents the present number of species per square kilometer, the red dot indicates the predicted number per square kilometer after extinctions, and the arrow connecting the two points shows the magnitude of change (MacDonald and Brown 1992).

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Top-Down Approaches

The biogeographic approach just summarized is an example of a top-down technique (for example, Holdridge life-zone classification, Fig. 9), in which data on abundances or range limits of vegetation types or biomes are overlain on data of large-scale environmental factors such as temperature or precipitation. When associations among large-scale biological and climatic patterns are revealed, biogeographic rules expressing these correlations graphically or mathematically can be used to forecast changes in vegetation driven by given climate changes. Price's maps of the changes in bird ranges (Fig. 11) are also an example of such a top-down approach. As noted earlier, though, such top-down approaches are not necessarily capturing the important mechanisms responsible for the association—the association itself may be a chance occurrence. Scientists therefore strive to look at smaller scales for processes that account for the causes of biogeographic associations, in the belief that the laws discovered at smaller scales will apply at large scales as well.

Bottom-Up Approaches

The next traditional analysis and forecasting technique is often referred to as bottom-up. Small-scale ecological studies have been undertaken at the scale of a plant or even a single leaf (Idso and Kimball 1993) to understand how, for example, increased atmospheric CO_2 concentrations might directly enhance photosynthesis, net primary production, or water-use efficiency. Most such studies indicate increases in all these factors, increases that some researchers have

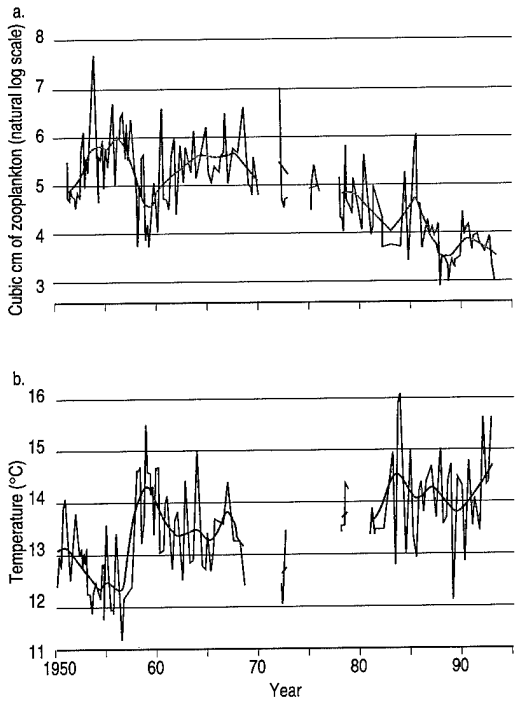

Fig. 14. a) Time series of zooplankton volume (cubic centimeters of zooplankton per 1,000 cubic meters of seawater strained in the Southern California Bight), and b) time series of the upper 100 meters of average temperature of seawater for a). On the logarithmic scale, a change of -1.6 is the change from the mean of the 1950–1970 data to the minimum in the 1990's and is equivalent to an 80% decrease (Roemmich and McGowan 1995).
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extrapolated to ecosystems (Idso and Brazel 1984; Ellsaesser 1990).

To what extent can we reasonably project from experiments that use single leaves or single plants to more complex and larger environmental systems, such as an entire tundra (Oechel et al. 1994) or forest ecosystem (Bazzaz 1990; Bazzaz and Fajer 1992)? Forest ecosystem models driven only by global climate change scenarios in which CO_2 was doubled in a global circulation model typically project dramatic alteration to the current geographic patterns of global biomes (Prentice 1992; Smith et al. 1992; Neilson 1993). But when such forest prediction models are modified to explicitly account for some of the possible physiological changes resulting from doubled CO_2, such as change in water-use efficiency, they use the empirical results from small-scale studies to extrapolate to whole forests. This bottom-up method dramatically reduces the percentage of land area predicted to experience biome change for any given climate change scenario (Vegetation/Ecosystem Modeling and Analysis Project 1995). Prentice et al. (1992), though, building on the work of McNaughton and Jarvis (1991), excluded extrapolations of the effects of direct CO_2/water-use efficiency from their model.

At the scale of a forest, the relative humidity within the canopy, which significantly influences the evapotranspiration rate, is itself regulated by the forest. In other words, if an increase in water-use efficiency decreased the transpiration from each tree, the aggregate forest effect would be to lower relative humidity. This, in turn, would increase transpiration, thereby offsetting some of the direct CO_2/water-use efficiency improvements observed experimentally at the scale of a single leaf or plant. Regardless of the extent to which this forest-scale feedback effect will offset inferences made from bottom-up studies of isolated plants, the following general conclusion emerges: the bottom-up methods may be appropriate for some processes at some scales in environmental science, but they cannot be considered credible without some sort of validation testing at the scale of the system under study. Schneider (1979) has made the same point for climate models, as do several authors in Ehleringer and Field (1993) for vegetation modeling. Harte et al. (1995) used actual field experiments with heaters to simulate global warming as an experiment to demonstrate top-down/bottom-up connections.

Combined Top-Down and Bottom-Up Approaches

To help resolve the deficiencies of the top-down biome forest models mentioned previously, more process-based, bottom-up approaches such as forest gap models have been developed (Botkin et al. 1972; Pastor and Post 1988; Smith et al. 1992). These models include individual species and can calculate vegetation dynamics driven by time-changing climatic change scenarios. Such models typically assume a random distribution of seed germination in which juvenile trees of various species appear. Whether these trees grow well or just barely survive depends on whether they are shaded by existing trees or grow in relatively well-lit gaps, what soil nutrients are available, and other environmental factors such as solar radiation, soil moisture, and temperature. Under ideal conditions, individual tree species are assigned a sigmoid (S-shaped) curve for growth in trunk diameter. So far, this approach may appear to be the desired process-based, bottom-up technique, an impression reinforced by the spatial scale usually assumed, about 0.1 hectares. But the actual growth rate calculated in the model for each species has usually been determined by multiplying the ideal growth rate curve by a series of growth-modifying functions that attempt to account for the limiting effects of nutrient availability, temperature stress, and so forth. These growth-modifying functions for temperature are usually determined empirically at a large scale by fitting an upside-down U-shaped curve, whose maximum is at the temperature midway between the average temperature of the species' northern range limit and the average temperature of its southern range limit (Fig. 15). Growing degree-days (related to temperature but not temperature per se) are used in this scenario.

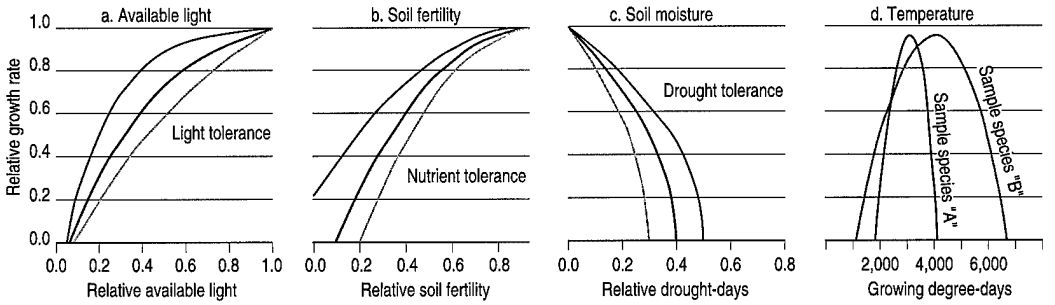

Fig. 15. Functions used to modify optimal growth of individual species in forest gap models (Smith et al. 1992): a) available light, b) soil fertility, c) soil moisture, and d) temperature.

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Understanding Climate Change Effects on Glacier National Park's Natural Resources

Determining past trends and the present status of biological resources is essential for effective decision making at national parks and other lands held in the public trust. Today, however, managers have a more powerful tool for making decisions—the ability to reliably forecast resource conditions under various future scenarios. This is particularly evident when considering potential effects of climatic change on national biological resources.

Although predicting the future has always been an uncertain business, with support from the U.S. Geological Survey Global Change Research Program, scientists have further developed the capability for simulating the function and structure of northern Rocky Mountain ecosystems (Fig. 1). The Regional Hydro-Ecological Simulation System (RHESSys) provides quantitative estimates of key ecosystem processes for any specified point in time or space (White and Running 1994).

A concurrently developed model, FIRE-BGC (biogeochemistry), can translate RHESSys estimates into the probable age, size, and species composition of a forest 100 years in the future on any specified mountain slope in Glacier National Park (Keane et al. 1996; Fig. 2). The predictions are spatially explicit, meaning that future forests can be calculated and mapped for each slope and aspect of the mountain landscape. The models are also mechanistic, meaning that components such as trees are "grown" in the virtual reality of computer memory by using biophysical principles and calculations, rather than by being estimated through empirical means. Finally, future landscapes can be generated by using various projections of future climates. These climatic scenarios can be imported to RHESSys from larger-scale climate modeling efforts.

RHESSys does not predict future climates; instead, it translates projected climate scenarios into tangible ecological changes on landscapes at Glacier National Park. Because RHESSys is spatially explicit in describing future conditions and can be displayed on a computer monitor or map, it can convey a powerfully intuitive understanding of potential landscape changes.

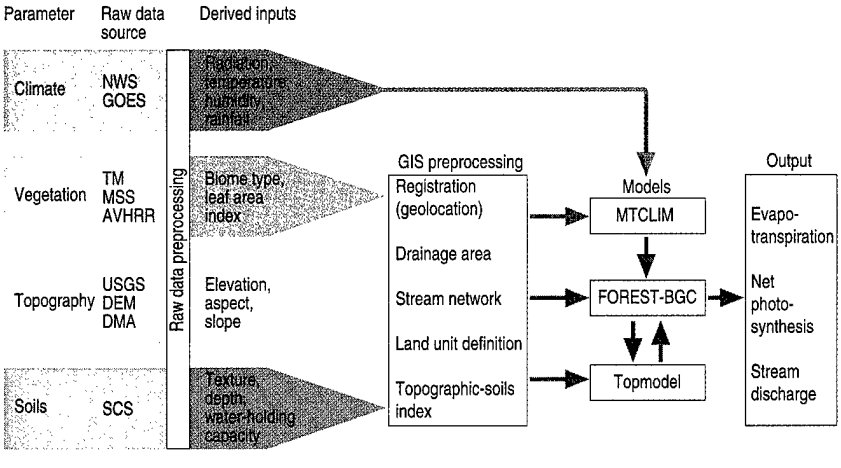

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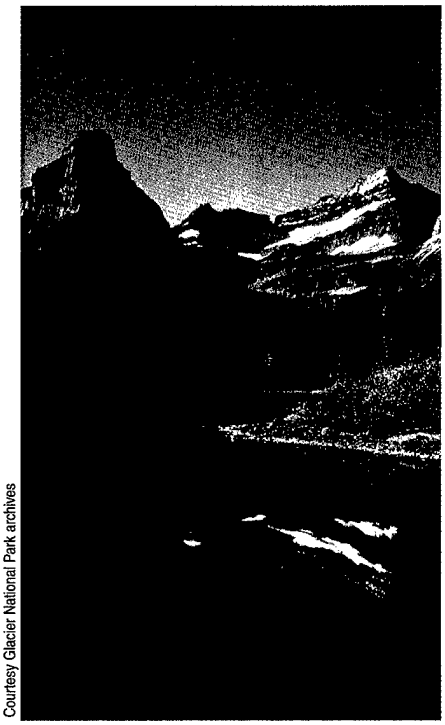
Fig. 1. RHESSys, the Regional Hydro-Ecological Simulation System, integrates data from various standard sources into a series of interacting models that provide quantitative estimates of ecosystem functions (modified from White and Running 1994).



Courtesy Glacier National Park archives

Fig. 2. Glacier National Park encompasses a 4,078 square-kilometer forested, mountainous landscape with numerous alpine lakes and streams.

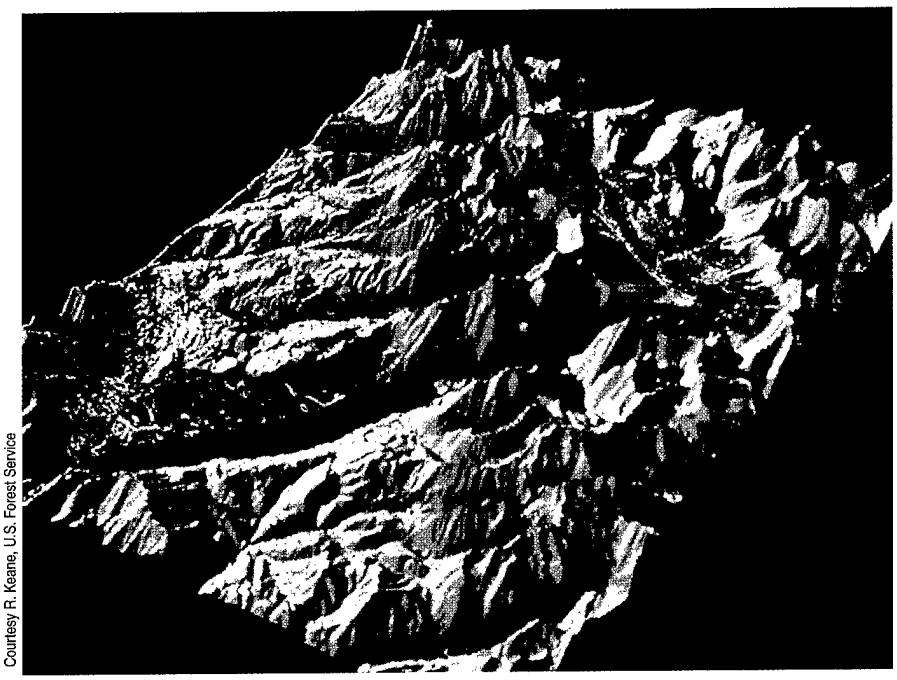
How Modeling Works

RHESSys uses remotely sensed imagery and other satellite data to provide the geographic distribution of vegetation cover types for Glacier National Park. By combining this information with elevation data in a geographic information system (GIS), the computer can create a three-dimensional digital landscape. Estimates of biomass or rates of photosynthetic activity for each vegetation cover type in the park are made from satellite data by using other tested techniques (Running et al. 1989). RHESSys then "knows" approximately what is on the landscape and where it is; next it needs to estimate landscape response to environmental changes.

A microclimate model (MTCLIM) takes daily meteorological measurements and, by using mathematical expressions of physical principles, extrapolates those data to every point in the mountainous terrain (Hungerford et al. 1989). Thus, the daily changes in microclimate experienced by each stand of trees in the park is calculated. A forest biogeochemistry model (FOREST-BGC) uses the microclimate calculations (such as relative humidity or solar radiation) and appropriate biophysical principles to estimate daily tree response (Running and Gower 1991). The net result is that RHESSys can simulate forest ecosystem processes daily for many years and across large areas of Glacier National Park.

Of course, tree growth is determined by more than just daily weather, which is why the various models within RHESSys interact. For instance, the responses of a forest stand to changes in microclimate are passed along to calculate the effects of increasing tree growth on soil moisture. Reductions in soil moisture provide feedback to another model, which estimates streamflow in each forested drainage. Changes in soil moisture also provide feedback to the model, which estimates rates of tree growth and so on. An advantage to the RHESSys structure is that the individual models can be tested and improved independently without changing the entire simulation system. This allows RHESSys to quickly take advantage of continuing improvements in ecological modeling.

RHESSys estimates ecological processes such as rates of evapotranspiration, hydrological balance, or net primary productivity (Fig. 1). FIRE-BGC is a biogeochemical succession model that uses those estimates to generate the physical structure and species diversity of forests. FIRE-BGC defines homogeneous landscape units (like forest stands) and calculates individual tree growth, death rates, seedling survival, organic matter accumulation, and decomposition both daily and annually. The replacement of one stand of trees by another stand (succession) can be tracked through time as tree demographic processes take place. The role of ecological disturbances, such as large forest fires, has also been integrated (Finney and Ryan 1995; Fig. 3).

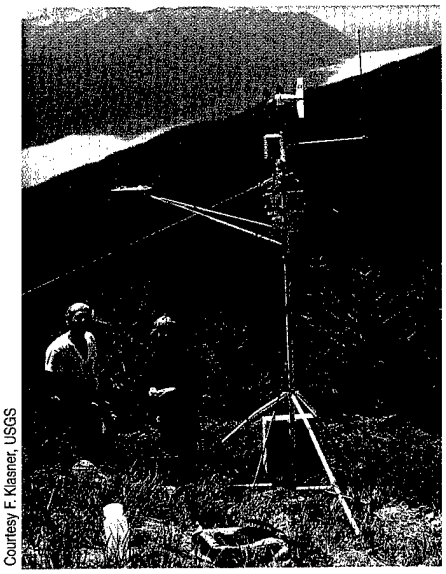


Courtesy R. Keane, U.S. Forest Service

Fig. 3. A forest succession model, FIRE-BGC, predicts the occurrence of two major forest fires in the upper McDonald watershed during simulation year 163. Blue colors are the cooler part of the fire, pink the hottest parts. The boundaries and intensity of the potential future fire are calculated by another model, FARSITE, based on such parameters as fuel loads and simulated daily meteorology.

How Well Do the Models Work?

We can test model performance by comparing ecosystem processes simulated for present conditions with measurements of the real ecosystem. Climate data for Glacier National Park's Lake McDonald basin have been used to drive a RHESSys simulation for the same period when numerous field measurements were being taken. For instance, thousands of snow depth measurements were made to verify the RHESSys estimates of snowpack distribution and moisture content. This test was critical because snowpack provides significant moisture during summer months for many ecosystem functions. Automated weather stations were placed on remote mountain slopes to confirm that the microclimate model was making reasonable predictions of climatic variables (Fig. 4). Many other ecosystem measurements were taken, including stream discharge volume and timing. Figure 5 shows the relation between the streamflow that actually occurred and what RHESSys predicted would occur (Comanor et al. 1997). Other comparisons of modeled and measured ecosystem phenomena showed similar relationships.



Courtesy F. Klasner, USGS

Fig. 4. Research scientists from the U.S. Geological Survey and National Park Service at an automated climate station above Lake McDonald, Glacier National Park. Data collected from this station will help verify the meteorological estimates generated by a submodel of RHESSys.

RHESSys is able to reasonably simulate the underlying dynamics that drive ecological changes in Lake McDonald basin. These

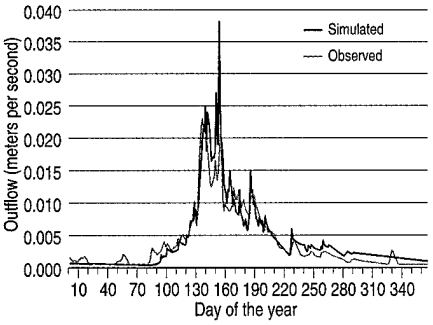


Fig. 5. A comparison of the observed and simulated outflow (meters per second) from the upper Lake McDonald watershed, Glacier National Park, 1993. Simulated outflows were calculated by RHESSys.

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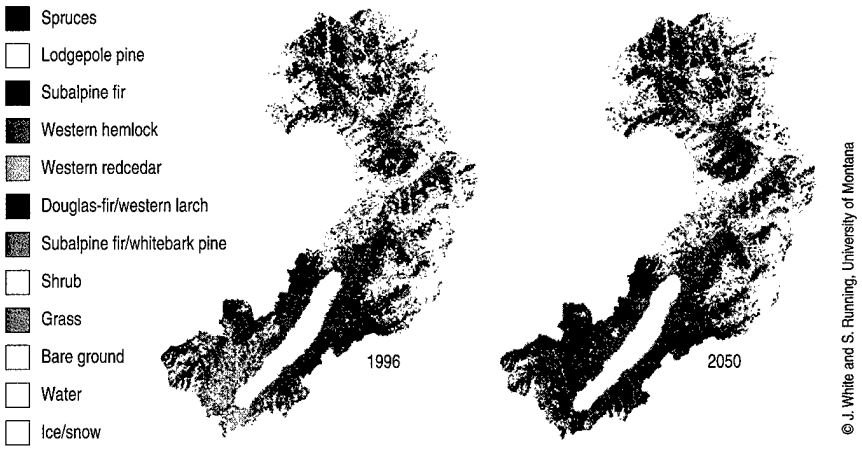


Fig. 6. Estimated changes in vegetation cover by 2050 for the Lake McDonald watershed, Glacier National Park, following climate change. Changes were estimated by RHESSys by using a climate change scenario of a 30% increase in annual precipitation and a 0.5°C increase in average annual temperature.

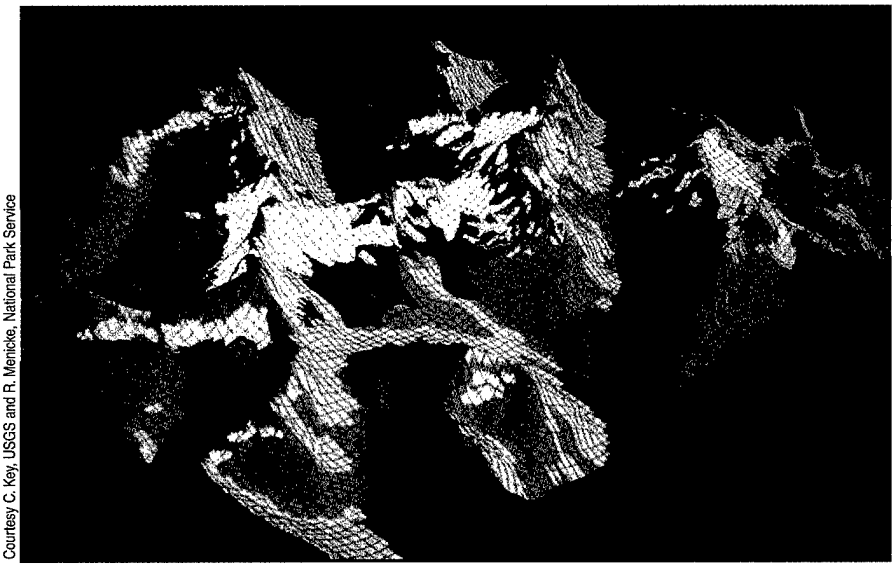
simulations indicate that the Glacier National Park landscape is dynamic and will change over time even with a stable climate. We cannot assume, however, that the climate is not changing.

Predicting Climate Change Effects

Forecasting future climates is both difficult and controversial. The value of models like RHESSys is that a variety of climate scenarios can be used to simulate the range of outcomes for Glacier National Park. As climate models improve, RHESSys can use the new forecasts to identify increasingly probable ecosystem changes.

The simulation for the Lake McDonald basin in Figure 6 is based on the assumption that the regional climate will be 0.5°C warmer and will have a 30% increase in annual precipitation 50 years from now. Predicted changes in vegetation include expanded cedar–hemlock forests, making Glacier National Park resemble the wetter forests of the Pacific Northwest. A different climate scenario suggests Glacier National Park stream temperatures will rise, especially in late summer, because of changes in streamflow timing and volume. Such changes would affect temperature-sensitive aquatic organisms; for example, different species live in each section of stream as the water becomes colder with increasing elevation. Predictable shifts of these organisms upstream and to higher elevations will occur under the RHESSys-projected changes.

RHESSys accurately predicted snowfall distribution at Glacier National Park, identifying areas where snow never melted completely before the onset of the next winter. These are the same areas that currently support glaciers (White and White 1994). These glaciers have been steadily receding during this century (Fig. 7), and RHESSys suggests that future snowpacks will not survive through summer to nourish glaciers. A separate modeling effort extrapolated glacial melt rates into the future by using different scenarios for global warming (Hall 1994). In this model, whether current warming trends continue or are accelerated by increasing atmospheric carbon dioxide, glaciers will not exist in Glacier National Park by 2030.



Courtesy C. Key, USGS and R. Mernicke, National Park Service

Fig. 7. A geographic information system representation of glacier shrinkage from 1850 to 1993 in Glacier National Park. The Blackfeet–Jackson glaciers are in the center. The yellow areas reflect the current area of each glacier; other colors represent the extent of the glaciers at various times in the past.

Future Models

Ecosystem modeling systematically organizes our current ecological knowledge to provide quantitative estimates we can test in the field. Once underlying ecological principles have been affirmed in the model by successful field tests, we can use a model to glimpse the future and help prepare for it. Like climate change models, simulation systems like RHESSys and FIRE-BGC will be continually improved. It seems clear, however, that these ecosystem models will challenge us to think more specifically about the effects of climate change and will be an essential tool for understanding the future status and trends of our biological resources.

See end of chapter for references

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In essence, this technique combines large-scale, top-down empirical pattern correlations into an otherwise mechanistic bottom-up modeling approach. Although this combined technique refines both approaches, it has been criticized because such large-scale, top-down inclusions are not based on the physiology of individual species and lead to confusion about the fundamental and realized niches (Pacala and Hurtt 1993). (The fundamental niche is the ecological space in which a given species could theoretically survive—for example, if its competitors were absent—and the realized niche is where it actually exists.) The question then is: what limits the realized niche, particularly at the southern boundary? Further, more refined models should include factors such as seed dispersal, so that plant recruitment is related to the preexisting population and is not simply the result of a random number generator in the computer code.

Studies of More Refined Approaches

As noted, problems with the singular use of either top-down or bottom-up methods have led to well-known criticisms. For bottom-up models, the primary problem is that some of the most conspicuous processes observable at the smaller scales may not be the dominant processes that generate large-scale patterns. The mechanisms that create larger-scale responses can be easily obscured by noisy (for example, random or unrelated) local variations, often leading to an inability to detect at small scales a coherent pattern of associations (that is, mechanisms) among variables needed for ecological impact assessments at large scales. As Dawson and Chapin (1993:318) noted, too much "information about detailed mechanisms may be inefficient, incorporating excessive detail and ignoring other aspects that are critical to understanding processes at the higher levels."

Top-down approaches suffer because of the possibility that the discovered associations at large scales are statistical artifacts that do not, even implicitly, reflect the causal mechanisms needed for reliable forecasting. As Jarvis (1993:121) stated, "A major disadvantage of a top-down model is that predictions cannot be made safely outside the range of the variables encountered in the derivation of the lumped parameter function."

A search of the literature (Wright et al. 1993; Root 1994; Harte et al. 1995) provides examples of a refined approach to analyzing across large and small scales, which Root and Schneider (1995) labeled strategic cyclical scaling. This method builds upon the combined techniques in which top-down and bottom-up approaches are applied cyclically in a strategic design that addresses a practical problem: in our context, the ecological consequences of global climatic change. Large-scale associations are used to focus small-scale investigations; this helps ensure that tested causal mechanisms are generating the large-scale relations. Such mechanisms become the laws that allow more credible forecasts of the consequences of global change disturbances. "Although it is well understood that correlations are no substitute for mechanistic understanding of relationships," Levin (1993:14) observed, "correlations can play an invaluable role in suggesting candidate mechanisms for (small-scale) investigation." Strategic cyclical scaling, however, is not only intended as a two-step process, but also as a continuous cycling process between large- and small-scale studies, with each successive investigation building on previous insights from all scales. This approach is designed to enhance the credibility of the overall assessment process (see also Vitousek 1993 and Harte and Shaw 1995), which is why strategic is the first word in strategic cyclical scaling.

If the rate at which humans are injecting greenhouse gases into the atmosphere is not greatly decreased, there is a significant chance that the Earth's climate will warm by several degrees Celsius by the year 2050 (Titus and Narayanan 1995). With that in mind, Root (1988a) examined the biogeographic patterns of all wintering North American birds. She chose this group of species because birds are important parts of ecosystems and because of the availability of the necessary data—large-scale abundance data requires a veritable small army of census takers. The National Audubon Society and the U.S. Geological Survey have such volunteer forces amassed to aid in the collection of Christmas Bird Count data and Breeding Bird Survey data, respectively. By using Christmas Bird Count data, Root determined that for a large proportion of species, average distribution and abundance patterns are associated with various environmental factors (for example, northern range limits of some species apparently may be limited by average minimum January temperature; Root 1988b, 1989; Repasky 1991). Because the Christmas Bird Count and Breeding Bird Survey do not cover the Mexican or Central American portions of wintering or breeding ranges, only characteristics of the northern limits or of species that winter entirely north of the Mexican border could be considered.

The scaling question is: What mechanisms (such as competition or thermal stress) at small scales may have given rise to the large-scale associations? Root first tested the hypothesis that local physiological constraints may be causing most of the particular large-scale, temperature-range boundary associations. She used

published small-scale studies on the wintering physiology of key species to determine that about half of the songbird species wintering in North America extend their ranges no farther north than the regions where, to avoid hypothermia during winter nights, they need not increase their metabolic rates more than roughly 2.5 times their basal metabolic rate (Root 1988c). The actual physiological mechanisms generating this 2.5 rule (Diamond 1989) required further investigation at small scales.

Field and laboratory studies examining various physiological variables (for example, stored fat) are being examined on a subset of those species that seem to follow the 2.5 rule. On a large geographic scale—along a longitudinal transect running from Michigan to Alabama (Fig. 16)—Root found that the amount of stored fat may be a limiting factor. The estimated amount of available fat at dawn under extreme conditions was much lower for those individuals near the northern boundary of their range than for those in the middle of their range (Root 1991). Root embarked on a larger, regional study to determine whether the longer nights—hence, fewer hours of daylight available for foraging—or the colder temperatures in the more northerly locations are relatively more important.

In addition to the one longitudinal transect, Root incorporated a second transect that runs from Iowa to Louisiana (Fig. 16), with the field sites on each transect paired such that pairs at the same latitude (that is, sites in Michigan and Iowa, Indiana and Missouri, Tennessee and Arkansas, and Alabama and Louisiana) have the same day length. In addition, because winter minimum isotherms run at an angle to latitude in this area of the continent, Root was able to form different pairs of the sites so that temperatures were similar (that is, sites in Missouri and Michigan, Arkansas and Indiana, and Louisiana and Tennessee have roughly the same average nightly January temperature). This larger-scale design was selected based on previous small-scale studies because it allows a decoupling of the effects of day length and minimum temperature, which is important to the strategic problem of determining whether scenarios of global warming might have a large effect. Preliminary results indicate that changing temperatures are more likely than day length to explain this effect (Root, unpublished data). Thus, global temperature changes would probably cause a rapid range and abundance shift, at least by selected bird species. Indeed, Root found significant year-to-year shifts in ranges and abundances; these shifts are apparently associated with year-to-year changes in winter temperatures.

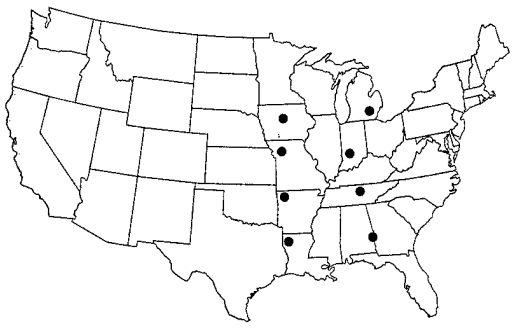

Fig. 16. Two north–south transects used to distinguish effects of day length from temperature for the northern cardinal (Root 1997).

This shift in year-to-year ranges and abundances observed at several field sites led to another large-scale, top-down study. Root has embarked on a continentwide examination of northern range boundaries of wintering birds, but this time is looking for year-to-year variations rather than average limits or abundances. Her first step was to quantify the year-to-year variations of selected species (Root 1994), the next to perform time-series analyses of 30 years of wintering bird abundance data and to compare these analyses with key climatic variables (for example, number of consecutive days below $^{-}4°C$). Preliminary analysis for only one species at two sites shows that in warmer years, more individuals winter farther north than in colder years (Fig. 17). No claim is made at this point in the research for the generality of the preliminary results indicating strong and quantitative links between bird disturbances and climate. This example does permit, however, a clear demonstration of refined methods for cycling across scales to estimate ecological responses to climatic change.

A second example of refined methods—this time from a consortium of researchers rather than a single investigator—is the Cooperative Holocene Mapping Project effort referred to previously. (See Cooperative Holocene Mapping Project 1988; Wright et al. 1993; and the discussion in Root and Schneider 1995 for further details.)

Three-way Linkages Among Plants, Animals, and Climate on a Large Scale

The anticipated changes in plant ranges will probably have dramatic effects on animals, both on the large biogeographic scale and on the local regional scale. The ranges of many animals are strongly linked to vegetation. For example, red-cockaded woodpeckers are endemic to mature longleaf pine and pine–oak forests (Mengel and Jackson 1977), and the winter range of Sprague's pipit is coincident with bluestem, a grass (Root 1988a). Most

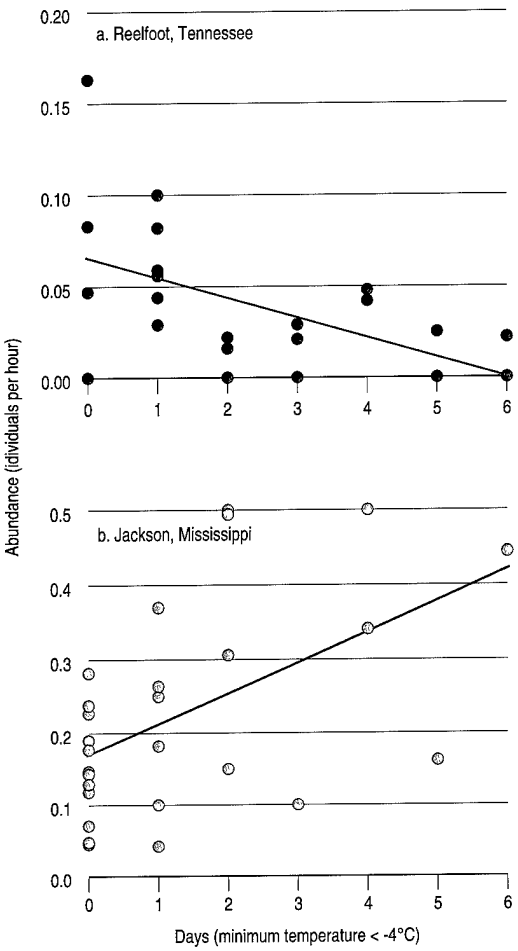

Fig. 17. The relation between annual winter abundance of the eastern phoebe from 1959–1960 to 1988–1989 and the harshness of the winter weather at two locations along the same longitudinal gradient: a) Reelfoot, Tennessee, and b) Jackson, Mississippi. In cold years, the birds move south, and in warmer years they stay farther north.

plant-eating insects are specific to plants at the generic or family level (P. A. Opler, U.S. Geological Survey, Fort Collins, Colorado, personal communication). Consequently, the ranges of various animals that rely on specific vegetation will change as the ranges of these plants shift, assuming that some other factor is not limiting them. If the climate changes more rapidly than the dispersal rates of the plants, it will result in extensive plant die-offs in the south or downslope before individuals can disperse and become established in the north or upslope. Thus, the ranges of animals relying on these plants could become compressed, and in some instances, both the plants and the animals could become extinct. For instance, the red-cockaded woodpecker needs mature, living trees for nesting sites (Jackson 1974), and if rising temperature causes most large trees to die before the newly established dispersing trees grow large enough, then this woodpecker, federally listed as endangered, could easily become extinct.

Community Disruption

Many animal species have ranges that are not directly limited by vegetation but are instead restricted by temperature. This is true for most ectotherms (insects and related arthropods, amphibians, reptiles) as well as some endotherms (mammals and birds). For example, the eastern phoebe, a North American songbird, winters in the United States in areas with average minimum temperatures warmer than -4°C (Root 1988a; Fig. 18). As the Earth warms, those species directly limited by temperature will be able to expand northward as rapidly as their dispersal mechanisms will allow, again assuming other factors are not limiting them. The animals limited by vegetation will be able to expand their ranges only as rapidly as the vegetation changes. Consequently, the potential for significant disruption among communities is high. For instance, some animals may no longer be able to coexist because an invading species disrupts the balance between competing species or between predator and prey. Therefore, to understand the ecological consequences of global climatic change on animals, the three-way linkages among animals, plants, and climate must be understood. It is critical to realize that this is not simply a one-way process whereby climate influences biota, but a three-way process, because animals and plants affect each other and are affected by climate. At the same time, altered surface vegetation can affect climate because midcontinental summer precipitation is significantly influenced by water vapor from evapotranspiration (Ye 1989; Salati and Nobre 1991).

Information Gaps

Climate Forecasts

Improve Regional Analysis, Study Transients, and Include Many Variables

The most reliable projections from climatic models are for global-scale temperature changes. Ecological impact assessments, however, need time-evolving (transient) scenarios of regional-to-local-scale climate changes. Included are changes in precipitation; severe storm intensity, frequency, and duration; drought frequency, intensity, and duration; soil moisture; frost-free days; intense heat waves; ocean currents; upwelling zones; near-ground ozone; forest canopy humidity; and ultraviolet radiation and total solar radiation reaching the surface, where photosynthesis is important. Data gathered at many scales and by coordinated volunteer and professional sources are needed for archives of these regional and local variables, which, in turn, can be used to develop and test models or other techniques for climatic forecasting.

Fig. 18. The winter range of the eastern phoebe and the -4°C isotherm for average minimum January temperature (Root 1988b).

Abrupt Climatic Changes

We have argued that *sustained globally averaged* rates of Earth and ocean surface temperature changes from the past Ice Age to the present were about 1°C per 1,000 years. Alarmingly, this is a factor of 10 or so slower than the expected changes of several degrees Celsius per 100 years typically projected for the twenty-first century due to human effects. We emphasize the words sustained globally averaged because comparably rapid regional variations have occurred. For example, about 13,000 years ago, after warm-weather fauna had returned to northern Europe and the North Atlantic, there was a dramatic return to ice age-like conditions in less than 100 years. This Younger Dryas miniglacial lasted about 1,200 or 1,300 years before the stable recent period was established (Berger and Labeyrie 1987). The Younger Dryas was also accompanied by dramatic disturbances to plants and animals in the North Atlantic and Europe (Coope 1977; Ruddiman and McIntyre 1981). During the same period, fewer dramatic shifts occurred globally, and no significant climate change is evident in Antarctic ice cores. Even so, studies of fossils in the North Atlantic show that the warm Gulf Stream current deviated many degrees of latitude to the south and that the overall structure of deep ocean circulation may have returned to near ice age form in only decades—a weakening of the vertical circulation known as the conveyor-belt current (Broecker et al. 1985).

Plausible speculations about the cause of the Younger Dryas center on the injection of fresh meltwater into the North Atlantic, presumably associated with the breakdown of the North American ice sheet (Boyle and Weaver 1994; Paillard and Labeyrie 1994). Could such a rapid change to the conveyor-belt current be induced today by pushing the present climatic system with human disturbances such as greenhouse gases or sulfur oxides? The potential for this is speculative, of course, but its possibility has concerned many scientists (Broecker 1994).

Even more perplexing is an ice core recently drilled in Greenland; this core's record stretches back to the previous interglacial age 140,000–120,000 years ago (Greenland Icesheet Project 1993). Unlike ice in Antarctica, which tells the standard story of a relatively stable 2°C warmer interglacial period (Fig. 1), the Greenland core contains several dramatic fluctuations during the slightly warmer Eemian interglacial, equivalent to the occurrence of some 5°C changes happening within a century or less (locally, at least). Could a human-caused global warming of 2°C—expected as likely in the decades ahead (Intergovernmental Panel on Climate Change 1996a)—trigger such "surprise" climatic instabilities as may have occurred 140,000–120,000 years ago? Again, this is speculation based on a possible but unconfirmed result. Still, the prospect of climatic surprises in general is chilling enough to lend considerable urgency to the need to speed up the rate of our understanding, slow down the rates at which we are forcing nature to change, or both.

Adaptability

Our current inability to credibly predict time-evolving regional climatic changes

has many implications, one of which concerns the adaptability of agricultural ecosystems. That is, any experience farmers might have with anomalous weather in, say, the 2020's, may not help them adapt to the evolving climate change in the 2030's, because a transient climate change could differ dramatically over time. This would inhibit learning by doing, creating a potential lack of adaptability associated with the difficulty of reliably predicting regional climatic consequences (Schneider 1996). Such rapid climate changes would be especially difficult for natural ecosystems to adapt to because habitats do not have the luxury of "choosing" to plant new seeds or change irrigation systems, soil tillage practices, or other agricultural practices.

Ecological Applications-Driven Climatic Research

Regional projections of climatic changes arising from a variety of greenhouse gas and sulfur oxide emissions scenarios are essential for ecological applications. Such studies must stress the climatic variables most likely to have significant effects on biological resources. For example, extreme variability measures such as high temperature and low relative humidity are important for evaluating the risk of forest fires (Torn and Fried 1992). Identifying such variables of ecological importance and communicating this information to climate scientists require close interdisciplinary, multi-institutional, and cross-scale research efforts to ensure that combinations of variables relevant to ecological applications receive research priority by climatologists. A focus of climate research toward changing climatic variability (Mearns et al. 1984, 1990; Rind et al. 1989) might be more useful for ecological impact assessments than the current focus among climatic modelers on climatic means.

Ecosystem Responses

Interactive, Multiscale, Ecological Studies Needed

Most ecological studies project the response of one species at small scales or shifts in biomes at large scales to an equilibrium, CO_2-doubled climate model (for example the Vegetation/Ecosystem Modeling and Analysis Project 1995). What is needed for more realistic and useful ecological impact assessments is a multiscale, multispecies, multitaxa analysis driven by regionally specific, transient climatic change forecasts. The construction of ecological forecast models first requires large-scale data sets gathered locally by professional (for example, U.S. Geological Survey land-cover data sets) and volunteer (for example, National Audubon Society Christmas Bird Count) workers. Without such data sets, virtually no credible progress is possible in determining large-scale patterns of associations among ecological and climatic variables. Small-scale studies informed by large-scale patterns are then needed to refine causal mechanisms underlying such large-scale associations, thereby testing the formulas used to make projections of various species or biome responses to hypothesized global changes. For example, Pacala and Hurtt (1993) suggested small- to medium-scale experiments to improve forest gap models. Their criticisms suggest that largely first principles, bottom-up models may still be unrealistic if some top-down parameters (that is, growth-modifying functions in the instance of gap models) are not appropriately derived from data at the scale at which the model is being applied (Root and Schneider 1995).

One obvious truism emerges: credible modeling required for forecasting across many scales and for complex interacting systems is a formidable task requiring repeated testing of many approaches. Nevertheless, tractable improvements in refining combined top-down and bottom-up techniques can be made. It will, however, take more than one cycle of interactions to reliably address the cross-scale and multicomponent problems of ecological assessment—what we (Root and Schneider 1995) have elsewhere labeled strategic cyclical scaling.

Synergistic Effects

One of the most potentially serious global change problems is the synergistic or combined effects of habitat fragmentation and climate change. People fragment natural habitats for farmland, settlements, mines, or other developmental activities (see chapter on Land Use). If climate changes, individual species of plants and animals will be forced to adjust if they can, as they have in the past. It seems unlikely that all of the migrating species that survived the Ice Age would be able to safely reach refuges after migrating across freeways, agricultural zones, industrial parks, military bases, and cities of the twenty-first century. An even further complication arises with the imposition of the direct effects of changes in CO_2, which can change terrestrial and marine primary productivity as well as alter the competitive relations among photosynthesizing organisms.

One representative instance of synergism is that of the Kirtland's warbler in northern Michigan; this species is restricted to a narrow area of jack pines that grow in sandy soil (Botkin et al. 1991). Forest gap models of growth and decline of jack pines indicate that this species will move north with warming, but

the Kirtland's warbler will not likely survive the transition. This bird nests on the ground under relatively young pines, and the soil to the north is not generally sandy enough to allow sufficient drainage for successful fledging of young (Cohn 1989). Consequently, global warming could well doom the warbler to extinction in 30–60 years. This potential for extinction indicates how the already high rate of extinctions around the world would be exacerbated by climatic changes occurring more rapidly than species can adapt (see Pimm 1991; Peters and Lovejoy 1992; Wilson 1992).

The synergism question raises a controversial management problem of anticipating global change risk and responding by setting up interconnected nature reserves to ensure against some species becoming extinct in the event of climate changes. Alternatively, we could simply let the remnants of relatively immobile wildlife and natural plant communities remain in isolated reserves and parks as now exist. If we do opt for more environmental safeguards by interconnecting our parks, the question then becomes how we interconnect the nature reserves. Priorities must be set and money made available for constructing natural corridors through which species can travel. For example, elevated sections of highways may be needed to allow for migration routes, similar to what was done for the caribou in the Arctic when the Alaskan pipeline was built.

Policy Implications

Climatic change as now envisioned is not necessarily a threat to the well-being of all climate-sensitive species. However, the transient nature of most projected human-induced climatic change scenarios suggests that significant alterations are likely on a scale of decades, whereas the adaptability of many species—especially those upon which faster responding species depend—is on a scale of centuries. These different rates of climate change and species adaptability imply that substantial disequilibrium within ecosystems could be created because of maladaptations, significant shifts in the ranges of some species, and inevitable extinctions that result from the need to migrate rapidly through fragmented habitats and areas where traditional migratory routes are disturbed by human land-use changes. Consequently, the only outcomes that can be predicted with virtual certainty are major surprises. The only forecast that seems unassailable is that the more rapidly the climate changes and the more extensively other human disturbances are forced on nature, the higher the probability of substantial disruption and surprise within natural systems.

Dramatic disruption of communities can be expected to occur in the next century under these conditions. To forecast possible consequences of the projected climate changes, single-species studies should be guided by the overall effects that climate may have at the large scale or on range limits and abundance patterns, and on the interactions among species. Coupling such results with information from climatologists, geologists, and others will allow interdisciplinary teams to more reliably forecast the possible biological consequences of scenarios of global warming and other global changes. These forecasts can then be used by policy makers and the general public to determine what types of actions might be effective to mitigate potential impacts of forecasted climate changes. Research can help put such policy making on a firmer factual basis, but any plausible level of effort is not likely to reduce all important uncertainties before the global change experiment now under way on Earth is played out (for example, Schneider 1997). This fact lends a real sense of urgency to research and policy communities concerned about biological conservation.

Acknowledgments

T. L. Root acknowledges partial support for this work from the National Science Foundation (IBN-9058031), U.S. Fish and Wildlife Service Global Change Program, and Pew Scholars Program in Conservation and the Environment. S. H. Schneider acknowledges support from the U.S. Department of Agriculture grant (94-G-237) to the National Center for Atmospheric Research, which is sponsored by the National Science Foundation. Opinions are only those of the authors and do not necessarily reflect the views of the sponsoring agencies. We appreciate the programming help from L. McDaniel and the many useful comments on draft manuscripts by E. J. Brennan, R. Burke, and J. Harte.

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Nonindigenous Species

Invasion by nonindigenous species is one of the most important issues in natural resource management and conservation biology today. The ability of nonindigenous species to alter population, community, and ecosystem structure and function is well documented (Elton 1958; Mooney and Drake 1986; Vitousek et al. 1987; Drake et al. 1989). Ecosystem-level changes that alter water, nutrient, and energy cycles; productivity; and biomass directly affect human society. Ecosystem-level consequences of invasive nonindigenous species have major ecological and economic implications and directly affect human health. Complex technology has addressed the cleanup of chemical pollutants and contaminants and has reversed some of the damage from physical alteration of the environment. However, little attention has been paid—and almost no progress has been made—in addressing the problem of nonindigenous species.

The problem of biological invasion of the United States is not new. In the continental United States, it began with the arrival of the first European settlers more than 500 years ago and has continued at an increasing rate. In Hawaii, it began more than a thousand years ago with the arrival of the Polynesians, who introduced several plants into their new landscape. Many of the early introductions of plants and animals were intentional and generally viewed as a welcome enrichment of the American biota. Among early introductions were the domesticated animals and plants, which were essential to the survival of settlers as dependable sources of food and fiber. As invasive nonindigenous species have increased and their effects on native biota have become apparent, the perception about many introductions has shifted from welcome additions to pests. Today, although the economic and recreational benefits of selected nonindigenous species are considerable, evaluation of the economic and ecological costs reveals that introductions of nonindigenous species can also be expensive. The nonindigenous species problem has reached proportions that demand development of a coherent national policy to guide future actions.

Definitions of invasive nonindigenous species have been inconsistent, leading to confusion in lay and scientific literatures. First, the distinction between natural biological invasions, which are generally considered as range expansions, and introductions involving human activities is important. Exotic, alien, transplanted, introduced, nonindigenous, and invasive are words that have been used to describe plants and animals that were moved beyond their native ranges by humans. For consistency, we adopted the definition from the Nonindigenous Aquatic Nuisance Prevention and Control Act of 1990 (Public Law 101-646, 16 USC 4701-4741, approved 29 November 1990), which defines nonindigenous species as, "The condition of a species being moved beyond its natural range or natural zone of potential dispersal, including all domesticated and feral species and hybrids." This definition embodies the most critical biological aspect of nonindigenous species—the movement or introduction of a species beyond its native range by humans. Some resource managers have used political boundaries, such as state or national borders, as a standard to determine the status of an introduction (Shafland 1986); however, they did not consider that species moved beyond their native ranges within state boundaries or within the United States (for example, from the east coast to the west coast) as nonindigenous species. Regardless, ecosystems receiving nonindigenous introductions respond based on a suite of biological and ecological interactions irrespective of the political boundaries from which the species originated. Today, many biologists recognize that any species

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moved beyond its native range by human activities is a nonindigenous species, and they realize that when such an action is taken, it is hazardous to the economic and ecological foundations of the country (Office of Technology Assessment 1993).

Origin and Magnitude of the Nonindigenous Species Problem

Today, biologists estimate there are more than 6,500 species of established, self-sustaining populations of nonindigenous animals, plants, and microbes in the United States (Office of Technology Assessment 1993; U.S. Geological Survey, Gainesville, Florida, unpublished plant and fish data). Of this number, more than 6,271 are native to areas outside of the United States (Table 1). These numbers point to a serious problem and become alarming when one considers that some evidence indicates that 5%–10% of introduced species become established, and 2%–3% are able to expand their ranges (di Castri 1989). Equally alarming is the increasing number of introductions that result primarily from the increased movements of people, their transportation of products, and the reduced travel time between destinations, which allows more species to survive (Office of Technology Assessment 1993).

Table 1. Estimated number of established nonindigenous species in the United States. Numbers are minimum estimates, especially of species that are native to the United States (modified from Office of Technology Assessment 1993). INA = information not available.

	Species with origins outside United States	Species with origins within United States
Plants	3,723	INA
Terrestrial vertebrates	142	51
Insects and arachnids	>2,000	INA
Fishes	76	203
Mollusks (nonmarine)	91	INA
Plant pathogens	239	INA
Total	>6,271	254

This continued homogenization of the world's flora and fauna, which represents at least millions of years of separate evolutionary histories, is an ecological holocaust of major proportions. In examining the ecological interactions of invasive nonindigenous animals and plants with native biotic communities, the introductions of nonindigenous species seem tantamount to an ecological surprise attack. The invaded community does not recognize the nonindigenous species that arrived in its midst and often has few or no natural controls to prevent establishment of the invader. Evolution of biotic communities in the absence of ecological interactions with a particular introduced organism may result in reduced resistance to the invasive nonindigenous species.

An examination of the origin of nonindigenous species introductions helps us understand the problem. Nonindigenous species can be divided into three categories: intentional introductions, intentional introductions with subsequent escape, and unintentional introductions. Intentional introductions are those nonindigenous species transported beyond their native range and released into the wild with the purpose and intention that they will become established; these include the house sparrow and the common carp. Intentional introductions with subsequent escape are those nonindigenous species transported beyond their native range under captive conditions and which subsequently escape into the wild, where they may establish reproducing populations; these include aquarium fishes and the African clawed frog. Unintentional introductions are those nonindigenous species that are transported, usually unnoticed or without detection, beyond their native range in the course of some unrelated activity; these include zebra mussels in ballast water or imported red fire ants on cattle boats.

Recognition of these three categories is important for the analysis of pathways used by invasive nonindigenous species. Intentional introductions have been made for a variety of purposes such as ornamental plants, food crops, livestock, game, pets, and biological control. Subsequent to their establishment, some intentionally introduced organisms escaped or were released and became harmful pest species. Some of the most harmful nonindigenous plants, including kudzu, saltcedar, and water hyacinth, were intentional introductions that subsequently escaped from confinement. The common carp, European starling, and burro are examples of intentionally introduced animals that have harmed native biota (Office of Technology Assessment 1993).

Unlike most intentional introductions, which are chosen for a suite of desirable traits, unintentional introductions were not selected for beneficial characteristics. Pathways of unintentional introductions are varied and include agricultural products, cut flowers, timber, seeds, and potted plants. Other species that have been unintentionally introduced have sneaked in with packing materials, ballast water, military vehicles, and containerized freight. A review of 1,364 nonindigenous species revealed that only 22% of the intentional introductions were harmful, whereas 47% of the unintentional introductions were harmful. Evaluations of terrestrial vertebrates, fishes, and mollusks, however, revealed that harm from intentional and unintentional introductions was approximately equal (Office of Technology Assessment 1993; Fig. 1). For these groups, the criteria for the screening and evaluation process seem to have

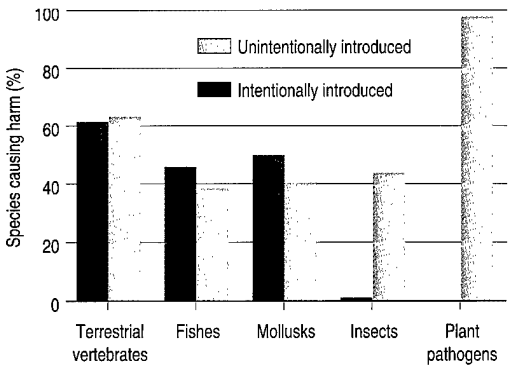

Fig. 1. Percentage of harmful effects by intentional and unintentional introductions (total for both of 1,364 species) of various groups of nonindigenous organisms (Office of Technology Assessment 1993).

been inadequate to determine the risk from these intentional introductions. Management of most intentional introductions is possible by legislation. Prevention of unintentional introductions requires stringent measures, however.

Attributes of Invading Species and Invaded Communities

Several questions are critically important for an understanding of invasive nonindigenous species and invaded communities. For example, do some characteristics make a species particularly subject to establishment and spread? Should some species cause more concern than others? Why is one ecological community more vulnerable to invasions than another community? Do rules exist by which the success or failure of a particular invasion may be predicted? Research is needed to answer such questions and to help us understand the phenomenon of species invasions, as well as to aid in the prevention or treatment of invasions.

Researchers generally agree that not all species are equally invasive and not all ecological communities are equally susceptible to being invaded (di Castri 1989). Although the ability of a particular nonindigenous species to successfully invade seems to be an individualistic phenomenon depending on the species and ecosystems, general patterns may aid in predicting the results of invasions. Not all introduced species succeed in becoming established. In fact, many fail, although failures are reported far less often than successes. Chance—or at least unknown factors—apparently plays a large role, because some intentional introductions failed several times before they succeeded (Office of Technology Assessment 1993). For example, most introductions of game birds into the United States—including seven species of pheasants, quails, and their relatives—failed initially and succeeded only under optimal circumstances (Pimm 1991). The European starling successfully colonized New York's Central Park in 1891, and then most of North America, only after several previous failed introductions (Long 1981).

Determining which nonindigenous species introductions may succeed or fail in a given situation requires a wealth of ecological knowledge about the organisms. For example, proposed introduction of a nonindigenous species should provide biological data indicating whether the species can tolerate the physical conditions of its new home, whether it can reproduce at its initial low densities, whether food in the new location is appropriate and plentiful, and whether predators, parasites, or pathogens will allow it to prosper.

Beyond these basic biological questions, though, are there species characteristics that lend themselves to greater likelihood of success as an invasive? That is, do successful invasive nonindigenous species tend to have certain characteristics in common that contribute to their success? In general, highly successful nonindigenous invaders seem to have one or more characteristics that further their establishment and expansions (Table 2). These, however, are merely generalizations, and exceptions are many. These characteristics do not guarantee that a particular nonindigenous invader will be highly successful, and the absence of most of the characteristics does not preclude the invasion of a species in a given circumstance. Also, different investigators focused on different characteristics depending on the taxonomic groups under investigation. For example, Ashton and Mitchell (1989) listed three significant factors for the success of invasive nonindigenous aquatic plants: vegetative reproduction, rapid rate of reproduction, and association with human activities that further expansion. Baker (1965:157) described a highly invasive nonindigenous plant (the *ideal* weed) as one which was "a plastic [i.e., adaptable] perennial which will germinate in a wide range of physical conditions, grows quickly, flowers early, is self-compatible, produces many seeds which disperse widely, reproduces vegetatively and is a good competitor." Lodge (1993) stated as general rules that most invasions fail, invaders with the highest probability of conspicuous success have a novel functional role such as top predator, and communities with a long history and a draw on a large species pool are most able to resist invasion.

Thus, many different perspectives pervade views of invasive nonindigenous species. In reference to the many rules of nonindigenous invaders that have been proposed, Brown (1989:86) stated that, "These rules are of limited utility in making specific predictions about the probability of establishment of a particular

Table 2. Some generalized characteristics of successful invasive nonindigenous species. The list is not exhaustive, and not every characteristic applies to each species in every case (modified from Ehrlich 1989; Lodge 1993; Meffe and Carroll 1994).

Characteristics of invaders
High rate of reproduction; pioneer species; short generation time
Long-lived
High dispersal rates
Single-parent reproduction (for example, a gravid or pregnant female can colonize)
Vegetative or clonal reproduction
High genetic variability
Phenotypic plasticity
Broad native range
Abundant in native range
Tolerant of wide range of conditions
Habitat generalist
Broad diet (polyphagous)
Gregarious
Human commensal

species in a certain region or habitat. This unpredictability is due to the uniqueness of species and places, which in turn is in large part a consequence of their distinct histories." The success of invasive nonindigenous species is highly variable, and predictability of invasions is limited in spite of well-established general patterns of invasions (Office of Technology Assessment 1993).

What are the characteristics of a community that is successfully invaded by plants or animals? Like species, ecological communities have characteristics that promote invasion by organisms (Table 3). One of the most important features that makes a community susceptible to invasion by nonindigenous species is the level of human-induced disturbance (Hobbs 1989). A disturbed state is a common feature of invaded communities and seems to provide opportunities for the invasion of many nonindigenous species. For example, the ability of nonindigenous fishes in the American Southwest to invade riverine ecosystems is greatly enhanced by disturbances stemming from dams, water diversions, destruction of riparian habitat, and other factors (Minckley and Deacon 1991). Few or no nonindigenous species reside in the few remaining free-flowing streams, and nonindigenous species that do colonize these streams are usually washed out of the stream by natural flooding (Meffe 1984; Minckley and Meffe 1987). Likewise, imported red fire ants are most successful in disturbed areas such as roadsides and agricultural fields and rarely penetrate intact, closed forests (Frank 1994). Similarly, kudzu invades from the disturbed edges of forests and from roadsides, where light availability is greater than in the interior forest (Schmitz 1994). Nonindigenous birds such as European starlings and house sparrows do well in disturbed areas such as cities, suburbs, and farms. In general, human disruptions of natural communities, such as by soil alterations, removal of vegetative cover, or suppression of natural disturbance regimes, seem to promote the invasion of a community by nonindigenous species. The invasion of intact communities may be more difficult.

The separation of the effects of disturbance from other features that allow or promote species invasions is difficult because of the absence of controls for comparisons with the disturbed sites. Whether a disturbance or other factors promoted or permitted the colonization and expansion of a nonindigenous species often cannot be determined. Because most of the world is disturbed by humans, the question may be moot anyway. If disturbed ecosystems are indeed more likely to be invaded, then nearly the entire world is being made an easier target for invasive nonindigenous species. The presence of nonindigenous species is a disturbance that further alters an ecosystem, perhaps promoting colonization by still other nonindigenous species. For example, a nonindigenous grass that inhibits germination of native trees makes the community more vulnerable to invasion by other nonindigenous grasses. In turn, a disturbed ecosystem may offer better opportunities for nonindigenous, grass-eating insects, which further perturb the community, making invasion of other nonindigenous species more likely, and so on. Disturbance and nonindigenous species interact in complicated ways, but usually to the detriment of native community structures.

Brown (1989) presented five rules of biological invasions that are broad generalizations about the conditions under which nonindigenous invasions may succeed (Table 4). These rules, he believed, are broadly applicable to vertebrates, invertebrates, and plants. Of vital importance among these rules is the ecological isolation of the invaded habitat, which seems to be critical to its vulnerability to invasion by nonindigenous species. It also helps if the physical characteristics of the new environment are similar to those in the native environment of the invasive nonindigenous species and if other species are not present in similar niches of the invaded habitat. Finally, disturbance and close association with humans are common characteristics of a community that is vulnerable to invasion by nonindigenous organisms.

Do the same rules apply to terrestrial and aquatic nonindigenous species, or do the ecosystems function differently? Differences in the modes or patterns of invasion of terrestrial and aquatic ecosystems by nonindigenous species are not consistent. The general characteristics of a successful invader or a community that is vulnerable to invasion by nonindigenous species exist regardless of the nature of the community. For example, single-parent reproduction is as advantageous in colonizing a new habitat for a pregnant rodent or lizard as it is for a pregnant livebearing fish in a new lake. High dispersal rates and broad diets are advantageous on land or in water, as are high rates of reproduction once colonization is realized. Likewise, characteristics of communities that are vulnerable to invasion by nonindigenous species are equally beneficial to the invaders on land and in

Table 3. Generalized characteristics of communities more likely to be invaded by nonindigenous species (from Meffe and Carroll 1994; modified from Lodge 1993).

Characteristics of communities
Climatically similar to original habitat of invader
Early successional (recently disturbed)
Low diversity of native species
Absence of predators on invading species
Absence of native species morphologically (form or structure) or ecologically similar to the invader
Absence of predators or grazers in evolutionary history (naive prey)
Absence of fire in evolutionary history
Low-connectance food web
Disturbed by humans

Table 4. Five generalized rules for the potential success of a biological invasion (from Brown 1989).

	Generalized rules
Rule 1	Isolated environments with a low diversity of native species tend to be differentially susceptible to invasion
Rule 2	Species that are successful invaders tend to be native to continents and to extensive, nonisolated habitats within continents
Rule 3	Successful invasion is enhanced by similarity in the physical environment between the source and target areas
Rule 4	Invading nonindigenous species tend to be more successful when native species do not occupy similar niches
Rule 5	Species that inhabit disturbed environments and those with a history of close association with humans tend to be successful in invading human-modified habitats

water. For example, one would expect the absence of predators of the nonindigenous species or a low diversity of native species to equally promote invasion. Some disturbance events occur in only certain ecosystems, but the general rules (Tables 2, 3, and 4) apply to any type of ecosystem.

Loss of Biodiversity and Ecosystem Changes Due to Invasions

When biodiversity is defined to include only the genetic, species, and ecosystem diversity native to an area, then invasive nonindigenous taxa clearly degrade biodiversity. However, frequent inclusions of species from any place of origin render a misleading and inflated measure of biodiversity. Measurements of biodiversity should include only native species. When the addition of nonindigenous species causes losses of native species, it causes a net loss of biodiversity and a degradation of the ecosystem.

One of the major effects of invasive nonindigenous species on biodiversity is outright loss of native species (Nott et al. 1995); this is a common and repeated pattern after establishment of nonindigenous species occurs. Invasive nonindigenous species are known to have caused the extinction of at least 109 vertebrate species around the world (Cox 1993), a significant proportion of overall identified causes of extinction of vertebrates (Table 5). In Hawaii, nonindigenous species introduced as biological-control agents have been implicated in extinctions of 15 native (endemic) moth species (Howarth and Ramsay 1991). The unintentional introduction of the brown tree snake caused the extinction of five species or subspecies of birds on Guam and significant declines of many other species (Savidge 1987). In Arizona, a pupfish endemic to a single spring became extinct within 1 year when largemouth bass were introduced to its sole habitat (Minckley 1973).

Group	Human exploitation	Invading species	Habitat disruption	Other	Unknown
Mammals	24	20	19	1	36
Birds	11	22	20	2	37
Reptiles	32	42	5	–	21
Fishes	3	25	29	3	40
Total number	**70**	**109**	**73**	**6**	**134**
Total % of known causes	27.1	42.3	28.3	2.3	–

Table 5. Major known causes of vertebrate extinctions around the world (modified from Cox 1993).

Island species tend to be especially vulnerable to the effects of nonindigenous species. A review of worldwide animal extinctions since 1600 revealed that 75% were island species (Groombridge 1992). Hawaii and other Pacific Islands are infamous for their endemic species that have been driven to extinction by colonization of nonindigenous species (Office of Technology Assessment 1993). The nation's highest rate of nonindigenous species' invasions and native species' extinctions is in the Hawaiian Islands (see chapter on Pacific Islands). Hawaii receives more nonindigenous species annually than any other state and has the highest proportion of established nonindigenous species in the wild, the highest concentration of threatened and endangered species, and the highest number of extinct species (Office of Technology Assessment 1993).

Evolution in isolation has produced the high rate of endemism of island species and also has resulted in especially "naive" faunas and floras, that is, species that have not historically had to cope with many types of competitors or predators. These species are especially susceptible to the effects of invading nonindigenous species. Consequently, two-thirds of all plants and birds that have become extinct in the United States were from Hawaii (Opler 1976; Vitousek et al.

American Chestnut Blight

At the end of the nineteenth century, the American chestnut was a major component of eastern deciduous forests from Maine to Georgia and west to Illinois, in some places constituting more than 40% of overstory trees (Krebs 1985). Early in the twentieth century, chestnut blight, a nonindigenous fungal disease from Asia, broke out near New York City and quickly spread and infected almost all American chestnuts on the continent, driving the species to ecological extinction. American chestnuts now exist only as scattered small trees that become infected and die as they mature.

Because the American chestnut was such a prominent component of eastern deciduous forests, the nonindigenous fungal disease has had far-reaching effects. Although no vertebrates became extinct because of the loss of American chestnuts, seven moth species fed exclusively on American chestnuts and are now extinct (Opler 1978). Another 49 moth species also feed on American chestnuts, but because of broader diets, they are able to feed on related trees and shrubs, including the introduced Chinese chestnut. The structure of the forests significantly changed because of the blight, and other tree species became dominant.

See end of chapter for references

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1987). The Hawaiian Islands have lost more than 50% of their native bird species, 50% of their plants, and 90% of their native land snails. Many of these extinctions are directly or indirectly due to nonindigenous species (Scott 1995).

An invasive nonindigenous species need not drive native species to extinction to have serious effects on the ecosystem (see box on American Chestnut Blight). Other effects include general decline in abundance of native species, change in ecosystem structure and function, and rearrangement of trophic relations.

Some invaders displace native species. For example, several nonindigenous grasses in the American West suppress the seedlings of oaks, pines, and other native species. In Arizona, at least 10 native plant species declined in abundance because of the spread of African lovegrass (D'Antonio and Vitousek 1992). Other invaders change basic ecosystem structure or dynamics. For example, zebra mussels decrease food availability for other filter feeders and increase light penetration by rapidly filtering and removing particles from water (Britton 1991). The Australian melaleuca tree has modified soil characteristics and topography of large areas of the Florida Everglades, displacing native vegetation and changing habitat structure for native wildlife (Schmitz 1994; Figs. 2 and 3). Saltcedar has similarly altered riparian ecosystem structure and water-flow patterns in desert streams of the southwestern Great Plains and Southwest (Loope and Sanchez 1988). Feral hogs throughout the Southeast, California, Hawaii, and the Great Smoky Mountains National Park trample, uproot, and destroy native vegetation, changing understory structure and displacing leaf litter and soil organisms (Peine and Farmer 1990). Aquatic equivalents are the grass carp and common carp, which destroy aquatic vegetation, increase water turbidity, and destroy habitat for smaller fishes (Moyle et al. 1986). The list could go on and on.

In some cases, the effects of an invasive nonindigenous species have cascaded throughout an ecosystem's food web. One of the best-known examples is the introduction of opossum shrimp into Flathead Lake, Montana. Heavy feeding by shrimp caused populations of zooplankton to drop, which in turn greatly reduced populations of forage fishes, which caused declines in predators such as bald eagles, river otters, bears, and coyotes (Spencer et al. 1991). Overall, harmful effects generally outweigh any beneficial effects of invasive nonindigenous species in the United States (Fig. 4).

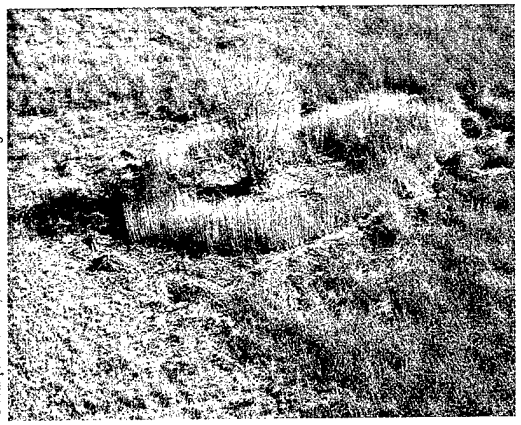

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Fig. 2. Melaleuca seedlings encircle a dead adult Australian melaleuca tree. After the adult tree in the middle of the picture was treated with herbicides, the stressed tree released seeds, illustrating the difficulty of controlling exotic species.

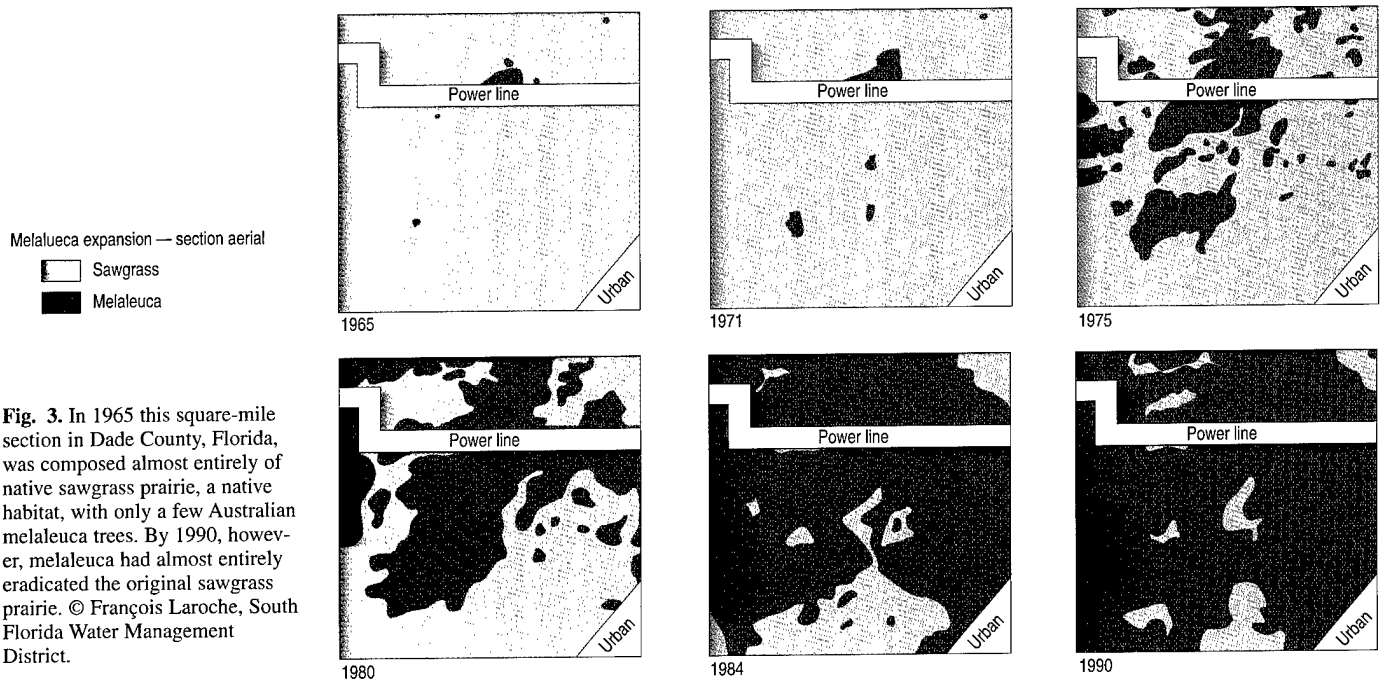

Fig. 3. In 1965 this square-mile section in Dade County, Florida, was composed almost entirely of native sawgrass prairie, a native habitat, with only a few Australian melaleuca trees. By 1990, however, melaleuca had almost entirely eradicated the original sawgrass prairie. © François Laroche, South Florida Water Management District.

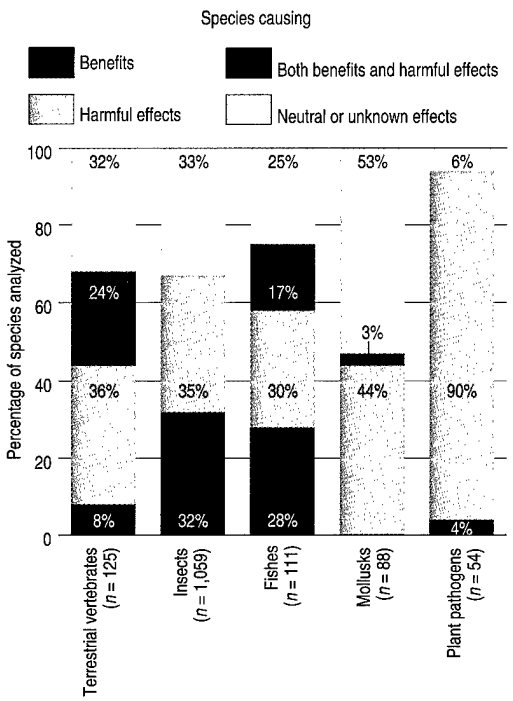

Fig. 4. Percentage of nonindigenous species that cause beneficial, harmful, both beneficial and harmful, and neutral or unknown effects (Office of Technology Assessment 1993).

Threats to Parks and Endangered Biota

Federal parks and natural areas account for about 3% of the total land area of the United States. An additional 27% of the land is managed by federal agencies such as the U.S. Bureau of Land Management, the U.S. Forest Service, the U.S. Fish and Wildlife Service, and the Department of Defense for a variety of purposes, but most land remains largely in an undeveloped state. While lands in public ownership are critical to efforts to maintain biodiversity, all suffer, to varying degrees, from invasive nonindigenous species. The National Park Service manages its lands with an aggressive policy to control or remove existing nonindigenous species and prohibit establishment of new invaders. This policy extends to management of invasive nonindigenous species adjacent to park lands with the consent of private land owners. Parks frequently exist as islands of natural communities surrounded by a sea of disturbance, providing invasive nonindigenous species with excellent opportunities to move into protected areas.

Still, the number of nonindigenous species in national parks is increasing to the point that removal and control cannot keep pace with new invasions (Office of Technology Assessment 1993). Most problems from invasive nonindigenous species in parks involve nonindigenous plants, which is not surprising because more than half of all nonindigenous species in the United States are plants. The large number of nonindigenous plants in each state (Fig. 5) is indicative of the problem in parks.

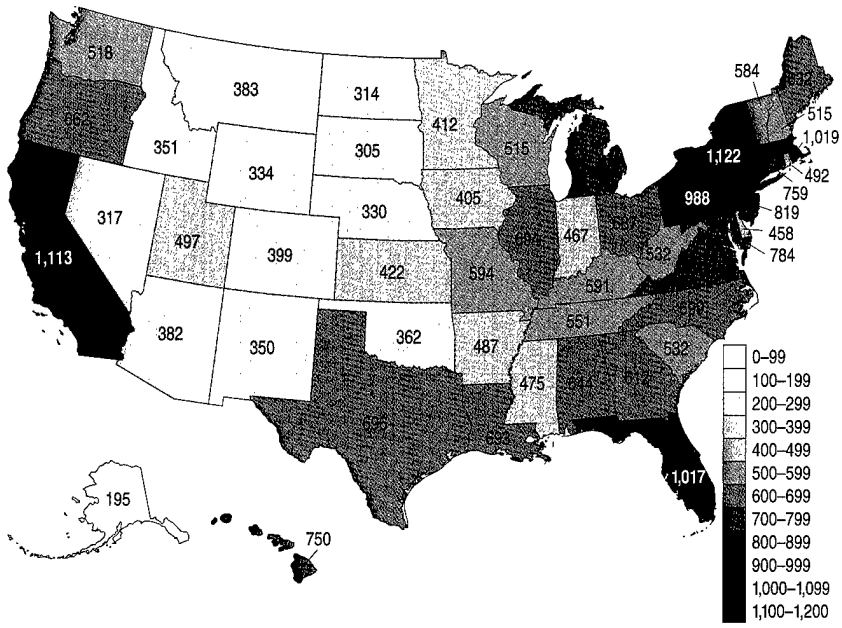

Fig. 5. Number of nonindigenous plant species (from outside the United States) introduced into each state (data on number of native and introduced species from a phytogeographic data summary in preparation by J. T. Kartesz, Biota of North America Program of the North Carolina Botanical Garden, Raleigh).

Nonindigenous species are a major threat to endangered and threatened biota. Invasive nonindigenous plants and animals should be treated as biological pollutants that can, in the presence of physical habitat alteration or chemical pollution, push native biota to or past the brink of extinction. In some environments, the association of nonindigenous species and disturbed habitat makes the evaluation of the effects of invaders on threatened biota difficult to assess. There is no question, though, that invasive nonindigenous species represent an additional stress to threatened biota.

Nonindigenous species do contribute to a significant proportion of listings of threatened and endangered species in the United States; about 315 native species and subspecies listings are attributed, at least in part, to nonindigenous species (Fig. 6). Based on U.S. Fish and Wildlife Service Federal Register listing documents for endangered and threatened species, nonindigenous species have contributed to the decline of approximately 35% of listed taxa. One-third of the 35% of the listed taxa affected

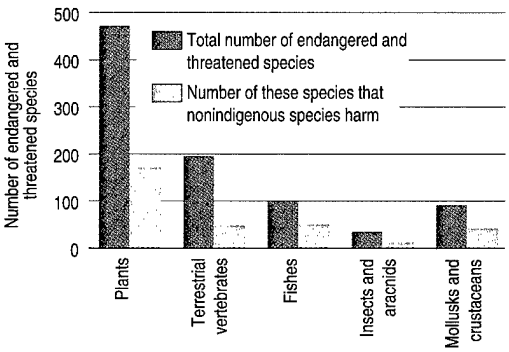

Fig. 6. Number of United States species listed under provisions of the U.S. Endangered Species Act of 1973 (U.S. Fish and Wildlife Service 1994) whose status is attributed to threats from nonindigenous species (Office of Technology Assessment 1993; updated by present authors through 1995).

Eastern and Western Mosquitofishes

The eastern and western mosquitofishes are small, harmless-looking, guppylike fishes native to rivers, ponds, lakes, and springs of the United States from New Jersey south through the Atlantic Coastal Plain, up the Mississippi River to Illinois, and west to Texas. These fishes were purposely introduced throughout the world in the mistaken belief that they control mosquitoes better than native, larvae-eating fishes (Courtenay and Meffe 1989).

Almost everywhere, introduced mosquitofishes have harmed aquatic ecosystems and faunas because of their highly predaceous habits, and they have reduced or eliminated populations of at least 20 other species of fish, including largemouth bass (Schoenherr 1981) and numerous invertebrate species. They have been especially devastating in the American Southwest, where they interact with a wide range of endangered and threatened native fishes, most notably the Gila topminnow. The topminnow was formerly the most abundant fish in the southern half of Arizona but is now endangered, with only 13 remaining natural populations (Meffe et al. 1983). One of the major reasons for the decline of the Gila topminnow is predation by nonindigenous mosquitofishes, which prey on juvenile topminnows, harass adults (Meffe 1985), and swarm through whatever stabilized habitat they colonize. Mosquitofishes also reduce or eliminate endangered pupfishes and springfishes in Arizona, California, and Nevada (Minckley et al. 1991). Mosquitofishes are difficult to eliminate once established (Meffe 1983; Marsh and Minckley 1990), and the best way to reduce their effects is to control their further spread. One of the main avenues of spread is continued, intentional release by mosquito-control agencies.

See end of chapter for references

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by nonindigenous species are from island ecosystems, primarily Hawaii and Puerto Rico. Although island taxa seem to be more susceptible to the adverse effects of nonindigenous species, the mainland biota is far from immune.

Freshwater ecosystems are similar to islands because they are surrounded by land. Aquatic organisms, like island species, are especially vulnerable to the effects of nonindigenous species—in fresh water such effects have been magnified by widespread habitat disturbance.

One hundred fishes were on the U.S. Fish and Wildlife Service list of endangered and threatened species as of 20 August 1994; nonindigenous species contributed to the decline of 49. Of the 30 extinct fishes in the United States, nonindigenous species were a factor in the extinction process of 24. Nonindigenous species involved in the extinction of fishes included the parasitic sea lamprey, mosquitofish (see box on Eastern and Western Mosquitofishes), trouts, sunfishes, and basses. The mechanism of extinction varied from predation and competition for food and space to genetic swamping through hybridization (Miller et al. 1989).

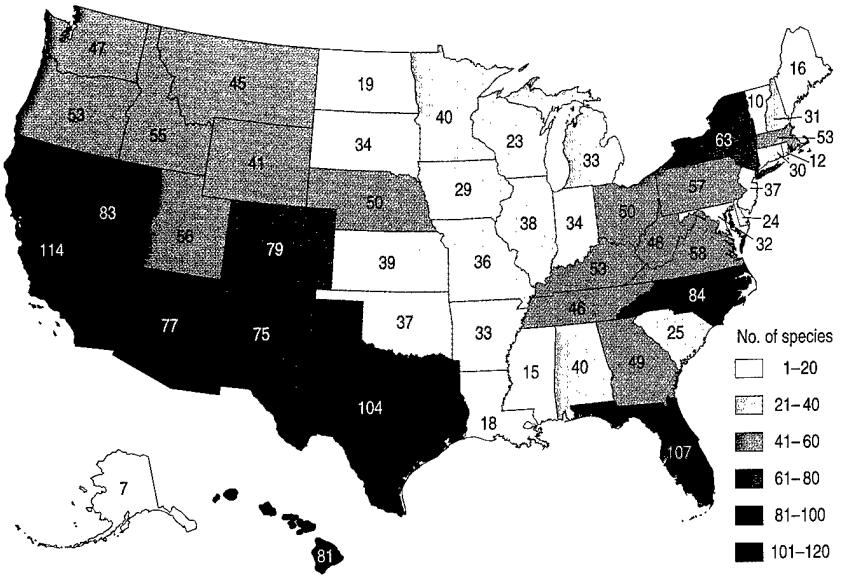

Fig. 7. Number of nonindigenous fish species introduced into inland waters of the United States, 1850–1995 (data are from the U.S. Geological Survey, Florida Caribbean Science Center, Gainesville, Florida, March 1995).

The effects of nonindigenous fishes on endangered species and aquatic biodiversity will probably significantly increase during the next 25 years because of the drastic increase in introduced fishes during the past 45 years. Analysis of more than 12,000 records of introduced fishes reveals that between 1831, the date of the first known release of nonindigenous fishes, and 1950, a period of 120 years, fewer than 117 known fish species were introduced. Between 1950 and 1995, a span of only 45 years, more than 458 additional fish species were introduced. Introductions of nonindigenous fishes were made in all states, but were most numerous in California, Florida, Hawaii, Colorado, and Texas (Fig. 7).

Nonindigenous fishes originate from a variety of locations. Intentional introductions have been made by management agencies as part of game or forage fish stocking. In addition, many game fishes were illegally stocked by well-intentioned but misguided anglers (U.S. Geological Survey, Florida Caribbean Science Center, Nonindigenous Fishes Database,

Gainesville, Florida). Several species, such as grass carp, were widely introduced for biological control of aquatic plants, many of which were also introduced (Schmitz 1994). Aquarium fishes represent another group of nonindigenous fishes that are now found in many habitats. Although many of these fishes escaped from fish-culture facilities, more were released by aquarists (Fig. 8). The tropical origin of most aquarium fishes limited their distribution to the extreme southern portion of the nation or to thermal springs in colder areas (Courtenay et al. 1984).

Native fishes throughout the desert Southwest are in serious jeopardy from nonindigenous fishes (Minckley and Deacon 1991; also see Southwest chapter). This region, characterized by low native fish richness and high endemism, has received the most fish introductions and suffered the greatest loss of native fishes. Species such as the bonytail chub and razorback sucker, which inhabit large rivers in the Colorado River basin, and the Sonoran topminnow and several pupfishes and springfishes, inhabitants of small desert springs, are directly threatened by numerous predaceous nonindigenous fishes.

Of the approximately 300 freshwater mussels found in the United States, about 73% are considered imperiled (Williams et al. 1993). Scientists believe that two nonindigenous bivalve mollusks, Asian clams and zebra mussels, have contributed to the decline of native mussels (Ricciardi et al. 1995). Asian clams, the most widespread nonindigenous mollusks in the United States, entered the west coast in the 1930's and invaded the southeastern United States in the 1950's (McMahon 1983). In some areas, Asian clams carpet stream bottoms, reaching densities of several thousand individuals per square meter (J. D. Williams, U.S. Geological Survey, Florida Caribbean Science Center, Gainesville, Florida, personal observations).

Nonindigenous plants also threaten endangered species; for example, the endangered snail kite has difficulty feeding when its waters are covered by invasive nonindigenous plants such as water hyacinth (Sykes 1987), and the nesting of endangered sea turtles is hampered by growth of Australian-pines (National Research Council 1990).

Economic Consequences of Successful Nonindigenous Species

Examples of the economic cost of introductions of nonindigenous species can be found in every state and in a wide range of terrestrial, freshwater, and saltwater habitats. Of the more than 6,500 nonindigenous taxa in the United States, about 15% are considered economically or ecologically harmful. In the United States, documented economic losses from only 79 taxa during this century are estimated conservatively at $97 billion, and this figure does not include many costly agricultural weeds with little or no economic loss data (Office of Technology Assessment 1993).

The thousands of established nonindigenous species in the United States that are not known to have caused ecological and economic damage to date should not be viewed as benign biota but as potential biological time bombs. For example, purple loosestrife existed in low numbers for more than a century before populations exploded, displacing valuable native wetland plants. Every year, more than 190,000 hectares of wetlands are taken over by this invasive nonindigenous plant (Thompson et al. 1987). Purple loosestrife is typical of nonindigenous species that eventually become an economic liability after existing at low population levels or in geographically limited areas for decades and then undergoing explosive growth and expansion of range.

One of the most costly unintentional introductions, the zebra mussel, arrived in United States waters via ballast water of cargo ships. Since its detection in the Great Lakes in 1988, the zebra mussel has already caused economic damage to Great Lakes industries. The anticipated costs to the power industry during the next 10 years exceed $3 billion (Office of Technology Assessment 1993). The assignment of a cost in dollars to the severe alteration of aquatic ecosystem structure and function and the local extirpation of native species is more difficult, however. The economic cost of species extinction and ecosystem alteration is generally not included in the cost of invasive nonindigenous species unless a commercial commodity is lost. Also, loss of nonconsumptive uses of a resource is usually not included in the cost of nonindigenous species. For example, if a forest is destroyed by a nonindigenous insect or pathogen, the damage to timber is calculated in assessing cost, but the loss of nonconsumptive uses of forests—hiking, camping, bird watching, photography—is usually ignored.

Beyond direct economic cost from the loss of a product, human health is at risk from some nonindigenous species. Imported red fire ants, an unintentional introduction, arrived in the southern United States at Mobile, Alabama, in dry ship ballast, in the early 1940's (Office of Technology Assessment 1993). Fire ant stings are painful and can produce a severe allergic reaction that requires hospitalization and which is sometimes fatal (Fig. 9). Some nonindigenous plants also present health hazards; for

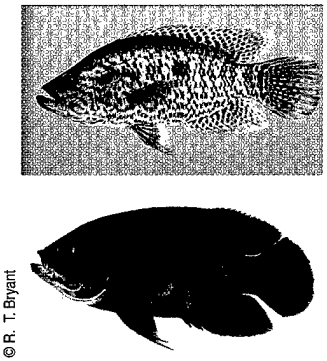

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Fig. 8. The jaguar guapote (top) and the oscar are two nonindigenous fish species that were either released by aquarists or escaped from aquarists into Florida waters. The jaguar guapote is likely to spread while the oscar, now considered a game fish, has already spread throughout southern Florida (U.S. Geological Survey, Florida Caribbean Science Center, unpublished information).

Courtesy U.S. Department of Agriculture

Fig. 9. Reaction to imported red fire ant stings on the arm of a teenager.

© L. Mytinger-Tyson, University of Florida

Fig. 10. Brazilian pepper, a nonindigenous pest species in south and central Florida, has multistem growth habits (top); its flowering (center) and fruiting foliage (bottom) cause skin irritation and respiratory problems in many people.

example, Brazilian pepper (Fig. 10) produces allergens that cause contact dermatitis and respiratory difficulty in many people. Likewise, the blood fluke planorb, an introduced aquatic snail, which is established in Florida and Texas, is the required intermediate host for human blood flukes that cause the debilitating disease schistosomiasis (Office of Technology Assessment 1993). If blood-fluke disease becomes established in the United States, it will be a major human health problem in Florida and Texas where the intermediate host snail became established.

Africanized honey bees also represent a threat to human health and the economy in the southern United States (Frank 1994). Queens of African honey bees were brought from Africa to Brazil in 1956 to increase commercial honey production. Since their initial introduction, these honey bees have spread north through Central America and Mexico; they invaded Texas by 1990 and Arizona by 1993. More than 2,000 human deaths and immeasurable loss of livestock, especially horses, have been attributed to stings of Africanized honey bees since their introduction into Brazil. In Texas, more than 200 serious stinging incidents and one death have been reported since 1990 (Frank 1994). Economic threats from the aggressive Africanized honey bees will come from their effects on tourism and agriculture. The most severe economic impact is expected in Florida, where Africanized honey bees are expected to occupy the entire state (Frank 1994).

Beekeepers have found that management of Africanized honey-bee colonies is more difficult because of several traits, most notably extremely defensive stinging. This resulted in serious setbacks of the beekeeping industry as the Africanized honey bees spread north through Brazil and Central America. In the United States, Africanized honey bees are expected to compete for food and to hybridize with the managed European honey bee. Managed European honey bees are an important agricultural commodity, used nationwide for crop pollination, at an estimated annual value of $9 to $19 billion. The estimated value of crops in Florida that depend on honey-bee pollination is $1.5 billion. Each year, thousands of Florida honey-bee colonies are shipped as far as Maine and North Dakota to pollinate crops (Frank 1994).

Federal Laws About Invasive Nonindigenous Species

Before the early 1900's, there were no laws concerning nonindigenous species, and decisions about these introductions were made by individuals or agencies with little or no examination of their possible effects. After experiencing the economic and ecological damage of some early introductions, federal legislation (Table 6) requiring more formal review obviously was required to prevent future problems. Federal legislators sought to improve the screening of introductions, but the patchwork of laws has numerous gaps. Federal laws (Library of Congress 1972; Office of Technology Assessment 1993) generally address specific incidents, providing a remedy for only a small fraction of the problem. Although these laws have prevented some ill-conceived intentional and unintentional introductions, the process is imperfect and represents little more than a token response to the problem.

Federal laws (Library of Congress 1972) for formal review with structured methods—for example, protocol and decision models, economic benefit–cost analysis, and risk assessment—are needed for screening nonindigenous species, including biological-control agents, before introduction. Although protocols exist for the evaluation of intentional introductions of some groups of organisms, these lack enforceability except when adopted by law, which is rarely the case (Welcomme 1986; Carlton 1989). For example, a protocol and decision model for evaluating proposed introductions of fishes was proposed by Kohler and Stanley (1984) and further refined by Kohler and Courtenay (1986). This model consists of five levels of review, each level requiring a more stringent evaluation of the proposed fish introduction. Although this model was adopted by the American Fisheries Society, it has been used rarely (perhaps fewer than five times) during the past 20 years and is not required by any state or federal law.

Future Direction of the Nonindigenous Species Issue

To meet the challenge of established nonindigenous species and future introductions of nonindigenous species requires policy development, enforcement, education, and research. The most critical need is in the area of policy development and enforcement, supported by aggressive public awareness and educational campaigns. Public awareness of the ecological, economic, and health risks from nonindigenous species is essential to successful implementation of policy and enforcement.

Existing legislation on nonindigenous species is fragmented, reductionist, and lacks comprehensive coverage and policy philosophy. Research is needed into how best to develop a policy, what it should look like, and how it

could be enforced. At this point, prevention of further introductions of invasive nonindigenous species is unquestionably the most prudent policy, one that could save billions of dollars in damage as well as prevent extensive perturbations to native ecosystems and endangered species. How such policy should be framed remains to be seen, but it needs to be developed by interdisciplinary thinkers who understand potential biological, social, and economic problems and limitations.

Research should also be conducted on ecosystem effects of invasive nonindigenous species, as well as on economic fallout from ecosystem changes. Humans receive many free ecosystem services from nature, such as pollination of agricultural crops, development and protection of soils, oxygen production and purification of air, water filtration, coastal protection by wetlands, and production of food resources in estuaries. How these services have been affected by invasive nonindigenous species is largely undocumented, as is how the services will continue in the face of disruptions by invasive nonindigenous species.

Implementation of a nonindigenous species policy demands a firm scientific basis, which will require the acquisition of information not currently available. Our knowledge of biology, physiology, ecology, and behavior of most nonindigenous species is rudimentary at best. Compilation and analysis of information on chronology of introductions, their pathways, and their rates and modes of dispersal are essential to the development of policy for nonindigenous species. Research in these areas is critical to understanding the nature of biological invasions and how to prevent or limit their effects.

Table 6. Federal laws prohibiting or restricting introduction and movement of nonindigenous species.

Federal laws	
Lacy Act (1900)	Strengthens and supports state wildlife conservation laws and promotes agricultural and horticultural interests by prohibiting importation of injurious wildlife
Plant Quarantine Act (1912)	Regulates imports or interstate shipments of plants or their parts and propagules to prevent introduction of plant diseases and insect pests
National Park Service Organic Act (1916)	Promotes the eradication and control of nonindigenous species and prohibits most introductions in national parks
Federal Seed Act (1939)	Authorizes U.S. Department of Agriculture to set standards for seed purity and to reduce the interstate movement and importation of nonindigenous plants
Public Health Services Act (1944)	Regulates entry of living organisms that may carry or cause human diseases
Federal Insecticide, Fungicide and Rodenticide Act (1947)	Controls movement of nonindigenous microbes into and through the United States
Importation of Certain Mollusks (1951)	Provides for the inspection and treatment of goods entering the United States from areas infested with any terrestrial or freshwater mollusks to control entry of such organisms
Department of Agriculture Organic Act (1956)	Animal and Plant Health Inspection Service is authorized to conduct an eradication program in countries adjacent to or near the United States
Federal Plant Pest Act (1957)	Restricts agricultural pests (pathogens, noxious weeds, animal and plant pests) from importation and interstate movements
Federal Noxious Weed Act (1974)	Provides program support to control undesirable plants on federal lands
Executive Order 11987 Exotic Organisms (1977)	Restricts the introduction of exotic species into natural ecosystems under federal agency authority
Cooperative Forestry Assistance Act (1978)	U.S. Forest Service is responsible for detecting, identifying, surveying, and controlling forest pests
Agricultural Quarantine Enforcement Act (1989)	Prohibits shipping of plants, fruits, and vegetables via first-class mail
Food, Agriculture, Conservation and Trade Act (1990)	Genetic Resources Program—purpose is to collect, classify, preserve, and disseminate genetic material important to agriculture
Great Lakes Fish and Wildlife Restoration Act (1990)	Controls the sea lamprey
Toxic Substances Control Act (1990)	Enables the Environmental Protection Agency to regulate nonindigenous microbes
Nonindigenous Aquatic Nuisance Prevention and Control Act (1990)	Controls and reduces the spread of aquatic pest species

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Environmental Contaminants

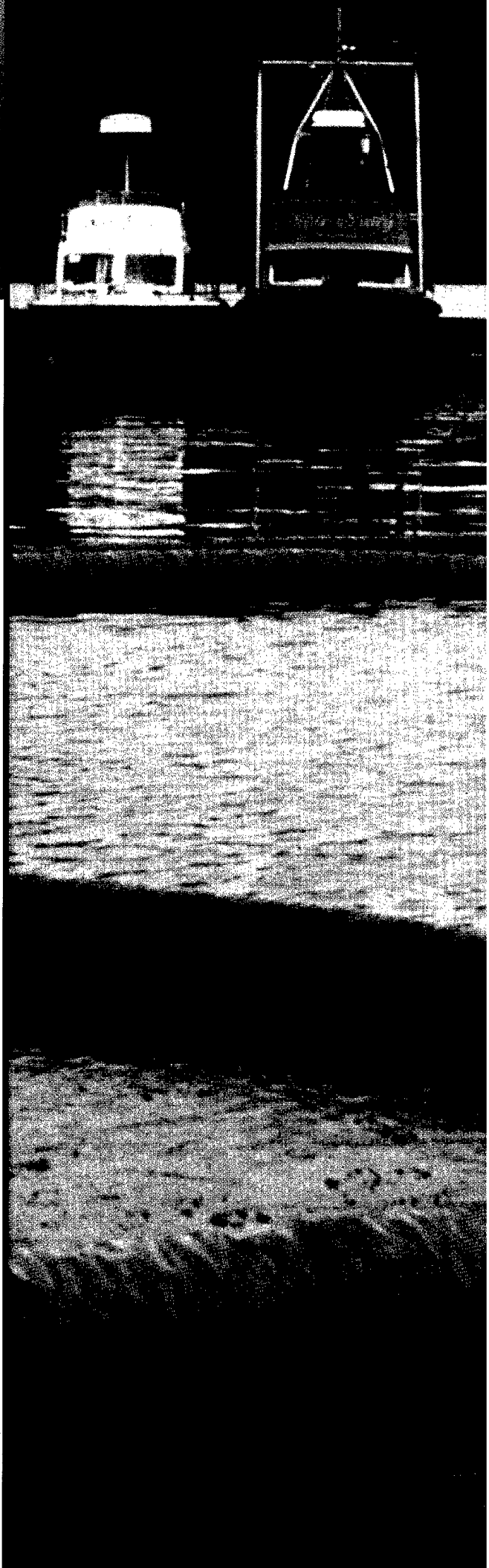
Chemical contamination of the environment is a pervasive, insidious side effect of human population growth and technological development. Unlike many other environmental stressors, casual observers often become aware of chemical pollutants only after some catastrophic event, such as an oil or chemical spill that kills many animals. Typically, chemical discharges that can be seen or smelled—or barren mine spoils (Fig. 1) and fishless streams—call attention to chemical pollutants. More commonly, sophisticated instruments are needed to detect toxic chemicals.

The effects of chemical contaminants on individual organisms, populations, and ecosystems may also be difficult to detect. The imperceptible accumulation of DDT (Table 1) and its metabolites in bald eagles and other predatory birds led to eggshell thinning, reproductive failure, and, ultimately, greatly reduced populations over much of North America (for example, Carson 1962; Colborn 1991; Wiemeyer et al. 1993). Much of this happened before the problem was understood sufficiently to take the steps necessary to correct it; populations of bald eagles are now recovering (U.S. Fish and Wildlife Service 1994).

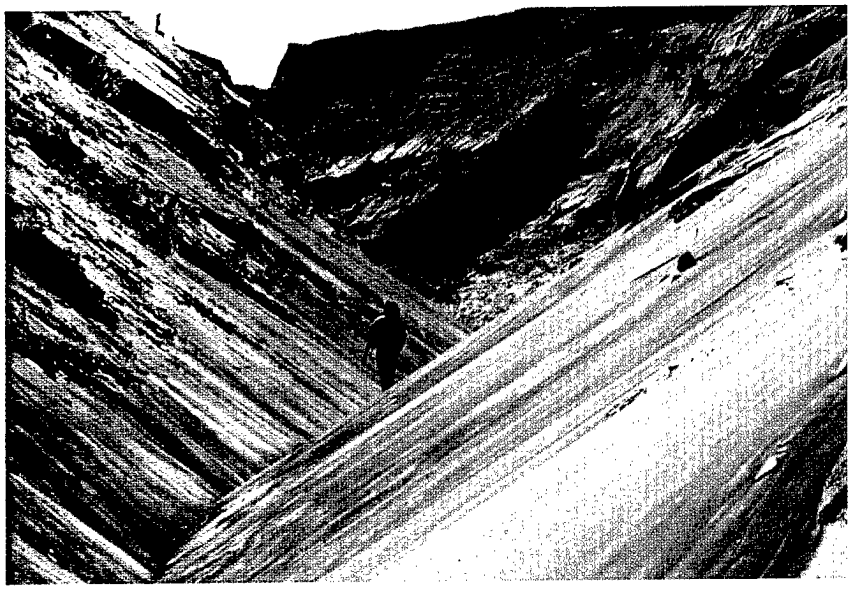
Effects of other contaminants on less visible species may be more subtle and localized. In addition to killing plants and animals, contaminants may reduce growth and reproduction or cause animals to avoid contaminated areas or to become more vulnerable to predators. The effects of chemical contaminants may also be masked by the more obvious effects of human population growth and technological development with which chemicals often co-occur. Sedimentation occurs in mined areas (Fig. 1); pesticides accompany sediments, nutrients, salts, and physical habitat changes as a consequence of intensive mechanized agriculture; and industrial chemicals, petroleum, pesticides, sewage, and combustion products accompany manufacturing, commerce, and urban growth.

Contaminants may be transported long distances in air and water, be modified in form and toxicity on release into the environment, and cause ecological injury far from their original sources. The resiliency of biological systems at all levels of organization—from subcellular through organism, population, and ecosystem—may also mask the effects of chemicals.

Environmental contaminants are generally perceived as a twentieth-century problem. Although this is true for synthetic organic chemicals, some of our most ecologically significant contaminant problems derive from the historical use of older technologies. Other contaminant problems existed for decades until technology and knowledge advanced sufficiently to detect and understand them. Some—including those resulting from mining, irrigation, and energy extraction—represent the accumulation of naturally occurring substances to harmful concentrations as a result of human-induced acceleration of natural weathering processes. In this chapter, it is not possible to discuss the thousands of potentially toxic substances released to the environment nor to evaluate their individual and combined effects on U.S. biota. Instead, I will present a historical overview of those human activities from which contaminant releases have been most significant—mineral and energy exploitation, agriculture, and industrial and urban growth. I also summarize the extent to which the ecological effects of the releases are known, and I present some information on future contaminant threats to biological diversity and some suggestions for where information is most needed.



Courtesy M. Mac, USGS



Courtesy C. Schmitt, USGS

Fig. 1. Mine tailings from historical lead mining near Desloge, Missouri.

Mineral and Energy Exploitation

The extraction and processing of minerals and fossil fuels have had widespread environmental consequences. Mining, drilling, smelting, refining, and other technologies associated with the extraction and exploitation of minerals and fossil fuels produce toxic by-products that can be released into the environment and transported long distances. Mineral and energy extraction activities also physically disrupt habitats and ecosystems.

Nonferrous Metals

Obtaining metals from ores requires separating the sought-after materials from the host rock and other minerals in the ore, a process that generates large quantities of wastes: noncoal-mining wastes in the United States totaled 50 billion metric tons in 1985 and were accumulating at an estimated 1.3 billion metric tons per year (U.S. Environmental Protection Agency 1985). Ores vary, but metal carbonates, oxides, and sulfides constitute the majority of commercially exploitable U.S. mineral deposits. Of these, the mining of sulfide minerals—which constitute important copper, nickel, lead, zinc, and silver deposits—has been the most environmentally significant. In the process of extracting metals, sulfur is oxidized and lost to the atmosphere as SO_2, which reacts with water and other atmospheric constituents to produce sulfuric acid. Therefore, smelters contribute substantially to acid precipitation. Because most ores are mixtures of minerals, potentially toxic elements other than the sought-after metals—including arsenic, cadmium, and mercury—may also be present and released into the environment. Following extraction—which varies in efficiency but is never complete—the natural oxidation of metal sulfides remaining in the solid wastes can produce acidic, metals-rich leachates, which may contaminate surface- and groundwaters. In addition to toxins, the large volumes of solid waste generated by mining and milling may also cause environmental problems (Fig. 1).

The technology for extracting and purifying gold, silver, copper, lead, and other metals from sulfide ores was brought to the Western Hemisphere by Europeans. North American colonization and subsequent westward expansion in the United States were stimulated first by the search for precious metals and later by the needs of industry. As the United States grew westward, new ore deposits were discovered and exploited. Although extraction efficiency also improved, the nineteenth and twentieth centuries brought tremendous increases in scale to the mining industry through the advent of steam, internal combustion, and electric power. The basic methods for extracting metals, though, continued to rely largely on mechanical separation, gravity, water, and heat. Consequently, the increasingly large quantities of toxic metals and by-products released into the environment left their marks on U.S. biota. No information on the cumulative effects of metals mining and refining on biota exists, but 557,650 abandoned mines in the United States are estimated to have contaminated 728 square kilometers of lakes and reservoirs and 19,000 kilometers of streams and rivers (Mining Policy Center 1994). Areas where toxic releases to the environment from mining and smelting have caused large-scale effects on United States biological diversity or have jeopardized particularly rare or valuable living resources are numerous; some examples are listed in Table 2.

In addition to the toxic releases generally associated with extracting metals from sulfide ores, gold and silver mining caused additional problems—placer and hydraulic mining and amalgamation with mercury. A placer is a sediment deposit from which gold and silver are mined; the sediments are dredged and washed in place. In hydraulic mining, water is pumped from a stream to wash the precious metals from surrounding banks and hillsides. Placer and hydraulic mining alter habitats and release metals, other toxins, and suspended solids directly into waterways. Aquatic plant, invertebrate, and fish production is generally reduced in placer-mined streams (Cordone and Kelley 1961; Lloyd et al. 1987). Both historical and ongoing instream mining still affect streams in California and Alaska (for example, Buhl and Hamilton 1990).

Table 1. Chemical names, common names, and acronyms of compounds mentioned in text.

Chemical name, common name, or acronym	Primary use(s)
Alachlor [Lasso® ; 2-chloro-2',6'-diethyl-N-(methoxymethyl)-acetanilide]	Herbicide
Aldrin (1,2,3,4,10,10-hexachloro-1,4,4a,5,8,8a-hexahydro-1,4:5,8-dimethanonaphthalene)	Organochlorine insecticide
Atrazine (Aatrex®; 2-chloro-4-ethylamino-6-isopropylamino-s-triazine)	Herbicide
Azinphos-methyl {O,O-dimethyl S[4-oxo-1,2,3-benzotriazin 3(4H)-methyl] phosphorodithioate}	Organophosphate insecticide
BHC (Benzene hexachloride; 1,2,3,4,5,6-hexachlorocyclohexane)	Organochlorine insecticide
Butylate (S-ethyl diisobutylthiocarbamate)	Carbamate insecticide
Carbofuran (Furadan®; 2,2-dimethyl-2,3-dihydro-7-benzofuranyl-N-carbamate)	Carbamate insecticide
Carbaryl (Sevin®; 1-naphthyl N-methylcarbamate)	Carbamate insecticide
CFC's (Chlorofluorocarbons, a family of gases comprising halons and freons)	Refrigerants, propellants, and fire supressants
Chlordane (1,2,4,5,6,7,8,8-octachloro-2,3,3a,4,7,7a-hexahydro-4,7-methanoindane, and other similar compounds)	Organochlorine insecticide
Chlorinated dibenzofurans (a family of compounds that are structurally and toxicologically similar to chlorinated dioxins)	Impurities; combustion products
Chlorinated dioxins (a family of structurally similar compounds, of which 2,3,7,8 tetrachloro-*p*-dibenzodioxin [TCDD; dioxin] is the most toxic)	Impurities; combustion products
Cyanazine [Bladex®; 2-chloro-4-(1-cyano-1-methylamino)-6-ethylamino-s-triazine]	Herbicide
2,4-D (2,4-dichlorophenoxyacetic acid)	Herbicide
2,4,5-T (Silvex®; 2,4,5-trichlorophenoxyacetic acid)	Herbicide
DDD {Rhothane®; TDE; [1,1-dichloro-2,2-bis(*p*-chlorophenyl) ethane]}	Organochlorine insecticide; DDT breakdown product
DDE [1,1-dichloro-2,2-bis(*p*-chlorophenyl)ethylene]	DDT breakdown product
DDT [1,1,1-trichloro-2,2-bis(*p*-chlorophenyl)ethane]	Organochlorine insecticide
Dicofol (Kelthane; 1,1-bis(chlorophenyl)-2,2,2-trichloroethanol]	Miticide
Dieldrin (1,2,3,4,10,10-hexachloro-6,7-epoxy-1,4,4a,5,6,7,8,8a-octahydro-1,4:5,8-dimethanonaphthalene)	Organochlorine insecticide; aldrin breakdown product
Endosulfan (6,7,8,9,10,10-hexachloro-1,5,5a,6,9,9a-hexahydro-6,9-methano-2,4,3-benzodioxathiepin 3-oxide)	Organochlorine insecticide
Endrin (1,2,3,4,10,10-hexachloro-6,7-epoxy-1,4,4a,5,6,7,8,8a-octahydro-1,4:5,8-dimethanonaphthalene)	Organochlorine insecticide; aldrin breakdown product
Fonofos (Dyfonate®; O-ethyl-S-phenylethylphosphonodithioate)	Organophosphate insecticide
Glyphosate [Roundup®; N-(phosphonomethyl)glycine, isopropylamine salt]	Herbicide
Heptachlor (1,4,5,6,7,8,8-octachloro-2,3,3a,4,7,7a-heptahydro-4,7-methanoindane)	Organochlorine insecticide; chlordane constituent
Hexachlorophene (2,2'-dihydroxy-3,3'5,5'6,6'-hexachlorodiphenylmethane)	Disinfectant
Kepone® (chlordecone; decachlorooctahydro-1,3,4-metheno-2H-cyclobuta(cd)pentalen-2-one)	Organochlorine insecticide
Methomyl {S-methyl-N-[(methylcarbamoyl)oxy] thioacetamide}	Carbamate insecticide
Methoxychlor [1,1,1-trichloro-2,2-bis(*p*-methoxyphenyl)ethane]	Organochlorine insecticide
Methyl parathion (O,O-dimethyl-O-4-nitrophenyl phosphorothioate)	Organophosphate insecticide
Metribuzin [4-amino-6-(1,1-dimethyl)-3-(methylthio)-1,2,4-triazin-5(4H)-one]	Herbicide
Metolachlor [2-chloro-N-(2-ethyl-6-methylphenyl)-N-(2-methoxy-1-methylethyl)acetamide]	Herbicide
Mirex [dodecachlorooctahydro-1,3,4-metheno-2H-cyclobuta(cd)-pentalene]	Organochlorine insecticide; fire retardant
PAH's (polycyclic aromatic hydrocarbons; a family of compounds—some of which are toxic and carcinogenic—containing primarily carbon and hydrogen)	Combustion products and petroleum constituents
PCB's (polychlorinated biphenyls of varying composition and toxicity)	Dielectric, heat transfer, and hydraulic fluids; lubricants; plasticizers; copy papers; extenders in many products
Pentachlorophenol (PCP)	Wood preservative
TCDD	(see chlorinated dioxins)
Terbufos {Counter®; S-[[(1,1-dimethylethyl)thio]methyl] O,O-diethyl phosphorodithioate}	Organophosphate insecticide
Toxaphene (chlorinated camphene mixture averaging 62% chlorine by weight)	Organochlorine insecticide
Trifluralin [Treflan®; 2,6-dinitro-N,N-dipropyl-4-(trifluoromethyl) benzenamine]	Herbicide
VOC's (volatile organic compounds—trichloroethylene, tetrachloroethylene, carbon tetrachloride, chloroform, chlorobenzenes and related compounds, and methylene chloride)	Solvents, cleaning agents, industrial feedstocks

Amalgamation is a process in which pure liquid mercury is used to separate particles of gold and silver from other materials, a practice that has led to mercury contamination in many areas of the West. For example, mining of the Comstock Lode in Nevada, which began before 1900, led to the release of substantial quantities of mercury to the Truckee-Carson River system (Richins and Risser 1975); this system comprises wetlands, lakes, and rivers important to fishes and migratory birds. Mercury from historical gold and silver mining remains evident in biota on both sides of the Sierra Nevada in California (Phillips 1987; Schmitt and Brumbaugh 1990; Hallock and Hallock 1993).

The second half of the twentieth century brought environmental regulation and improved extraction efficiency to the mining and metal refining industry. The incorporation of flotation processes employing organic reagents, for example, enhanced the efficiency with which metals are recovered from tailings, so wastes contain lower concentrations of leachable metals; SO_2 is recovered from smelter stack emissions, which reduces acid formation; and flue dusts containing metals are trapped and

recycled (Baker and Bhappu 1974). Collectively, these improvements result in less toxic and less widespread emissions.

Some reagents and by-products of the newer technologies also affect biota, however. The organic reagents can induce algal growth and alter invertebrate communities in receiving streams (Hardie et al. 1974). Sodium cyanide, used to extract precious metals, is highly toxic (Baker and Bhappu 1974; Eisler 1991). Accidental discharges of cyanide from tailings ponds and other facilities have caused massive and well-documented fish kills (for example, Leduc 1984). Cyanide-leach ponds at gold mines attract waterfowl and other wildlife and have caused numerous wildlife kills—some recently (Eisler 1991). Consequently, mines and smelters remain ecologically significant sources of pollutants despite recent improvements (Nriagu 1984; U.S. Environmental Protection Agency 1993).

Ferrous Metals and Coal

Commercially important iron deposits occur as oxides from which little sulfur is lost to the environment. Consequently, iron mining is not a major source of toxic contaminants. Of much greater environmental significance than the iron itself is the reducing agent necessary for its recovery. Carbon is supplied to reduce iron from the oxidized to the metallic state; either charcoal or coke—hardwood or coal, respectively, from which elements other than carbon have been driven by slow burning under restricted airflow—is typically used. In North America, iron and steel were made with charcoal until about 1840, when the eastern hardwood forests were exhausted. This coincided with the development of steam power and, consequently, railroads, which opened the vast Appalachian coal fields to the iron and steel industry.

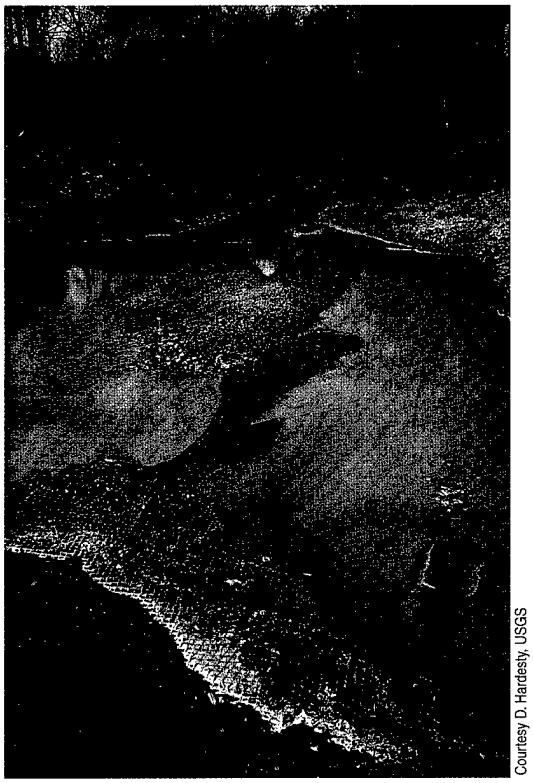
Acid Mine Drainage

The most direct and immediately obvious toxicological effect of the switch to coal was acid mine drainage. Acid drainage is caused by the oxidation of pyrite—iron sulfide—a common mineral constituent of rocks and soils that is often present in coal mine wastes and overburden. Streams affected by coal mine drainage are typically acidic (pH 2.5–6.0) and are characterized by high iron and sulfate concentrations. In addition, the iron, as ferric hydroxide, often precipitates as a fine flock that may coat stream bottoms and further affect aquatic life (Fig. 2). Acid mine drainage may also leach toxic concentrations of metals such as copper, aluminum, and zinc from rocks and soils (Barton 1978). The oxidation, or weathering, of pyrite and other metal sulfides is a natural process that may occur spontaneously on exposure of minerals to air, or it may be mediated by bacteria. Weathering of pyritic rock formations has resulted in naturally acidic streams in some localized areas of the Southeast (Huckabee et al. 1975) and Colorado (Bencala et al. 1987).

By the mid-1960's, a century of U.S. surface mining had disturbed about 8,000 square kilometers, including 21,000 kilometers of streams

Table 2. Examples of sites where mining and mineral exploitation have affected U.S. biological diversity or have affected particularly valuable biological resources.

Location	Effect
Copper Basin, Tennessee	SO_2 emissions from copper smelting beginning in 1843 eliminated vegetation over a 130-square-kilometer area (Tyre and Barton 1986) and may have contributed to the endangered status of Ruth's golden aster, a federally listed plant endemic to the Ocoee Valley. Metals and sediment have also contaminated Tennessee Valley Authority reservoirs on the Ocoee River (U.S. Environmental Protection Agency 1977; Tennessee Valley Authority 1991).
Palmerton, Pennsylvania	Zinc smelting emissions from 1898 to 1980 completely denuded an 8-square-kilometer area and affected plants and animals for a much greater distance (Jordan 1975). Stream aquatic communities were not measurably affected (Carline and Jones 1993).
Tri-State Mining District—Missouri, Kansas, Oklahoma	A century of zinc mining and smelting and attendant acidification and toxic metals releases have left bare areas and eliminated animal life from small streams. Among affected species are the Neosho madtom, a federally listed threatened fish (Williams et al. 1989), and the Neosho mucket, a rare mussel that is a candidate for federal listing (Missouri Department of Conservation 1992).
Torch Lake, Michigan	The disposal of tailings and other copper mining wastes from the late 1860's to the 1960's is believed responsible for an outbreak of liver cancer in sauger and walleye (Black and Baumann 1991). The sauger were ultimately eliminated, and the walleye are sustained by stocking (Ellenberger et al. 1994).
Leadville, Colorado	Mining in the headwaters of the Arkansas River system since the 1860's has resulted in acidification and toxic metals pollution that continues to affect aquatic communities for 50 kilometers downstream (Roline 1988; Kiffney and Clements 1993).
Clark Fork River system, Montana	Some 15 million cubic meters of mine tailings containing elevated metal concentrations, generated since mining began in 1880, have visibly contaminated and affected the aquatic biota in more than 230 kilometers of the Clark Fork main-stem (Woodward et al. 1994). Acidic, metals-laden mine drainage has also affected the benthic and fish communities and reduced the productivity of sport fisheries in the Blackfoot River, a tributary (Moore et al. 1991).
Blackbird Mine, Idaho	Mining contaminated 40 kilometers of Panther Creek, a tributary of the Salmon River. Releases of copper, colbalt, and other metals for more than 50 years decimated the resident fishery and the spring-summer run of chinook salmon, a threatened species.
Coeur d'Alene Valley, Idaho	Mining and smelting in and around Kellogg since 1879 have contaminated the South Fork of the Coeur d'Alene River, obliterated area vegetation (U.S. Environmental Protection Agency 1977), and contaminated biota (Henny et al. 1994; Hoiland et al. 1994). Mining wastes were responsible for repeated deaths of tundra swans into the late 1980's (Henny et al. 1991).
Iron Mountain Mine, Redding, California	Fish kills caused by metals released from mines and mine wastes have occurred in the Sacramento River for more than 100 years (Finlayson and Wilson 1979). Threatened are populations of steelhead (the sea-run form of rainbow trout) and chinook salmon, which have been denied access to all but 32 kilometers of Sacramento River spawning habitat since construction of Shasta Dam. Metals from Iron Mountain Mine, together with warm summer discharges from Shasta Dam, may be responsible for the imperiled status of the spring-run chinook salmon population (Finlayson and Verrue 1980; M. K. Saiki, Dixon, California, personal communication).



Courtesy D. Hardesty, USGS

Fig. 2. Iron hydroxide precipitate (orange) in a Missouri stream receiving acid drainage from surface coal mining.

(totaling 550 square kilometers), 281 natural lakes (419 square kilometers), and 168 reservoirs (168 square kilometers; Spaulding and Ogden 1968). Coal mining accounted for 41% of the total disturbed lands, the bulk of the injury coming from acid mine drainage occurring in the East and the Midwest (Spaulding and Ogden 1968). Acid drainage from coal mining affected 9,480 kilometers of streams in the Appalachians (Kinney 1964), with surface mining accounting for about 25% and underground mines about 75% (Amhad 1974). The Appalachian Regional Commission (1969) estimated that about 12,000 kilometers of streams and 120 square kilometers of impoundments in the eastern coal-mining regions were seriously affected by acid mine drainage. Acidified streams typically result in reduced diatom, benthic invertebrate, and fish communities (for example, Matter et al. 1978; Vaughan et al. 1978; Winger 1978).

Injury from acid mine drainage has been extensive and well-documented in the Cumberland River system of Kentucky and Tennessee. Streams of the Cumberland Plateau historically supported unique fish and invertebrate faunas that have been severely affected by surface mining; 23% (22 species) of the historical mussel fauna is either extinct or federally listed as endangered, and several other species have either been eliminated from significant portions of their historical ranges or reduced to small, nonreproducing populations (Layzer et al. 1993). Rare fishes and other invertebrates have also been affected (Layzer and Anderson 1992).

Injury to aquatic biota has also been extensive elsewhere in the East, but documentation on a species-by-species basis has not been undertaken. In the arid regions of the West, acid drainage is not typically associated with coal mining because deposits are generally overlain by alkaline soils and rocks (Moore and Mills 1977). In addition, the intensive mining of western coals is a relatively recent phenomenon; mining in the West has been more closely regulated and mined land reclamation has been more rigorously practiced than in historically mined areas farther east.

Current U.S. surface mining regulations mandate the restoration of disturbed lands. Moreover, restoration of abandoned coal mines has been under way since 1977; programs to seal mine openings and revegetate surface-mined lands have improved water quality in many areas and, through the incorporation of new technology, have the potential to improve more. Despite these gains, the National Stream Survey estimated that in 1986, 4,590 kilometers of streams—about 10% of the total in Pennsylvania, West Virginia, and Maryland—remained acidic because of acid mine drainage and that an additional 5,780 kilometers were strongly affected but not acidic (Herlihy et al. 1990). Other estimates range as high as 20,000 kilometers (for example, Girts and Kleinmann 1986). Moreover, the long-term success of remediation efforts on restoring biological diversity remains to be evaluated.

Acid Precipitation and Other Inorganic Contaminant Releases Into the Atmosphere

Coal is primarily carbon, but because it consists of decomposed plants and animals, it also contains variable concentrations of other elements, including sulfur, arsenic, selenium, aluminum, mercury, and cadmium. Eastern and midwestern coals are especially high in sulfur content. The combustion of these coals releases large quantities of SO_2, the major component of acid precipitation, to the atmosphere. Most of the high-sulfur coal consumed in the United States during this century has been used to make steel and to generate electricity in the East and Midwest. From there, atmospheric pollutants responsible for acid precipitation are transported northward and eastward by prevailing winds and storms (Haines 1981). These trends are reflected in the geographic distribution of rainfall pH (Fig. 3). Emissions from coal-fired electric generating plants (Fig. 4) presently constitute the largest source of atmospheric SO_2 (Placet 1991). Other constituents of acid precipitation,

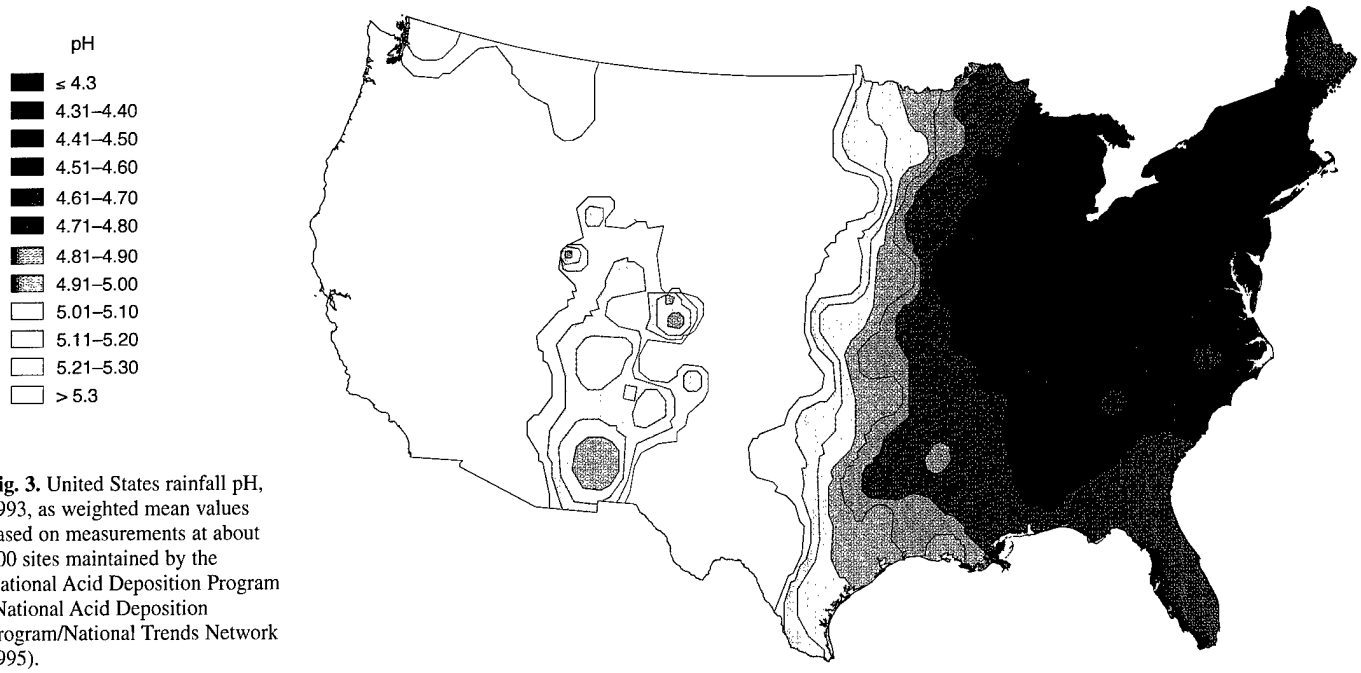


Fig. 3. United States rainfall pH, 1993, as weighted mean values based on measurements at about 200 sites maintained by the National Acid Deposition Program (National Acid Deposition Program/National Trends Network 1995).

including those from automotive exhausts, are distributed similarly (Sisterson 1991).

The chemistry of acid precipitation is complex and involves atmospheric and terrestrial components. Hydrogen ions in precipitation and their deleterious effects may be buffered by carbonates, organic matter, and other rock and soil constituents. Consequently, areas underlain by crystalline rock, shale, and sandstone are more susceptible to acidification than those underlain by limestones and other carbonate-rich rock. Potentially sensitive areas are widely distributed in North America and include much of the Appalachian Mountains, where rainfall is most acidic (Fig. 3); the Canadian Shield region of the upper Midwest (that is, the northern parts of Michigan and Wisconsin, as well as eastern Minnesota and parts of eastern and central Canada); the higher elevations of the Sierra Nevada, Rocky Mountains, and Cascade Range; and parts of the Ozark and Ouachita uplands, mid-Atlantic Coastal Plain, and Florida. Buffering by ions in groundwater and constituents leached from watersheds makes large lakes and rivers at lower elevations less susceptible to acidification than smaller, higher-elevation lakes and streams.

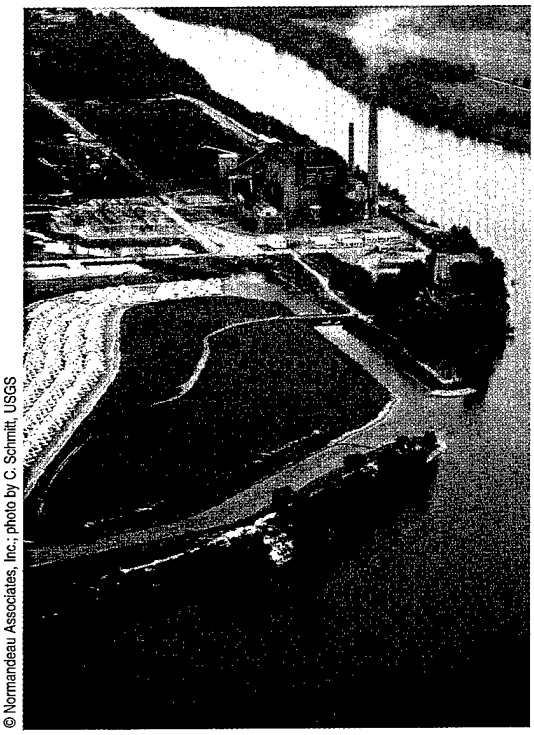


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Fig. 4. A coal-fired electric generating plant near Concord, New Hampshire.

The interactions of ions in precipitation (that is, H^+, SO_4^{+2}, NO_3^{-2}) with organic and inorganic constituents of soil and water affect toxicity. Particularly important is the leaching of potentially toxic elements, especially aluminum, from rocks and soils by acidic precipitation. Aluminum toxicity occurs in acidic waters with low organic content; organic matter binds aluminum, making it less toxic (Wright and Snevik 1978; Baker and Schofield 1980; Driscoll et al. 1980). Sensitivity to pH and aluminum varies with taxon and life stage, but acid-sensitive species occur among most groups of aquatic organisms, including mollusks, mayflies, zooplankton, and fishes (Haines 1981; Baker 1991a). Acidified waters typically contain zooplankton faunas dominated by a few resistant species, reduced benthic macroinvertebrate diversity and productivity, altered fish communities, and no mollusks (Haines 1981). Among fishes, certain minnows (Cyprinidae) and the early life stages of some salmonids, including Atlantic salmon and rainbow trout, are more sensitive than those of other taxa, such as brook trout (Haines 1981).

Toxicity attributable to pH and aluminum is often episodic, occurring during high surface-water discharge; pH during spring snowmelt is characteristically low and aluminum is correspondingly high in those areas that develop significant snowpack (Wigington 1991). Spring is also the time when salmonid alevins emerge from stream gravel, making them susceptible to episodic acidification and aluminum toxicity (Fiss and Carline 1993). Significant episodes can also occur during large rainfall events in other seasons (Wigington 1991).

Acid rain is defined as rainfall with a pH lower than about 5.0; the pH of distilled water in equilibrium with atmospheric CO_2 is 5.6, but other atmospheric constituents tend to make rainfall more acidic even in areas unaffected by air pollution. In eastern North America, the 1970–1971 mean pH based on weekly measurements was about 4.0 at monitoring stations in upstate New York and New Hampshire, with rainfall pH of individual storms regularly less than 4.0. Historical records indicated pH values as low as 2.1 in 1964 (Likens and Bormann 1974). The National Surface Water Survey (NSWS) estimated that in addition to waters acidified from coal mining, 1,181 lakes (4.2% of those surveyed) and 5,506 kilometers of streams (2.7%) were acidic and that potentially toxic aluminum concentrations were present in 3% of the lakes and 13% of the streams surveyed (Baker 1991b). Almost all the affected waters were in six susceptible areas—the southwestern part of the Adirondack Mountains, New England, forested mid-Atlantic highlands, Atlantic Coastal Plain, northern Florida highlands, and the eastern part of the upper Midwest (Baker 1991b).

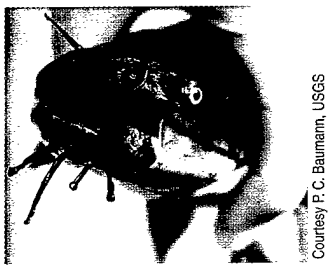
The biological consequences of acid precipitation in North America were first publicized with the discovery of fishless lakes—110 lakes above 610 meters elevation in the Adirondack Mountains (Schofield 1976). Significant changes in fish community composition, including the elimination of smallmouth bass, also occurred in many lakes that contained fish (Schofield 1976). Further study revealed more widespread ecological injury. The NSWS estimated that nearly 60% of headwater stream reaches in the mid-Atlantic Coastal Plain, 23% of Adirondack lakes, and 18% of mid-Appalachian streams are too acidic to support brook trout, an acid-tolerant species (Baker 1991a). Among Adirondack lakes, 24% have no fish; the 16% for which historical data are available have lost one or more fish species; and brook trout have been eliminated from 11% of those lakes that historically supported the species (Baker 1991a). Trends in Vermont and New Hampshire are similar to those reported for the Adirondacks, and acid-sensitive species have been eliminated from headwater streams in Massachusetts (Baker 1991a). In Maine, acidified lakes are unsuitable for natural reproduction of Sunapee char, a rare landlocked form of arctic char (Jagoe et al. 1984). In Pennsylvania, an estimated 3,000 kilometers of trout streams are affected by acid precipitation (Carline et al. 1992; Fiss and Carline 1993), as are 10% of trout streams in West Virginia (Cosby et al. 1991). Some precipitation-acidified headwater streams in Pennsylvania are toxic to salmonids, including brook trout, during spring runoff (Carline et al. 1992). In the Northeast as a whole, about 5% of lakes otherwise suitable for brook trout are too acidic, and 9% will not support other acid-tolerant species (Baker 1991a). In the mid-Appalachian region, about 30% of stream reaches surveyed by the NSWS will not support acid-sensitive species such as blacknose dace (Baker 1991a). Moreover, the NSWS did not survey small lakes (less than 4 hectares) and headwater streams and may have consequently underestimated the full extent of injury (Baker 1991a).

Acidification has also affected migratory fishes, amphibians, and terrestrial organisms in the Northeast. Atlantic salmon have been eliminated from coastal streams in northern Europe (Rosseland et al. 1986) and in maritime Canada (Elson et al. 1973; Watt 1986; Haines 1992). Although New England coastal streams receive acidic deposition (Fig. 3), they are not chronically acidic, and effects on Atlantic salmon have not been as severe. Nevertheless, parr production in tributaries of Maine coastal streams may occasionally be reduced by episodic acidification (Haines 1992). In tributaries of Chesapeake Bay, episodic acidification and elevated aluminum concentrations associated with spring rains may reduce the survival of larval striped bass (Hall et al. 1985, 1991). In addition, about 65% of the small coastal streams surrounding the upper Chesapeake Bay in Maryland are too acidic for blueback herring, an acid-sensitive species (Baker 1991a). Acidification of breeding sites in the Northeast was suspected of reducing the survival of larval frogs, toads, and salamanders (Haines 1981), but amphibians avoid the most acidified habitats (Freda 1986). Many northeastern amphibians breed in temporary pools fed by acidified spring meltwaters and rain; these small habitats may also have been overlooked by regional water-quality surveys (Blancher 1991). Elsewhere, studies on the effects of acid precipitation on amphibians have proven equivocal (for example, Bradford et al. 1994).

Acidification-induced changes in the aquatic fauna of small lakes in the Northeast have affected the distribution of fish-eating birds, including ospreys, common loons, belted

kingfishers, and common mergansers, as well as other ducks (Diamond 1989; Longcore et al. 1993; Desgrangies and Gagnon 1994). The reduced benthic macroinvertebrate productivity typical of acidified waters may indirectly depress production of American black ducks (Haramis and Chu 1987), a species that has been in decline in the Northeast since the 1950's (Steiner 1984). Acidification also reduces the availability of soil calcium to forest insects, which may ultimately lead to calcium deficiency and eggshell thinning in insectivorous birds (Drent and Woldendorp 1989; Blancher 1991). Direct injury by acid precipitation to forest vegetation is believed limited to red spruce at high elevations in the northern Appalachians (Barnard and Lucier 1991); however, indirect effects on wildlife caused by subtle vegetation shifts have been documented. The distributions of tree swallows and eastern kingbirds have been altered by acidification-induced forest changes—including effects on invertebrate food organisms (Diamond 1989; Longcore et al. 1993)—as was the production of birds in acidified areas of Europe (Graveland et al. 1994). The long-term effects of acidification on wildlife populations and on the productivity of terrestrial ecosystems have not been thoroughly assessed (Barnard and Lucier 1991; Blancher 1991; Schreiber 1995).

In addition to sulfur, the combustion of coal releases other potentially toxic elements, including arsenic, cadmium, lead, mercury, and selenium into the environment (Dvorak and Lewis 1978). Arsenic, cadmium, and selenium are concentrated in coal ash, from which they may be leached into surface waters and accumulated to toxic concentrations by aquatic organisms (Hall and Burton 1982). In North Carolina (Lemly 1985; Baumann and Gillespie 1986) and Texas (Garrett and Inman 1984), selenium from power plant ash caused mortality and reproductive failure in fishes. Mercury, some selenium, and other elements in coal are released into the atmosphere in stack emissions (Fig. 4) and may be transported long distances. Mercury, like selenium, tends to accumulate in birds, mammals, and predatory fishes; it is also highly toxic to most organisms. Mercury was formerly a pollutant associated with gold mining and point sources such as caustic soda (that is, sodium hydroxide) plants and paper mills (May and McKinney 1977). The accumulation of mercury in the biota of remote lakes in the Northeast (for example, Driscoll et al. 1994), however, has raised concerns about atmospheric transport and natural chemical processes that tend to keep mercury available for accumulation by organisms. Mercury of presumed atmospheric origin has accumulated in the biota of remote inland lakes in Maine, where it is believed to be the cause of reduced reproductive success in bald eagles relative to coastal populations (Welch 1994). Coal-fired electric generating plants are the greatest sources of atmospheric mercury; other important sources include municipal and hospital waste incinerators (U.S. Environmental Protection Agency 1993).



Courtesy P.C. Baumann, USGS

Fig. 5. External neoplasms (tumors) and deformed chin barbels on a brown bullhead from the lower Black River, a Lake Erie tributary, in Lorain, Ohio. Polycyclic aromatic hydrocarbons (PAH's) from coke ovens, long discharged to Great Lakes harbors and estuaries in steel-making cities, are believed responsible for outbreaks of these and other types of cancer in fishes. Fish populations in which the frequency of such lesions is high typically contain few old individuals, suggesting that the tumors are ultimately lethal (Baumann et al. 1990).

Polycyclic Aromatic Hydrocarbons

Coal combustion also releases organic chemicals, especially polycyclic aromatic hydrocarbons (PAH's; Table 1), into the atmosphere. Few of these are directly toxic; however, some are potent human and animal genotoxins (that is, mutagens, carcinogens, and teratogens). These compounds can also lower the disease resistance of many animals (Hodgins et al. 1977). The most toxic PAH's, including the genotoxins, are rapidly metabolized by vertebrates and hence do not tend to accumulate in food chains (Eadie 1984). Nevertheless, benthic invertebrates inhabiting contaminated sediments are a source of PAH's to fishes, shorebirds, and mammals. The full extent and significance of releases of PAH's from coal combustion are unknown (Heit 1985).

The production of coke from coal also generates PAH's, and the indiscriminate disposal of coking wastes has led to the contamination of many industrialized waterways. Contamination by PAH's is especially evident in the harbors of steel-making cities of the Great Lakes basin (Great Lakes Water Quality Board 1985; Baumann and Whittle 1988). The benthic invertebrate and fish faunas of these waters are characteristically reduced in diversity (Great Lakes Water Quality Board 1985; Smith et al. 1994), and bottom-dwelling fishes in some waters are afflicted with liver cancer and other tumors (Baumann 1989; Black and Baumann 1991; Fig. 5) that reduce life expectancy in affected populations (Baumann et al. 1990). Significant quantities of PAH's derived from coal are also released from other metallurgical sources, including foundries and electric arc furnaces that produce aluminum and steel (Quilliam et al. 1985; Thrane 1987).

The use and disposal of other coal-derived by-products, especially creosote, were also significant sources of PAH's to the environment. Creosote, a condensate distilled from coal tar, was used for decades as a wood preservative. Contamination from creosote wood treatment facilities is common, and such facilities have affected biota by inducing tumors in fish, reducing benthic diversity, or both, in many locations (Malins et al. 1984; Bender et al. 1988; Swartz et al. 1989; Pastorok et al. 1994). Creosote was also used to separate metals from ore and is among the possible causes of liver cancer in walleye and sauger of Torch Lake, Michigan

(Baumann 1989; Black and Baumann 1991). Creosote is no longer registered for use as a wood preservative, but nevertheless it continues to enter the environment from historical sites of use and formulation as well as from treated wood products.

Petroleum

Petroleum, like coal, is a complex mixture containing thousands of compounds derived from the decay of prehistoric plants and animals. The most abundant of these compounds are aliphatic (straight-chained) and aromatic (ring-structured) hydrocarbons (Clark and Brown 1977). Petroleum hydrocarbons are composed of mostly carbon and hydrogen, but some also contain oxygen, nitrogen, sulfur, and other elements and vary greatly in molecular weight, volatility, solubility, persistence, and toxicity (Clark and Brown 1977; Neff 1979; Robotham and Gill 1989; Shales et al. 1989). Crude oils and refined products, as well as wastes from petroleum production and processing facilities, are also highly variable in composition and toxicity. In general, the more volatile, water-soluble, and lower molecular weight aromatic components are the most directly toxic to aquatic organisms. These are also proportionally more abundant in refined products than in crudes (Shales et al. 1989; Mielke 1990).

In addition to direct toxicity by aromatic hydrocarbons, other petroleum components may harm biota through different mechanisms. Oil slicks may especially affect organisms concentrated at the air–water interface—including marine birds and mammals and the eggs and larvae of recreationally and commercially important fishes and invertebrates. Oil may coat shorelines, beaches, and tidal flats (Fig. 6), suffocating intertidal organisms. Several mechanisms may cause the incorporation of oil into marine particulates—including small planktonic organisms—which may result in the incorporation of petroleum hydrocarbons into pelagic food chains, or the particles may sink to the bottom and affect benthic organisms. The decomposition of petroleum hydrocarbons by bacteria depletes oxygen, which may cause oxygen stress, and the loss of insulating capacity caused by oil on feathers and fur increases the vulnerability of birds and mammals to cold (Geraci and Smith 1977; Holmes and Cronshaw 1977; Kooyman et al. 1977). Microliter quantities of oil transferred to eggs from the feathers of oiled birds can be toxic to developing embryos (Albers 1977; Hoffman 1979, 1990; King and Lefever 1979), and ingestion of a single dose by female birds may alter the yolk structure and reduce the hatchability of eggs (Grau et al. 1977).

Courtesy D. Chapman, USGS

Fig. 6. Oiled salt marsh in Corpus Christi Bay, a Texas estuary.

Large quantities of petroleum enter the environment, mostly from land-based sources. The National Academy of Sciences estimated that annual inputs of petroleum to the oceans during the 1970's were about 4.5 million metric tons annually, derived from the following major sources: land-based discharges other than refineries (including sewage, urban runoff, and waste oils), 53%; natural seeps, 13%; atmospheric transport and deposition, 13%; marine operations (bilge and ballast discharges, and so forth), 11%; offshore production, 4%; marine accidents (oil spills and well blowouts), 3%; and refineries, 0.4% (Clark and MacLeod 1977). Land-based, nonindustrial sources similarly predominate even in Raritan Bay, New Jersey, a heavily industrialized estuary ringed by petroleum storage, transport, and processing facilities. About 92,000 kilograms of petroleum hydrocarbons enter Raritan Bay daily. Of this total, sewage treatment effluents and urban runoff represent 76%; other industrial effluents, 19%; and spills about 2% (Connell 1982).

On release into the environment, the composition and potential toxicity of petroleum mixtures change rapidly and continuously as individual compounds are volatilized, solubilized, dispersed, and degraded at differing rates by physical, chemical, and biological processes. The rates of these weathering processes vary depending on temperature, currents, wind, concentrations of suspended and dissolved components of the receiving water, and biological activity. The timing of petroleum releases relative to the distribution and life cycles of organisms determines the potential exposure and, correspondingly, the biological effects of exposure. Ecosystems also vary in their susceptibility to oil (Gundlach and Hayes 1978; Getter et al. 1984). Nearshore areas, especially sheltered marshes and estuaries, are generally more vulnerable than those of the open ocean; coastal habitats are more diverse and productive, and the restricted circulation characteristic of some causes longer residence time at higher concentrations of the oil (Fig. 6). Arctic and subarctic

ecosystems may be more vulnerable than those in warmer climates because of the slower rates of dispersion and decomposition of petroleum components especially under ice, where oil decomposes very slowly. Animals dependent on openings in the ice may be at particular risk. The comparatively low productivity and regenerative capacity of cold-climate organisms also increase their vulnerability; arctic vegetation is also very sensitive and slow to recover from oil exposure (Clark and Finley 1977). Conversely, the toxicity of oil increases with temperature (Mayer and Ellersieck 1986). Collectively, these factors make the environmental fate and effects of oil highly variable and dynamic.

Oil Spills

Much of what is known about oil in the environment is derived from the study of transportation and production accidents, despite their relatively small contribution to the global flux of petroleum. Spills of varying proportions involving both crudes and refined products have occurred often during this century, and recent events have been widely publicized. Studies of major North American spills and well blowouts—and of many other smaller spills, and of those that occurred outside North America—have provided dramatic evidence of short-term ecological injury (Phillips and Lincoln 1930; Clark and Finley 1977; Mielke 1990). Massive direct mortalities of plants, shellfish, mammals, and birds are common, with regularly reported kills of tens and hundreds of thousands of birds as a result of individual spills (Holmes and Cronshaw 1977). A 1952 spill off Chatham, Massachusetts, for example, reduced the overwintering population of eiders from 500,000 to 150,000, and a 1969 well blowout in Santa Barbara, California, killed 64% of the loons and grebes in the area, which represented 7%–10% of the regional populations (Perry 1980). Direct deaths of adult fishes occur infrequently, but the early life stages of many fish species are vulnerable because the fishes are then highly concentrated in inshore areas and near the surface; losses, however, are difficult to observe and quantify. Inland spills also occur regularly, but they have received much less study than marine spills. Reported findings are nevertheless similar: short-term effects include kills of plants, invertebrates, fishes, amphibians, reptiles, water birds, and mammals; one 1988 Ohio River diesel spill killed an estimated 5,000 waterfowl and innumerable fish and invertebrates (Cronk et al. 1990). Unlike marine spills, however, long-term effects of inland spills have received little study (Shales et al. 1989).

The effects of the 1989 *Exxon Valdez* spill in Alaska are still being investigated, but findings to date indicate that about 40% of the estimated 6,500 endangered sea otters inhabiting Prince William Sound were killed (Garrott et al. 1993), and as many as 300,000 seabirds (Piatt et al. 1990), including 120,000 adult common murres, 12,000 marbled murrelets, and 150 bald eagles (*Exxon Valdez* Trustee Council 1994). Moreover, mortality figures based on counts of dead animals recovered or observed shortly after oil spills usually underestimate the total kill; in addition to dead animals being difficult to find, delayed deaths and indirect effects are also underestimated (Holmes and Cronshaw 1977). In Prince William Sound, for example, the number of dead birds recovered was estimated to be only 10%–15% of the total killed (*Exxon Valdez* Trustee Council 1994). By 1994, bald eagles in Prince William Sound had nearly recovered, and common murres and marbled murrelets were recovering, but numbers of northwestern crows, cormorants, arctic terns, and tufted puffins remained depressed in oiled areas (*Exxon Valdez* Trustee Council 1994). Survival of river otter pups was poor in years following the spill (*Exxon Valdez* Trustee Council 1994), and sublethal effects in adult otters remained evident in oiled areas (Duffy et al. 1993). Survival of larval Pacific herring was not affected despite the presence of large quantities of oil on spawning beaches (McGurk et al. 1990, 1992), but biochemical evidence of exposure remained evident in intertidal fishes 14 months after the spill (Woodin and Stegeman 1993). Lower than normal survival of eggs and larvae in oiled areas may have reduced the adult pink salmon population of Prince William Sound by as much as 10%, with further reductions possible from secondary effects (*Exxon Valdez* Trustee Council 1994).

Longer-term effects of spills on populations and communities are less obvious, and follow-up studies of individual events, when they have been conducted, have provided equivocal evidence of significance and persistence. In addition, it is not clear whether sufficient studies can be conducted to discriminate the effects of single events, especially in areas of natural seepages and repeated spills. Events such as spills are always difficult to evaluate because they are not repeatable and because prespill data are lacking for most locations (Norcross 1992). Generally, 10 years is the estimated recovery time for local effects from individual oil spills, but each spill is a separate event governed by different physical and biological constraints (Mann and Clark 1978). Coral reefs and mangroves are highly vulnerable to spills and may take longer to recover (Gundlach and Hayes 1978; Fucik et al. 1984; Getter et al. 1984). In addition, the long-term effects of spills in cold climates have not yet been fully evaluated and

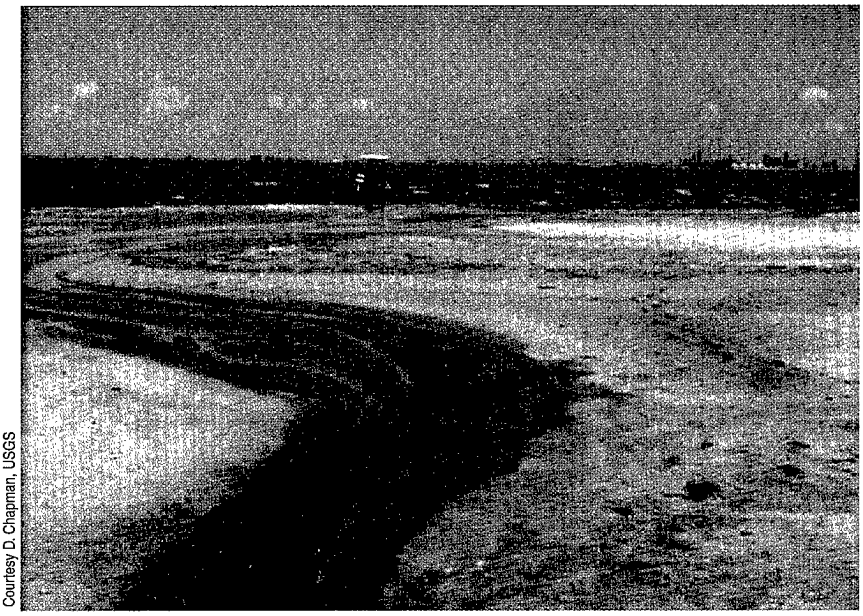
await the *Exxon Valdez* findings; the seabird colonies of Prince William Sound may take 20 years or more to recover (*Exxon Valdez* Trustee Council 1994).

Chronic Oil Pollution

Although chronic pollution has been studied much less intensively, chronic pollution by oil and other contaminants associated with petroleum production, transport, and refining is generally regarded as more widespread and serious than individual spills and other accidents (Holmes and Cronshaw 1977). In addition, at some point along a continuum, repeated spills become chronic pollution; such spills have been implicated as a factor responsible for the long-term decline of seabird colonies in parts of northern Europe and maritime Canada (Holmes and Cronshaw 1977). Annual bird losses from chronic oil pollution in the North Sea and North Atlantic Ocean were estimated as 150,000–450,000—murres, scoters, grebes, and gulls were the most commonly recovered groups (Perry 1980).

A significant component of chronic pollution from petroleum exploitation is produced water—the water that often accompanies oil and natural gas in geologic formations. Water may also be injected into wells to force oil to the surface. Produced waters may contain toxic concentrations of petroleum hydrocarbons, salts and other ions (including metals and radionuclides), and reagents used to enhance the separation of oil from water (Andreasen and Spears 1983; Woodward and Riley 1983; Roach et al. 1993). Some 36 billion liters of produced water are discharged annually to coastal waters in the United States (U.S. Environmental Protection Agency 1995). Historically, produced waters were discharged untreated; however, this practice has been regulated by most states, and the elimination of discharges to all coastal waters except Cook Inlet, Alaska, has been proposed (U.S. Environmental Protection Agency 1995).

Disposal of produced waters often represents a significant source of injury to biota in oil production areas (Leppäkoski and Lindström 1978; Armstrong et al. 1979), especially in estuarine marshes with restricted freshwater inflow and limited tidal exchange (for example, Nance 1991). In Texas, chronic pollution from produced water discharges has affected the biota of Nueces, Trinity, and Galveston bays (Armstrong et al. 1979; Henley and Rauschuber 1981; Carr 1993; Roach et al. 1993; D'Unger et al. 1996; Fig. 7); about 11 million liters of produced waters are discharged daily into Galveston Bay (Andreasen and Spears 1983). In freshwater streams that drain oil fields and refineries, the diatom, benthic macroinvertebrate, and fish communities are often affected by produced water discharges (Wilhm and Dorris 1968; Woodward and Riley 1983; Olive et al. 1992). At some inland sites, produced waters are stored in reserve pits or lagoons for evaporation, or they may be used to create wetlands. These may represent sources of continuing mortality for waterfowl and wading birds (Ramirez 1993). In arctic regions where evaporation rates are low and reserve pits must be discharged, benthic invertebrate diversity is reduced in receiving waters (West and Snyder-Conn 1987).



Courtesy D. Chapman, USGS

Fig. 7. Produced waters—the water accompanying petroleum in geologic formations—being discharged to Nueces Bay, Texas.

Because many point sources of water pollution associated with petroleum production and refining have been regulated, the contribution of nonpoint sources has become more apparent. As noted earlier, waste oils, discharges from marine operations, and urban runoff are significant, pervasive sources of petroleum hydrocarbons in the environment. Petroleum-derived aromatic hydrocarbons are present in the sediments of all urban waterways, and concentrations tend to be elevated in areas of petroleum storage and transport. Especially high concentrations occur in the sediments of Casco Bay, Maine; Boston and Salem harbors, Massachusetts; western Long Island Sound; Raritan Bay, New Jersey; Baltimore Harbor, Maryland; San Diego Harbor and parts of San Francisco Bay, California; Elliot Bay, Washington (Calder and Means 1987; Helz and Huggett 1987; Turgeon and Robertson 1995); and in many Great Lakes harbors and bays (Meyers 1984; Fabacher et al. 1991). Petroleum-contaminated sediments typically contain genotoxic PAH's, and tumors have been reported in bottom-dwelling fishes from many of these locations (Baumann 1989; Turgeon and Robertson 1995; Fig. 5). Fin rot, which may indicate reduced resistance to disease, is also

common in fish from areas chronically contaminated by petroleum (Minchew and Yarbrough 1977; Turgeon and Robertson 1995). The specific linkages between these disease outbreaks and petroleum pollution have been challenged (Mix 1986). It is also difficult to attribute such effects, which may have multiple causes, to one chemical or group of chemicals among the complex mixtures usually present in urban, industrial environments.

Air Pollution

Petroleum constituents and combustion products contribute significantly to air pollution. Refineries and fuel-handling and transport facilities are major sources of benzene and other organic components of smog, and the combustion of petroleum releases PAH's to the atmosphere. Although coal combustion, primarily by electric utilities (Fig. 4), is the greatest source of atmospheric SO_2, vehicular exhausts also contribute significantly. In addition, refineries emit large quantities of sulfur into the atmosphere. Vehicular emissions are the largest source of nitrogen oxides (NO_x), which contribute to smog and acid precipitation, as well as carbon monoxide (CO) and carbon dioxide (CO_2; Placet 1991). Both NO_x and CO are precursors of ozone, the air pollutant most responsible for injury to vegetation (Barnard and Lucier 1991). Automobile exhausts also contain ethylene, which is toxic to vegetation and also contributes to ozone formation (Heck and Anderson 1980). Methane, CO, and CO_2 are among the so-called greenhouse gases responsible for global warming; their concentrations are increasing in response to increasing global consumption of fossil fuels (Boden et al. 1994). The combustion of leaded gasoline, which was introduced in 1923 (Nriagu 1990), remains the greatest source of lead to the global atmosphere (Settle and Patterson 1980). Leaded gasoline also contributes to urban lead pollution; however, environmental lead concentrations in the United States have generally declined over the last decade (Fig. 8), ostensibly as a result of the removal of lead from gasoline and the control of emissions from mining and point sources (Smith et al. 1987).

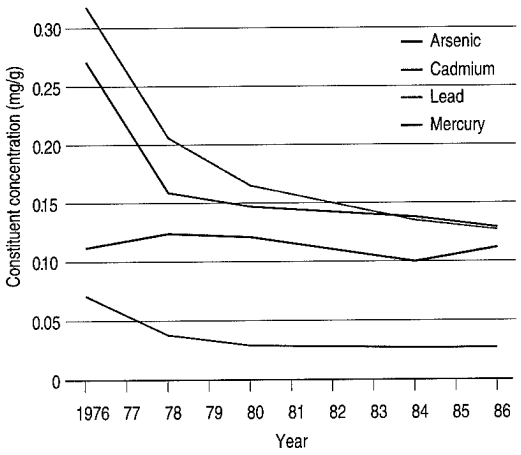


Fig. 8. Concentrations of arsenic, cadmium, lead, and mercury in United States freshwater fish, 1976–1986 (U.S. Fish and Wildlife Service, National Contaminant Biomonitoring Program, unpublished data).

Agriculture and Forestry

In the twentieth century, the advent of machinery run with fossil fuels greatly aided the conversion of vast expanses of native forests, prairies, wetlands, and deserts into croplands across North America. In addition to physical changes, the irrigation of formerly arid lands leaches minerals from soils at accelerated rates, resulting in accumulations of some elements to toxic concentrations. Agricultural conversion also simplifies complex natural ecosystems, which facilitates pest and disease infestations and creates a market for pesticides. Agricultural runoff may contain high concentrations of sediments and plant nutrients, which have profoundly affected stream biota in the Midwest and elsewhere (for example, Trautmann 1957). Nutrients (that is, nitrogen and phosphorus) from agricultural runoff, with increased temperature and light penetration, can stimulate the growth of algae and nuisance rooted aquatic vegetation. The decomposition of excess vegetation may cause oxygen deficiency in affected waters. Bacteria can also convert nitrogen from fertilizers and animal wastes to ammonia, which is highly toxic to aquatic organisms.

Toxic Minerals From Irrigation

Wetlands in the arid and semiarid regions of the West support migratory birds and rare endemic fishes, wildlife, and plants (Preston 1981; Thompson and Merritt 1988). That the evaporation of water from these "arid wetlands" (Lemly et al. 1993) could cause toxic accumulations of minerals was known to wildlife biologists since at least 1891, when an estimated 35,000 eared grebes and northern shovelers were found dead at Owens Lake, California (Phillips and Lincoln 1930). Subsequent extensive kills of ducks and other birds occurred on the Bear River and Great Salt Lake marshes of Utah during droughts early in the twentieth century. Similar incidents occurred widely during the 1920's, from the Dakotas and Canadian prairies to Oregon and California, and in Kansas, Oklahoma, Texas, and northern Mexico; particularly serious outbreaks occurred

in the Klamath River basin in Oregon (Phillips and Lincoln 1930). These episodes were termed alkali poisoning and were believed caused by the ingestion of plant and animal material containing toxic levels of salts—primarily of sodium, magnesium, and calcium—concentrated by evaporation (Phillips and Lincoln 1930). Subsequent studies revealed the involvement of selenium in these episodes (Twomey and Twomey 1936). It was known in the 1920's that evaporation and the concentration of salts to toxic levels were worsened by water withdrawals for irrigation (Phillips and Lincoln 1930).

Selenium, a natural constituent of the earth's crust, is essential to all plants and animals. At high concentrations, however, it can be toxic. Elevated concentrations commonly occur west of the Mississippi River in areas of arid, alkaline soils derived from marine shales (Lemly and Smith 1987). Irrigation of arid soils leaches selenium salts and those of other elements into surface waters. Once in solution, the salts may be concentrated by evaporation and are available for accumulation by aquatic organisms and animals that feed on them. Among the high-selenium areas of the West is the extensively drained, intensively irrigated Central Valley of California. Beginning in the 1970's, irrigation return water from selenium-rich Central Valley farmland was used to create and maintain wetland habitat at Kesterson National Wildlife Refuge; drain water constituted nearly all of Kesterson's water supply by 1981 (Lemly et al. 1993). Primarily selenium, but also boron, accumulated in the refuge, causing widely publicized incidents involving wildlife kills, poor hatching success, and embryo deformities in ducks and other birds (Fig. 9) in the early and middle 1980's (Ohlendorf et al. 1986; Lemly et al. 1993). Aquatic organisms were also affected: a massive fish kill and subsequent reproductive failure eliminated all fishes except mosquitofish from irrigation drains (Saiki 1986) and refuge ponds, and a high incidence of embryo deaths occurred even in this resistant species (Saiki et al. 1991). At Kesterson, selenium also accumulated to high concentrations in snakes, frogs, raccoons, and small mammals, but no deleterious effects were detected (Clark 1987; Ohlendorf et al. 1988; Clark et al. 1989).

Selenium also accumulated in reservoirs constructed in seleniferous areas of western Colorado; those impoundments became unable to support fish in the 1950's (Baumann and May 1984). Following the discoveries at Kesterson, further studies of irrigation drain water by the U.S. Department of the Interior revealed either overt symptoms of selenium poisoning, selenium concentrations sufficiently high to induce such symptoms, or both at nine other refuges in the West and in the Gunnison River basin, Colorado, and the middle Arkansas River basin, Kansas (Stephens et al. 1992; Lemly et al. 1993; Presser et al. 1994). Elevated selenium concentrations also occur in water (Dvorak and Lewis 1978; Stephens et al. 1992) and fishes (Schmitt and Brumbaugh 1990; Fig. 10) throughout much of the basins of the Colorado and Missouri Rivers. In the Colorado and Green River systems, irrigation and other water-development activities have further increased naturally elevated concentrations to the extent that selenium may be at least partly responsible for the currently imperiled status of the razorback sucker, humpback chub, bonytail chub, and Colorado squawfish—all federally listed threatened or endangered fishes (Williams et al. 1989; Stephens et al. 1992; Hamilton and Waddell 1994). Elevated selenium concentrations in the Rio Grande (International Boundary and Water Commission 1994) may also be caused by water withdrawals for irrigation.

Courtesy H. M. Ohlendorf, U.S. Fish and Wildlife Service

Fig. 9. An American coot embryo from Kesterson National Wildlife Refuge, California, with selenium-induced developmental abnormalities including a deformed lower bill and no eyes.

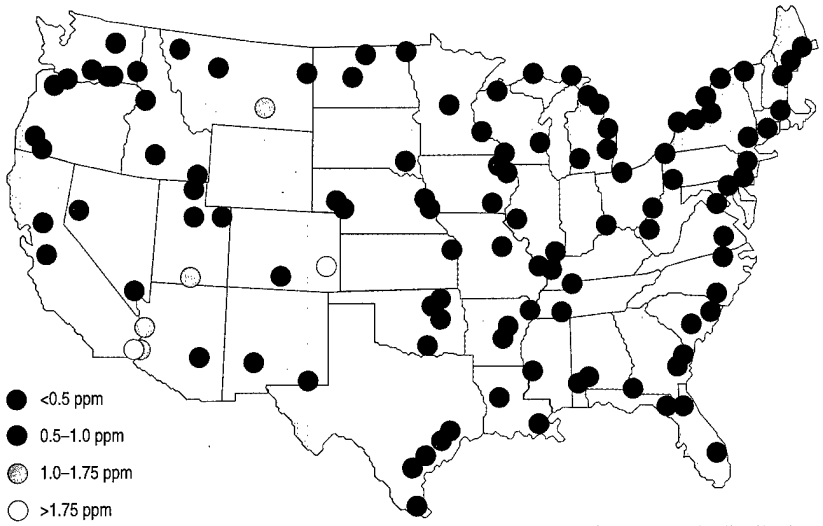


Fig. 10. Geographic distribution of selenium in freshwater fish collected from the indicated sites in the conterminous United States in 1986.

Pesticides

Widespread use of pesticides did not occur until the twentieth century; however, chemicals were used to control insects, fungi, and weeds much earlier. Inorganic pesticides, including copper sulfate, mercuric chloride, lead and sodium arsenates, sodium dichromate, hydrogen cyanide, and sodium chlorate became widely available in the nineteenth and early twentieth centuries (Clarkson 1991; Ghering et al. 1991; Stevens and Sumner 1991). These were followed by organo-metallic compounds (that is, organic chemicals containing arsenic, mercury, tin, and others), most of which remained in use until after World War II; some organo-arsenicals are still used (Clarkson 1991). Plant-derived organic pesticides, including pyrethrum and strychnine, were available commercially by the end of the nineteenth century (Ray 1991). Organic compounds obtained from coal and oil, including kerosene, naphthalene, and carbon disulfide, were in use as pesticides by 1900 (Ghering et al. 1991).

Organochlorine Pesticides

Synthetic organic chemicals containing chlorine, including carbon tetrachloride and trichloroethylene, were available commercially by 1925 (Ghering et al. 1991). Benzene hexachloride (Table 1) was first synthesized in 1825, and DDT in 1874; however, the insecticidal properties of these compounds were not recognized until around 1940 (Smith 1991). The military developed and produced DDT during World War II to control mosquitoes and, thereby, the spread of malaria and other diseases. Released into civilian markets in 1945, DDT was used heavily over the next two decades to control agricultural and forest insects as well as disease vectors; by 1961, 1,200 formulations were available for use on 334 crops (U.S. Environmental Protection Agency 1992). DDT was also used to control fishes, bats, and other wildlife. After World War II, additional organochlorine pesticides—including methoxychlor, aldrin, dieldrin, and chlordane—became available. These were followed in the 1950's–1960's by endosulfan, endrin, mirex, kepone, toxaphene, and others (Smith 1991; Table 1). In addition to being highly toxic, organochlorine pesticides are relatively insoluble in water, adhere strongly to soil particles, and are resistant to physical, chemical, and biological degradation. These properties were viewed as desirable, and negative consequences from bioaccumulation and toxicity to nontarget organisms were not foreseen.

The use of DDT in the United States peaked in the late 1950's; maximum production, 80–90 million kilograms per year, occurred in the early 1960's (Hayes 1991; U.S. Environmental Protection Agency 1992). Cotton farming in the Southeast, the Delta states, and the southern plains accounted for 74% of the 15 million kilograms of DDT used in 1964 on farms in the United States (Eichers et al. 1971). Other heavily treated crops included tobacco, soybeans, and fruits and vegetables. Cotton pests developed resistance to DDT, and it was replaced in the 1960's by newer compounds, especially toxaphene. Consequently, DDT represented only about one-third of the 34 million kilograms of insecticides applied to cotton in 1964, with toxaphene and nonorganochlorine chemicals accounting for the rest in about equal proportions (Eichers et al. 1971).

As the use of DDT declined, total organochlorine chemical use increased; in 1966, 18 million kilograms of organochlorine insecticides were used in agriculture, including 6 million kilograms of DDT and DDD (a DDT derivative; Table 1), 7 million kilograms of toxaphene, and 3 million kilograms of aldrin (Fox et al. 1968; Eichers et al. 1971; Andrilenas 1974). After the 1969 DDT ban, toxaphene became the most heavily used insecticide, averaging about 13 million kilograms annually through the early 1970's; most was used for insect control in cotton (Eichers et al. 1978). Cotton insects eventually developed resistance to toxaphene, and usage declined through the late 1970's, well before its registration was canceled in 1983.

Aldrin, heptachlor, chlordane, and similar compounds were used heavily to control insects in corn during the 1970's, and organochlorine chemical use in the Midwest increased accordingly (Eichers et al. 1978). As insect resistance and environmental concerns grew, use of these and other organochlorine compounds declined from 46% of the total used in 1971 to 29% in 1976 (Andrilenas 1974; Eichers et al. 1978). At present, only endosulfan and methoxychlor are registered for agricultural use, although other organochlorine insecticides are still manufactured for export.

The ecological consequences of organochlorine pesticides were extensive, and some remain evident. Because of their insolubility in water and resistance to complete metabolic degradation, many organochlorine compounds bioaccumulate. Upon accumulation by vertebrates, DDT is metabolized to DDE (Table 1), which is stable and toxic; it impairs calcium metabolism in the shell gland of adult female birds. At sufficiently high concentrations, eggshell thickness can be reduced to the extent that eggs cannot support the weight of the incubating parents. Shell breakage and death of the developing embryo can result. Susceptibility varies, but predatory birds are most vulnerable, both physiologically

A History of Aquatic Toxicology

Most disciplines of biology have evolved along a path of hypothesis testing, but the field of aquatic toxicology is an exception. Society's demand for information in an atmosphere of increasing litigation initially drove, then hastened, the development of the field of aquatic toxicology. Before 1962, pollution concerns were largely focused on sewage treatment facility operations and eutrophication of lakes, streams, and estuaries. With the publication of *Silent Spring* by Rachel Carson in 1962, however, the warning alarm was sounded, proclaiming that organic contaminants, particularly pesticides such as DDT, posed a threat to the health of natural resources and humans.

One of the most salient features of the development of environmental toxicology as a scientific discipline has been the expressed need for chemical detection and identification simultaneously with the need to determine the biological effects associated with chemicals. Lags in methodological progress, both chemical and biological, limited observable progress in the early years of environmental toxicology and chemistry. Thin-layer chromatography and gas chromatography were first used to detect and identify pesticides and organic chemicals; atomic adsorption spectrophotometry was used to detect metals and other inorganic materials. At the same time, acute lethality (in which the subject organism dies in 96 hours or less) toxicity tests were initially developed and standardized to bracket extreme biological effects.

In 1977, a group of scientists working in various areas within the field gathered to discuss the ideal attributes of a toxicity test. This group, made up of representatives from government, academia, and industry, determined that the following attributes were the most important in a toxicity test and ranked them in order of their significance:

- produces ecologically significant results;
- generates scientifically and legally defensible data;
- is based on methods that are routinely available for widespread application;
- is predictive;
- methods are widely applicable across a range of chemicals; and
- test is simple and cost-effective.

The group evaluated available aquatic toxicity tests and scored them on the basis of the previously listed criteria. A score of 100% (out of a possible 100%) was awarded to acute lethality toxicity tests because of their ecologically significant results (death ... unarguably important), applicability across chemical classes, simplicity and cost-effectiveness, and their scientifically and legally defensible results.

If evaluated today, acute lethality toxicity tests would still fare well for some of the same reasons but also for some different ones. Acute lethality tests allow for the rapid building of comparative data bases in which species can be compared in terms of their sensitivity to the same chemical or by which chemicals can be compared to one another using the same species. Additionally, water quality can be varied to evaluate potential interactions with toxicity (for example, as pH increases, the toxicity of some metals increases). When dealing with new chemicals, new formulations of existing chemicals, mixtures, changing environmental conditions, and so forth, a rapid screening toxicity test is often invaluable. Consequently, acute lethality tests remain a comparative framework for evaluation.

This approach, however, does not address the important and more likely situation encountered in natural systems, namely, longer-term, sublethal exposure and its ecological consequences. Scientists grew concerned about the inadequacy of so-called "kill 'em and count 'em" tests and developed methods to evaluate changes induced by contaminants that affected reproduction, behavior, physiological processes, biochemical function, and survival of young and other sensitive life stages. Although disruptions in these areas might render an organism "ecologically dead," it may not technically induce direct mortality. For example, courtship behavior may take place normally in the presence of sublethal concentrations of toxicants, but the larvae produced might be malformed or unable to make developmental progress. Because researchers needed chronic, sublethal tests to approximate effects more likely to occur in nature, they developed full life cycle (from birth until the organism reproduces) fish tests. Although the results are ecologically meaningful (such as contaminant effects on the number of eggs produced, percent successful hatch, survival to swim-up, and so forth), such tests are difficult and expensive to run without problems. For example, of the native warmwater, freshwater fishes adaptable to laboratory conditions for full life cycle testing, fathead minnows complete the life cycle in the shortest time; even so, a test on them can last 3 to 6 months depending on broodstock and test conditions. Consequently, to decrease the testing time required, partial life cycle testing began to replace full life cycle tests. Such partial life cycle tests decrease the probability of some test condition complications, can bracket sensitive life stages (such as reproduction), and can increase the potential for testing various species of interest even if their full life cycles could not actually or practically be completed in a reasonable time.

In the late 1970's and early 1980's, invertebrate tests became increasingly important because they took less time than full life cycle testing and because disruptions in food-chain dynamics at lower trophic levels can translate into severe ecological consequences for top predators and species of monetary and ecological concern. In addition, invertebrate testing requires less space and specialized equipment than fish testing.

Behavioral toxicity tests, although ecologically relevant if the endpoints measured are interpretable, have met with limited success because of their intrinsic variability when replicated. The very thing that contributes to their sensitive detection capabilities can backfire if the animals are not acclimated properly or standardized test approaches are not appropriately conducted. The expenditure of time and labor required, however, can be offset by the ecologically interpretable results of such tests.

Biochemical and physiological approaches have become important in aquatic toxicology over the last 5 to 8 years. Not only do such approaches demonstrate the relation between exposure and effects, but they can also sometimes explain the toxic action of the contaminant. As researchers have refined biomarker techniques, such techniques have become more specific and sensitive in detecting contaminants. Baseline information on the normal physiological and biochemical states of aquatic organisms has also grown, making perturbations due to contaminants more discernible.

Currently, scientists are emphasizing portable, field-oriented, sublethal yet acute detectors of dose–response. Microtox (trade name for a bioluminescing bacteria assay) and rotifer tests are receiving much attention. Field approaches, originally survey-oriented and aimed at detecting the presence of a problem, have moved more and more toward hypothesis testing and experimental manipulation. This is a great addition to field data because experimental information

can be expanded with more confidence past the geographic perimeters of the field site, and cause–effect relations can be more realistically investigated.

The realization that no single test approach meets all needs or answers all questions has become even more evident over the last decade. The fact is that many "tools" are needed and each should be selected and combined with others in diverse configurations depending on the contaminants of interest and the questions being addressed. Continued effort is required to further develop meaningful, cost-effective, and field-friendly methodologies to detect contaminants and their effects on aquatic biota.

See end of chapter for reference

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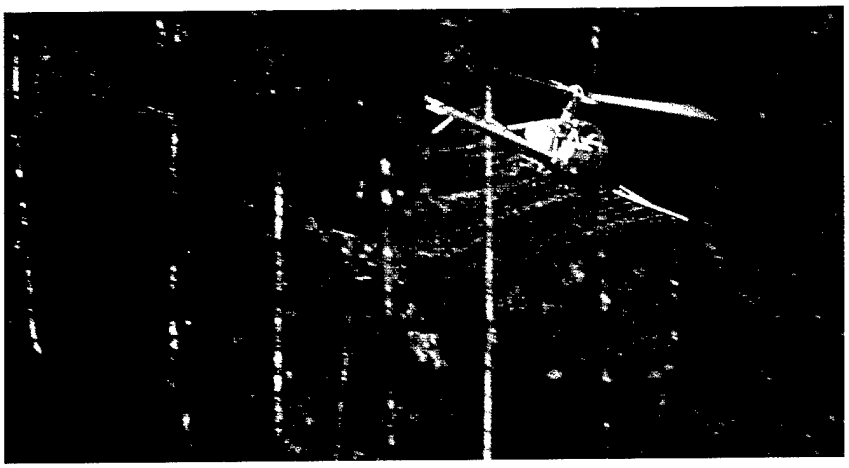
and because of their position at the apex of aquatic food chains (Cooke 1973). In North America, population declines attributable to DDE-induced eggshell thinning and reduced recruitment were documented in bald eagles, ospreys, prairie falcons, merlins, double-crested cormorants, and brown pelicans (Cooke 1973). Other contaminants and factors may also have contributed to the declines in these species, especially in the Great Lakes (Colborn 1991). Shell thinning was also documented in other species, including peregrine falcons and herring gulls, but many factors may also have been involved in their declines (Cooke 1973).

The use of DDT and other organochlorine insecticides in agriculture and forestry also affected aquatic organisms. In waters draining cotton-farming areas, the diversity of benthic invertebrate and fish communities was characteristically low, and the development of insecticide-resistant forage fishes led to elimination of predatory species in the 1960's (Ferguson et al. 1964). In addition to directly affecting bald eagle reproduction (Colborn 1991), DDT spraying of United States and Canadian forests in the 1940's and 1950's to control eastern spruce budworms (Fig. 11) and western spruce budworms reduced benthic invertebrate diversity and fish populations in streams over wide areas of the Northeast (Ide 1957; Warner and Fenderson 1962) and the West (Adams et al. 1949; Graham 1960; Cope 1961).



Courtesy U.S. Fish and Wildlife Service

Fig. 11. Forest insecticide spraying.

Agricultural and forest insect control accounted for more than half of organochlorine insecticide usage in the United States during the 1960's and 1970's (Andrilenas 1974; Eichers et al. 1978; Aspelin et al. 1992). Nevertheless, other pesticide uses, mechanisms of toxicity to birds other than eggshell thinning, and effects on other organisms were also significant. Application of chemicals to water for the control of mosquitoes, gnats, and black flies was common. Heavy applications of DDD for gnat control decimated western grebes at Clear Lake, California (Herman et al. 1969). Mosquito control using DDT led to reproductive failure of lake trout in Lake George, New York (Burdick et al. 1964), and of landlocked Atlantic salmon in Sebago Lake, Maine (Anderson and Everhart 1966), and was suspected of reducing the survival of juvenile winter flounder in a Massachusetts estuary (Smith and Cole 1970). During the 1950's, widespread use of DDT to control the bark beetles that transmit Dutch elm disease reduced American robin populations in many northeastern and midwestern communities (Cooper 1991); some 80 bird species were affected by the Dutch elm disease program in Michigan alone (Wallace et al. 1961). In southern Ontario, residual DDT and dieldrin from mosquito control have been suggested as a cause of local amphibian extinctions (Russell et al. 1995).

Accumulations of newer organochlorine insecticides—such as chlordane, aldrin, dieldrin, heptachlor, and endrin—caused many wildlife kills, including endangered gray bats in Missouri (Clark 1981; Clawson and Clark 1989). The use of endrin to control sugarcane borers and of heptachlor (Table 1) to control imported red fire ants in Louisiana during the 1950's–1960's led to repeated massive fish kills in the Atchafalaya and Lower Mississippi rivers and along the gulf coast (Biglane and Lafleur 1967). The consumption by waterfowl of seeds treated with heptachlor and other organochlorine pesticides caused frequent kills in agricultural areas. Dieldrin is suspected of contributing to the decline of the Great Lakes population of bald eagles (Colborn 1991). As presently known, however, the overall extent of

ecological injury attributable to these newer organochlorine insecticides has been less than that of DDT.

In response to declining organochlorine pesticide use in North America, residue concentrations of DDT and other persistent compounds in fish and wildlife declined steadily during the last decade (Mineau et al. 1984; Prouty and Bunck 1986; Bunck et al. 1987; Baumann and Whittle 1988; Schmitt et al. 1990; Wiemeyer et al. 1993; Weseloh et al. 1994; Mora 1995; Figs. 12 and 13). Elevated levels of DDT and other organochlorine insecticides persist in the Great Lakes, some cotton-growing areas of the South and Southwest (White and Krynitsky 1986; Schmitt et al. 1990; U.S. Environmental Protection Agency 1992; Schmitt and Bunck 1995; Fig. 14), and in the Mississippi River

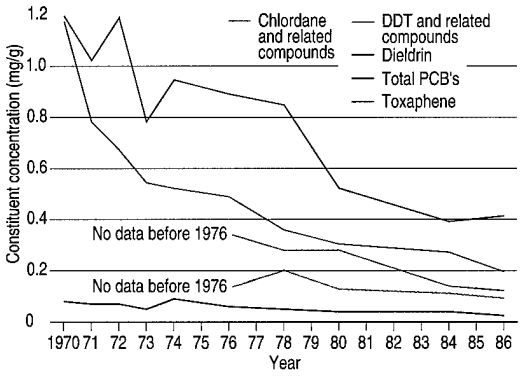
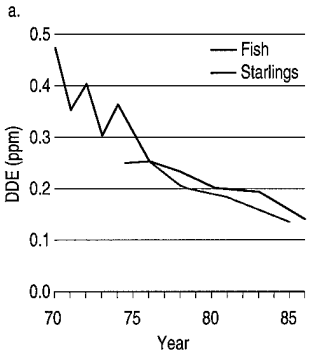


Fig. 12. Concentrations of organochlorine chemicals in U.S. freshwater fishes, 1970–1986 (U.S. Fish and Wildlife Service, National Contaminant Biomonitoring Program, unpublished data).



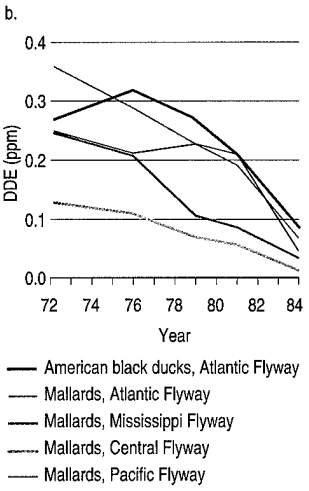
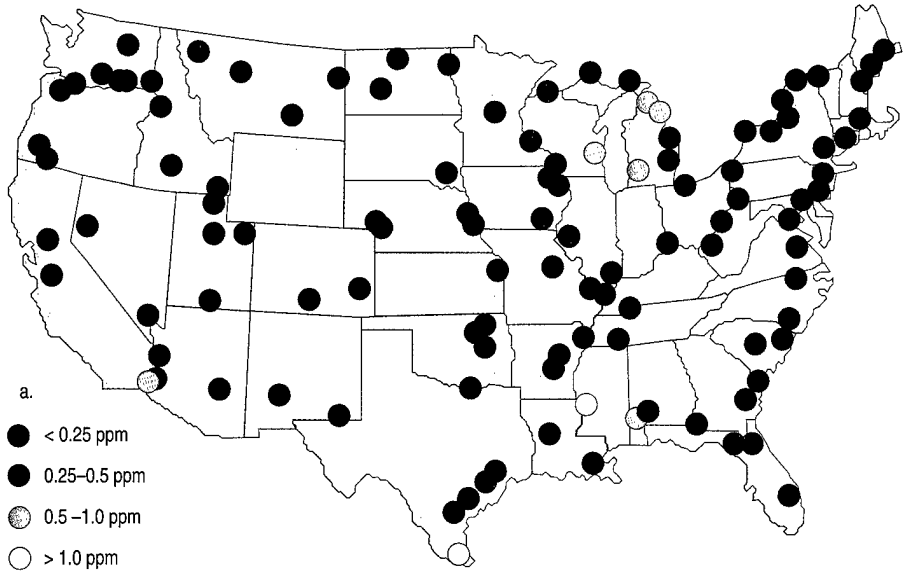


Fig. 13. Mean concentrations of DDE, the most stable metabolite of DDT, in U.S. Fish and Wildlife Service monitoring networks, 1970–1986: a) in freshwater fish and European starlings collected nationwide and b) in mallards and American black ducks from the four major flyways (from Schmitt and Bunck 1995).



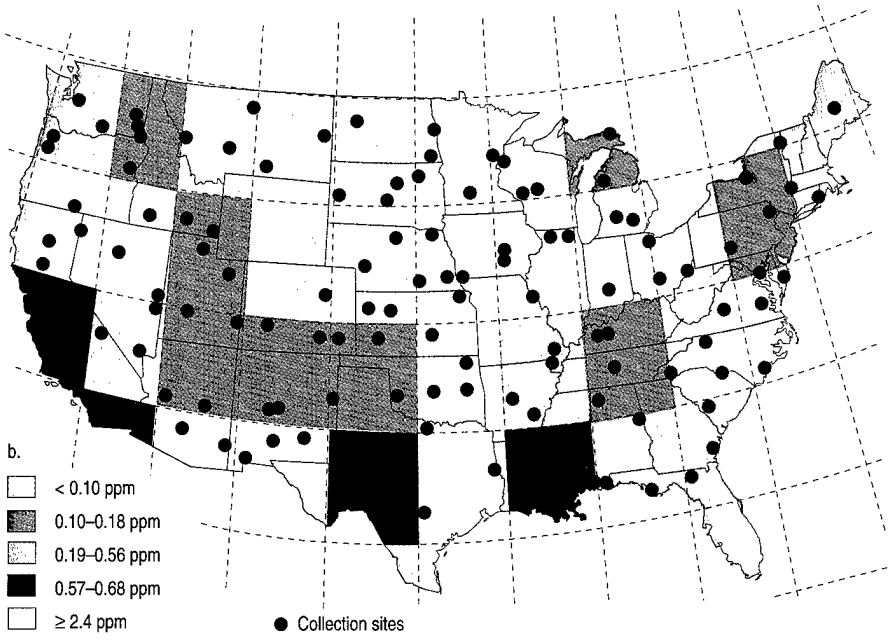


Fig. 14. Geographic distribution of DDE residues in the conterminous United States: a) in freshwater fish collected in 1986 from the indicated sites and b) in European starlings collected in 1985 from the indicated sites. Also shown are boundaries of the 5-degree (latitude and longitude) sampling blocks (dashed lines) and collection sites (red dots; from Schmitt and Bunck 1995).

Endocrine-Disrupting Compounds in the Environment

One of the most recent concerns associated with environmental contaminants is that some of these toxic chemicals may interfere with animal hormones. These compounds are referred to as endocrine disruptors because they disrupt normal functioning of the endocrine system. Many of the chemicals that may pose this threat have been in the environment for a long time (such as DDT), but only recently has this toxic mode of action been identified. The number of observations of aberrant endocrine functions in both human and wildlife populations that could be explained by contaminants working as endocrine disruptors is especially disconcerting (Colborn et al. 1993).

Some of the effects that have been attributed to endocrine disruptors have been dramatic enough to be described in the news media, including male American alligators with underdeveloped sex organs, vitellogenin (an egg and yolk protein normally found only in females) in male animals, and male Florida panthers with undescended testes and abnormal sex hormone ratios (Begley and Glick 1994; Raloff 1994). These examples typify estrogenic effects of endocrine disruptors, xenobiotic chemicals that, because of their chemical structures, can mimic estrogen, a female sex hormone. When the body's hormone receptors recognize the contaminant as estrogen, they respond as they would to the hormone, and the result is feminization of the exposed organism. Some of these effects may be more subtle than physical abnormalities and may manifest themselves as behavioral changes (Fox et al. 1978), such as aberrant behavior of birds during nesting, which can have significant effects on their nesting success.

Endocrine disruptors also may work in ways other than as estrogen mimics. Some compounds are thought to alter the activity of other sex hormones (androgens and progesterone), thyroxine, glucocorticoids, and possibly others. Endocrine disruptors may act not only by mimicking a hormone, as in the case of the estrogens previously described, but may also act as inhibitors (Kelce et al. 1995). Much current evidence points to early development (embryo, fetus, juvenile) as the most sensitive stages for exposure, although the effects on exposed young are often not apparent until an organism reaches sexual maturity, complicating the demonstration of cause and effect (Colborn et al. 1993).

Although some startling observations have been made in wildlife populations, epidemiological data from humans heighten concern about the endocrine disruption theory. There is evidence of a significant decrease in sperm counts in men over the last 50 years (Carlsen et al. 1992), with the exposure to endocrine-disrupting compounds a possible cause. Also, increasingly frequent human cancers over the last 20 years include those of the breast, ovaries, testes, and prostate (Reis et al. 1994), all tissues that are sensitive to sex hormones. One of the confounding factors in the theory of endocrine-disrupting contaminants as responsible for some of these observations is that naturally occurring compounds in some fruits and vegetables can also have estrogenic activity. Some scientists believe the amount of estrogenic activity an individual would receive from these naturally occurring chemicals in the diet is far greater than that from environmental contaminants.

These observations, and the implications of involvement of manufactured chemicals as a cause, prompted a national workshop sponsored by the U.S. Environmental Protection Agency in April 1995. This workshop brought together experts from human and ecological health research to discuss what was known about the potential for endocrine disruption due to environmental exposure, and to suggest what research is most urgently needed. While it appears that there is not enough scientific evidence to adequately address the health risks of endocrine disruptors, a dedicated research effort needs to be undertaken because of the magnitude of the potential impacts and the plausibility of this toxic mode of action.

See end of chapter for references

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delta waters of the Gulf of Mexico (Calder and Means 1987). Concentrations also remain slightly elevated in other areas where pesticide use was historically heavy, such as the California Central Valley (Saiki and Schmitt 1986) and the Yakima Valley, Washington (Johnson et al. 1988; Schmitt et al. 1990). Levels of DDT remain highest near sites of its former production and formulation (O'Shea et al. 1980; Calder and Means 1987; U.S. Environmental Protection Agency 1992; Schmitt and Bunck 1995; Turgeon and Robertson 1995).

Toxaphene concentrations also declined (Schmitt et al. 1990; Fig. 12), but residues of this insecticide may still affect biota. Although used most extensively on cotton in the South and Southwest, toxaphene is transported atmospherically to the Great Lakes (Rice and Evans 1984; Rice et al. 1986), where it accumulates in lake trout (Ribick et al. 1981). Toxaphene is a complex mixture of many compounds; it is especially toxic to fish. Although it degrades more rapidly than DDT and many other organochlorine compounds, the most toxic components resist degradation (Harder et al. 1983). Concentrations of these toxic components remain elevated in Great Lakes lake trout (Gooch and Matsamura 1987).

Elevated but declining concentrations of some organochlorine insecticides remain from agricultural use in the Corn Belt. They also persist near urban areas, where compounds such as aldrin, dieldrin, and chlordane were used to control termites; levels are especially high in Hawaii (Schmitt et al. 1990). Like DDT, concentrations of these insecticides also remain highest near sites of former manufacture and

formulation (U.S. Environmental Protection Agency 1992).

Many bird populations are recovering from the effects of eggshell thinning; for example, the U.S. Fish and Wildlife Service has proposed changing the status of the bald eagle from endangered to threatened in most of the conterminous states, the exception being the Southwest (U.S. Fish and Wildlife Service 1994), and herring gull populations are increasing in the Great Lakes (Weseloh et al. 1994). In parts of the Southwest, DDE concentrations remain somewhat elevated (Schmitt and Bunck 1995; Fig. 14), possibly from the continuing use of dicofol, an organochlorine miticide (Table 1) that may contain traces of DDT and DDE (Jarman et al. 1986). Historically, the accumulation of pesticides by migratory birds wintering outside of the United States was a concern (for example, Henny et al. 1982). Recently reported concentrations of DDE in migrating peregrine falcons sampled in southern Texas are low relative to the past (Mora 1995); nevertheless, migratory species are still exposed to organochlorine and other pesticides on their wintering grounds. Concentrations of DDE and other pesticides remain elevated in parts of the Rio Grande Valley (International Boundary and Water Commission 1994), however, and the peregrine falcon population of the trans-Pecos region is declining because of poor reproduction (McKinney 1994). Organochlorine insecticides have been shown to impair bird reproduction through mechanisms other than eggshell thinning in many species (for example, Fry and Toone 1981; Colborn et al. 1993). These insecticides also persist in soils, tending to accumulate in soil invertebrates (for example, Beyer and Gish 1980). Collectively, these findings indicate that organochlorine pesticides remain a threat to U.S. biological diversity.

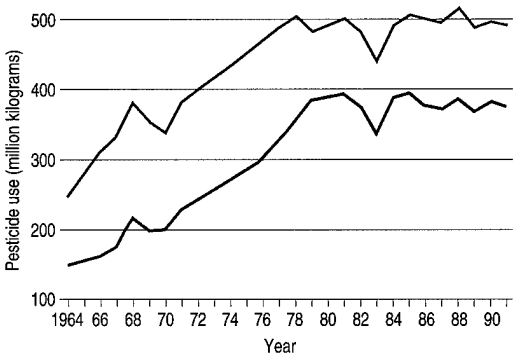

Fig. 15. Total and agricultural U.S. pesticide use, 1964–1991 (redrawn from Aspelin et al. 1992).

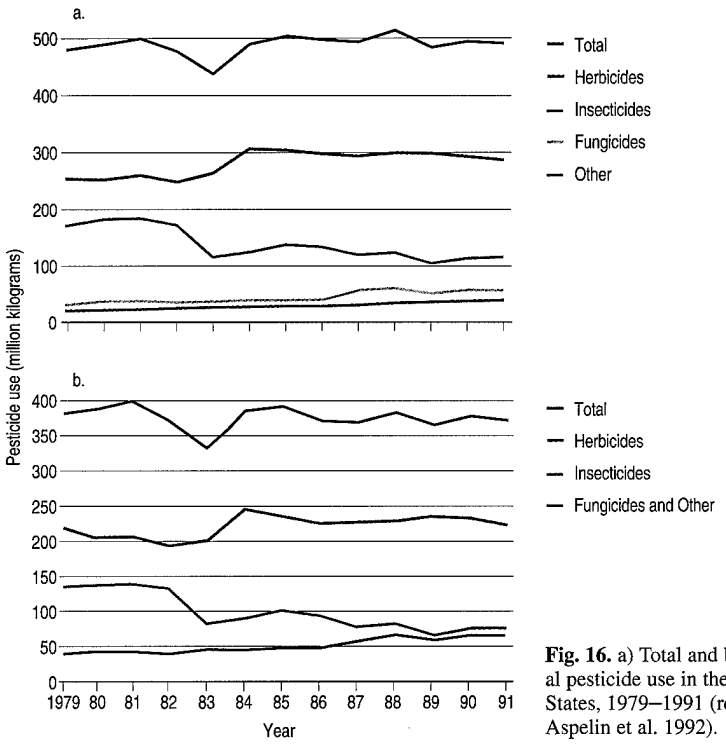

Fig. 16. a) Total and b) agricultural pesticide use in the United States, 1979–1991 (redrawn from Aspelin et al. 1992).

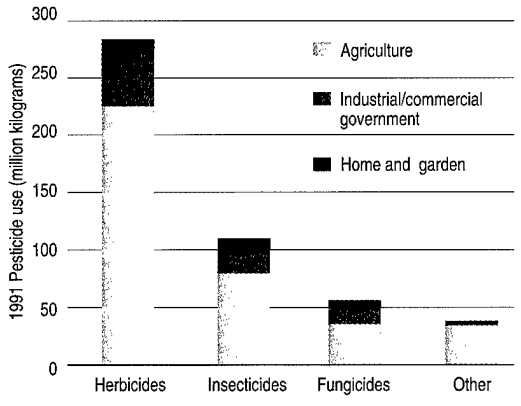

Fig. 17. United States pesticide use in three sectors, 1991 (redrawn from Aspelin et al. 1992).

New-Generation Pesticides: Organophosphate, Carbamate, and Synthetic Pyrethroid Compounds

Organochlorine pesticides began to be replaced in the late 1960's, first with organophosphorus and then carbamate and synthetic pyrethroid compounds. As these so-called soft pesticides, which degrade rapidly and do not accumulate, became more widely used from the mid-1960's through the late 1970's, pesticide use in the United States increased steadily (Fig. 15). Total pesticide use has remained at about 500 million kilograms annually since 1979, but total and agricultural insecticide use declined (Aspelin et al. 1992; Fig. 16). Agriculture accounted for 76%–77% of total United States pesticide use through 1990–1991 (Figs. 16 and 17), with corn and soybeans accounting for 62% of all pesticides used on crops (Gianessi 1986). The counties with the greatest total 1987 expenditures for agricultural chemicals were in the West, Midwest, mid-South, Texas, and Florida (Fig. 18). Highest values were in counties where fresh fruits and vegetables are grown for human consumption, in rice- and cotton-producing areas,

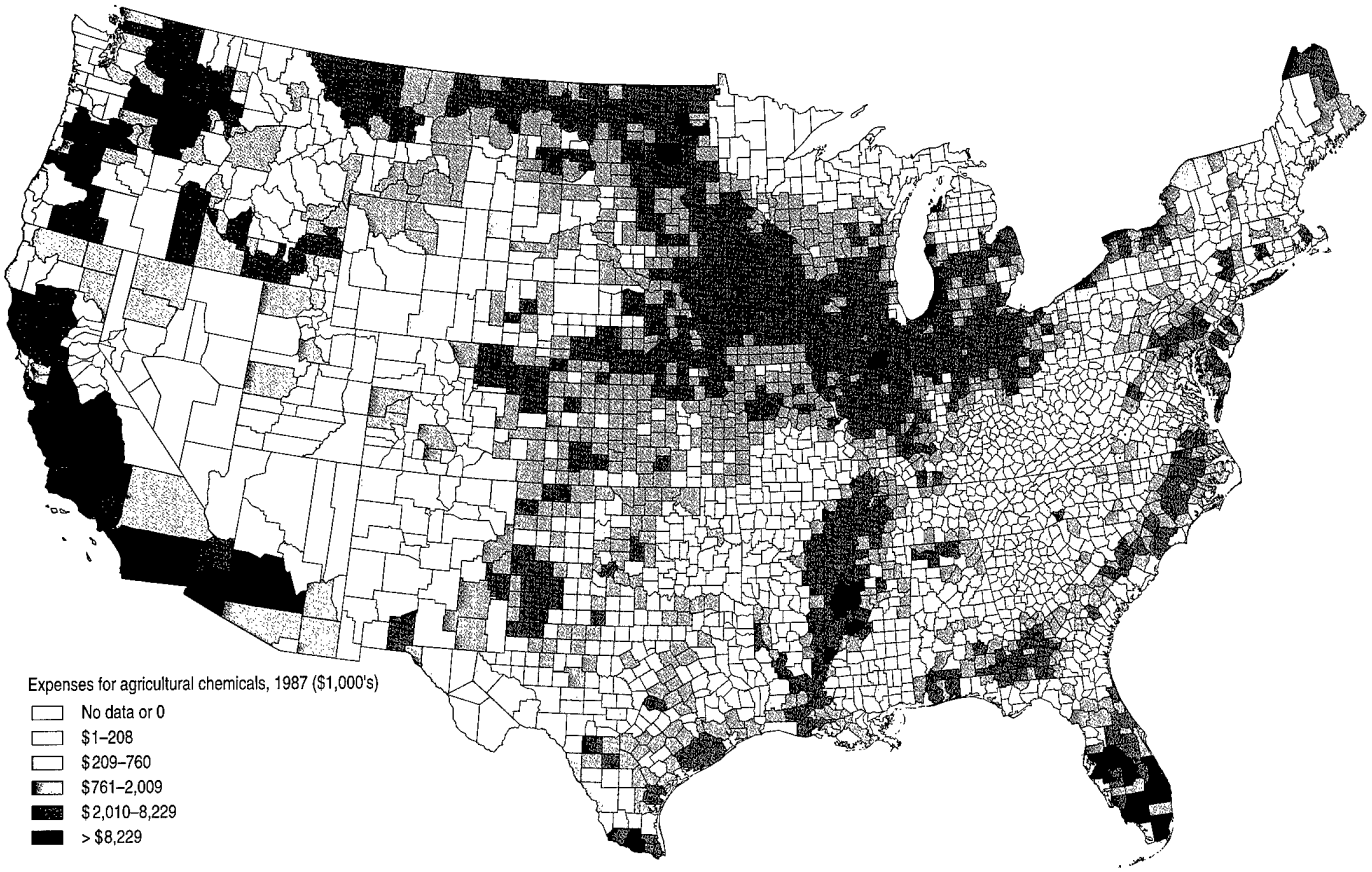

Fig. 18. Total 1987 expenditures for farm chemicals other than fertilizers, by county, in the conterminous United States (from Battaglin and Goolsby 1995).

and in the Corn Belt (Fig. 18). Among soft pesticides, the most heavily used compounds include methyl parathion, butylate, methomyl, carbaryl, terbufos, fonofos, and azinphos-methyl, all organophosphates and carbamates (Smith 1987; Table 1). Carbofuran (Table 1) was also heavily used in agriculture (Smith 1987), but its registration has been canceled (U.S. Environmental Protection Agency 1989).

Although soft pesticides are shorter-lived than organochlorines, do not accumulate, and the total amount in use has declined (Fig. 16), the high toxicity and fast action of many newer pesticides have resulted in increasing incidences of fish and wildlife kills (Glaser 1995).

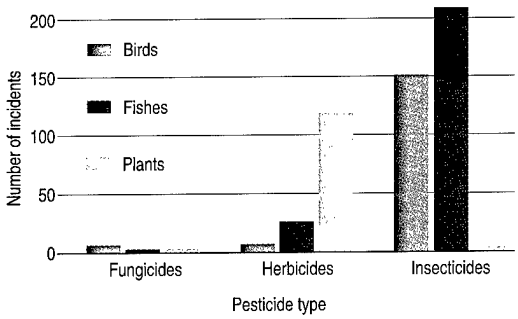

Fig. 19. Reported incidences of kills of birds, fishes, and plants from three classes of pesticides, 1988–1993 (U.S. Environmental Protection Agency, Office of Pesticide Programs, Ecological Effects Branch, unpublished data).

Insecticides account for most of these incidents (Fig. 19). Some 270 species of birds have been represented in more than 500 kills reported from 1988 to 1993. Incidents vary in size from a few to thousands of birds. Songbirds are most often affected; carbamate pesticides have been implicated most frequently as the cause in kills of songbirds and raptors, and organophosphates most often involved in kills of fish and waterfowl (U.S. Environmental Protection Agency, Office of Pesticide Programs, unpublished data). As described earlier for oil spills, exact numbers of organisms affected in pesticide-poisoning incidents are difficult to determine. Incident investigations are neither systematically nor uniformly conducted, and the reports are therefore difficult to interpret (for example, Greig-Smith 1994). Laboratory and field investigations have shown that delayed mortality and altered reproductive and predator-avoidance behavior occur, and losses attributable to these effects are not represented in kill numbers (for example, Mineau and Peakall 1987). Consequently, numbers of dead organisms reported are probably far lower than the true totals. Despite these difficulties, pesticides, primarily from agriculture, were estimated to have caused the deaths of 6–14 million of the 141 million fish that died annually in fish kills from

1977 to 1987, and 672 million birds are directly exposed to high concentrations of pesticides each year in the United States; 67 million of these birds die (Pimentel et al. 1992). Carbofuran was estimated to have killed 1–2 million birds annually in the United States during the early 1980's (U.S. Environmental Protection Agency 1989). Recent declines in some wildlife populations, including the endangered Indiana bat in Missouri (R. Clawson, Missouri Department of Conservation, unpublished 1994 annual survey data), have raised new concerns about currently used agricultural chemicals.

Soft pesticides are highly toxic to terrestrial and aquatic invertebrates, including beneficial predatory insects and those that pollinate plants. Insect losses from pesticide use can affect populations of insectivorous birds, mammals, and other wildlife (for example, Seidel and Whetmore 1995). No estimates of the cumulative effects of pesticides on invertebrate biological diversity or secondary effects on insect-dependent wildlife are available; however, annual U.S. economic losses attributed to the effects of pesticides on insect pollination (including losses of commercial honey bees) and other beneficial insects are valued at $840 million (Pimentel et al. 1992). Recent evidence indicates that new-generation pesticides may affect the homing behavior of honey bees at sublethal concentrations (Vandame et al. 1995); the total losses due to pesticides may therefore be much greater. Soft pesticides are also highly toxic to aquatic invertebrates, including pearlymussels and the larvae of many aquatic insects. A recent kill of endangered tar spinymussels in Nash County, North Carolina, was attributed to soft pesticides (Fleming et al. 1995). Pearlymussel die-offs have been reported with increasing frequency since the 1980's throughout the United States (Neves 1987), but the involvement of pesticides or other contaminants in these incidents has not been fully investigated. In general, exposure of organisms to soft pesticides is difficult to gauge because most compounds neither persist nor accumulate.

Herbicides

Stimulated by high fuel costs, chemical weed control became increasingly common in United States agriculture during the 1970's. Consequently, much of the increase in United States agricultural pesticide use since the 1960's is attributable to agricultural herbicide increases (Figs. 15, 16, and 17). Corn (45%), soybeans (18%), pasture (6%), cotton (6%), sorghum (5%), wheat (4%), and rice (3%) account for most U.S. agricultural herbicide use (Gianessi and Puffer 1991). Atrazine, alachlor, metolachlor, trifluralin, cyanazine, metribuzin, glyphosate, and 2,4-D (Table 1) are the most heavily used compounds (Gianessi and Puffer 1991; Aspelin et al. 1992). Herbicide use is heaviest in the Midwest, South, and mid-Atlantic regions, and in Florida, California, and Oregon (Battaglin and Goolsby 1995). Until recently, herbicides and defoliants containing arsenic were used heavily in orchards and in cotton production; consequently, arsenic concentrations in soils and in waters draining extensively treated areas can remain elevated (Sheets 1980). Arsenical herbicides remain registered for use in cotton and for weed control in turf, including lawns.

Although there are exceptions (for example, Eisler 1990; Fig. 19), most currently used herbicides do not accumulate in biota nor are they acutely toxic to animals at environmental concentrations (Hoffman 1990, 1994). Herbicides are highly toxic to nontarget terrestrial and aquatic plants (Kemp et al. 1983, 1985; Cunningham et al. 1985), however, which has raised new concerns. Because of their widespread use—and for some compounds, persistence—herbicide contamination of surface and groundwaters in agricultural areas has become common (for example, Paulson et al. 1993). Atrazine is heavily used in the Midwest and in the Chesapeake Bay watershed for weed control in corn (Fig. 20). Some 235,000 kilograms of atrazine were estimated to have been exported from the Mississippi River to the Gulf of Mexico in 3 months during 1991 (Goolsby et al. 1991). The effects of chronic herbicide pollution on aquatic vegetation in the Midwest (where concentrations are highest overall) and in the Gulf of Mexico have not been investigated. In Chesapeake Bay, atrazine and other herbicides were estimated to have contributed, along with nutrient enrichment and sedimentation, to the decline of submerged aquatic vegetation (Kemp et al. 1983; Sanders 1987). Aquatic vegetation has recovered somewhat in the brackish regions of Chesapeake Bay since the early 1980's but not in the freshwater areas of the upper bay (Pendleton 1995). The involvement of herbicides in declines of aquatic vegetation elsewhere has received less study.

A recent, comprehensive ecological risk assessment of atrazine revealed that atrazine application rates have declined somewhat over the last decade, and that concentrations in surface waters are not sufficiently high enough to represent a significant risk except in small reservoirs and streams receiving agricultural runoff (Solomon et al. 1996). Nevertheless, the long-term, cumulative risks of herbicide pollution have not been fully assessed. The distributions of aquatic and terrestrial animals are highly dependent on plant distributions (for example, Chick and McIvor 1994). Consequently,

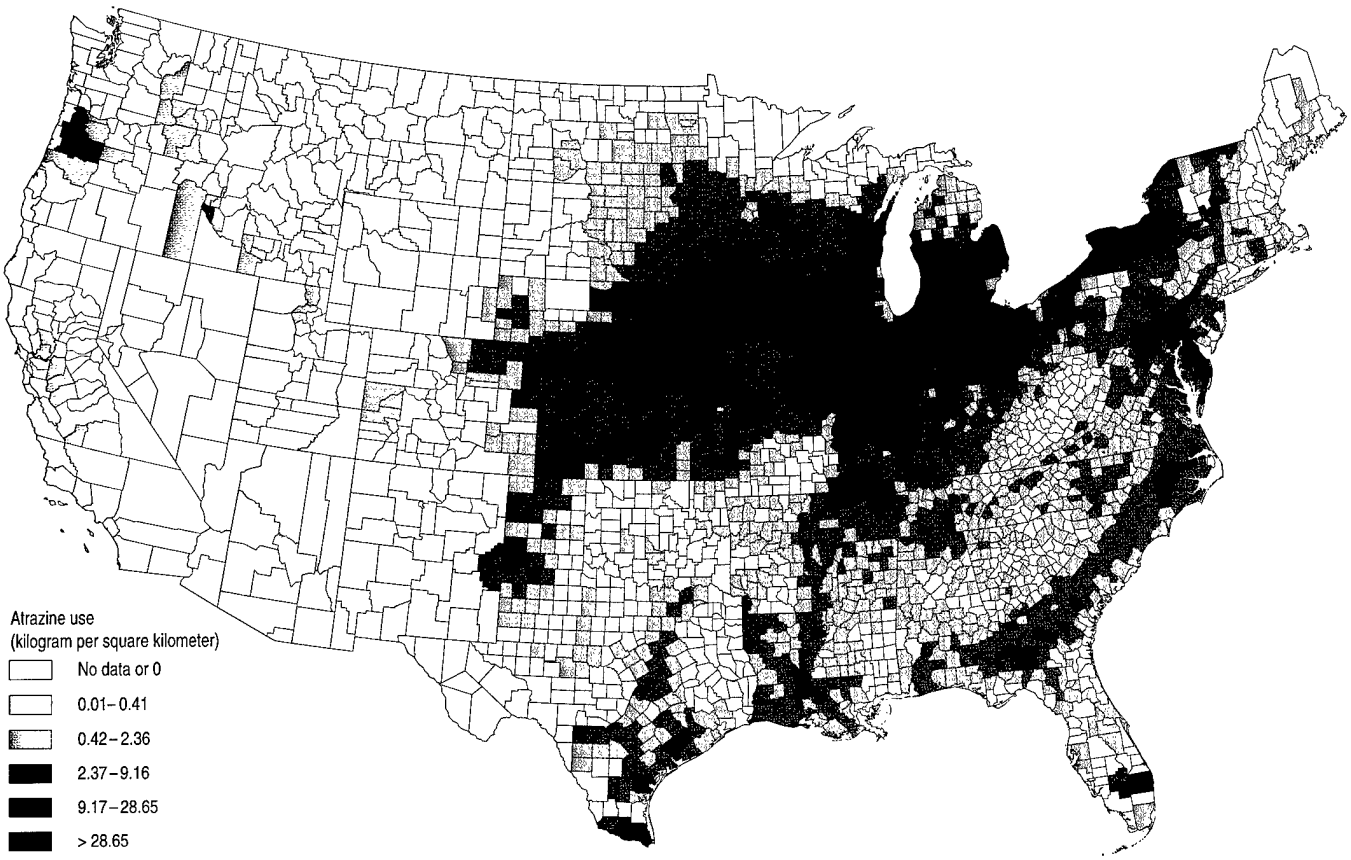

Fig. 20. Use of atrazine, by county, in the conterminous United States in 1987 (from Battaglin and Goolsby 1995).

chronic, low-level herbicide pollution may alter the structure of plant communities, which, in turn, can influence the distribution of animals (for example, Cooke 1977). Because the use of herbicides at current levels is unprecedented, long-term effects on nontarget vegetation and secondary effects on animal populations are unknown.

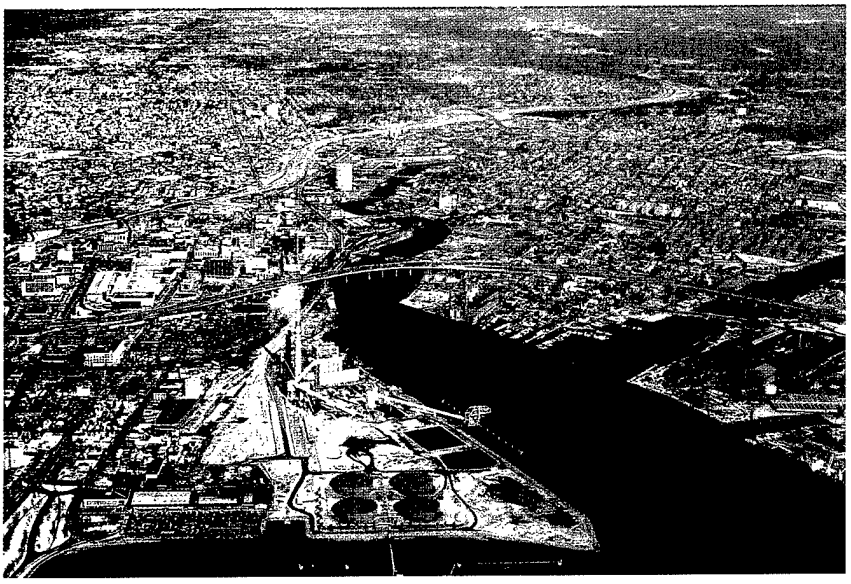

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Fig. 21. Aerial photograph of Bridgeport, Connecticut, an urban–industrial estuary.

Industrial and Urban Development

Many of the most environmentally significant contaminants that emanate from industries and population centers have already been discussed in the context of other human activities. These include contaminants associated with mineral and energy exploitation: lead, mercury, other metals, arsenic, and selenium—all from industrial and municipal discharges, fossil fuel combustion, and solid waste disposal (that is, landfills and incinerators); PAH's and other organic compounds from fuels, lubricants, solvents, and industrial processes; combustion gases (SO_2, NO_x, CO, CO_2) from domestic, industrial, and automotive fuel consumption; nutrients from wastewater treatment plants and urban runoff; and pesticides from manufacturing and formulation facilities and from runoff in urban and suburban areas (Fig. 21). Certain industries, including those already noted—pesticide manufacturing and formulation (pesticides and precursors), petrochemicals and petroleum refining (numerous industrial and commercial chemicals, PAH's and related compounds, metals), chlor-alkali production (mercury), and base and precious metal reduction and manufacturing (metals, PAH's, PCB's)—

were historically responsible for the release of large quantities of contaminants to the environment. The forest products industry, which includes pulp-making, paper-making, and wood-treatment facilities, released PCB's, dioxins, mercury, wood preservatives including creosote and pentachlorophenol (Table 1), and other toxic by-products at numerous locations throughout North America.

Relatively few of the thousands of industrial and consumer chemicals manufactured and released into the environment have been thoroughly tested and evaluated. Of those that have, even fewer (other than the contaminants already discussed) have been found to be toxic at environmental concentrations. Among toxic industrial chemicals, the industrial organochlorine compounds have been the most injurious to biota. These chemicals are structurally similar to organochlorine pesticides, with which they also share many toxicological and environmental fate properties. This group includes PCB's, chlorinated dioxins, and other structurally similar compounds (Table 1), some of which bioaccumulate and are highly toxic to fishes and wildlife. The group also includes chlorofluorocarbons (CFC's) and volatile organic compounds (VOC's)—air pollutants involved in global climate change and thinning of the Earth's protective ozone layer (Table 1).

Polychlorinated Biphenyls, Dioxins, and Dibenzofurans

Polychlorinated biphenyls (PCB's), dioxins, and dibenzofurans are families made up of many structurally similar compounds that vary greatly in toxicity and persistence. Among them are some of the most toxic and persistent chemicals yet investigated (for example, Safe 1990). Chlorinated dioxins were first discovered as toxic by-products of chlorophenols, which are feedstocks for the synthesis of many products (U.S. Environmental Protection Agency 1992; Table 1). Early formulations of the wood preservative pentachlorophenol and of the herbicide 2,4,5-T (Table 1) were also contaminated with chlorinated dioxins; wood treatment and herbicide manufacturing facilities synthesizing, formulating, or using these materials were significant sources of these compounds to the environment (U.S. Environmental Protection Agency 1992). Chlorinated dioxins were also produced by bleaching processes used historically in paper manufacturing and are released into the atmosphere from many combustion sources including municipal waste incinerators and cigarette smoke (Muto and Takizawa 1989; U.S. Environmental Protection Agency 1992).

Trace quantities of chlorinated dioxins occur widely in North America because of their persistence and diversity of sources. Concentrations tend to be highest in waters that received direct discharges from point sources, such as sites of herbicide and hexachlorophene synthesis and formulation. Examples include the Passaic River and Newark Bay, New Jersey; the Kanawha River, West Virginia; Bayou Meto, Arkansas; the Brazos River, Texas; and tributaries of Saginaw Bay, Michigan. Concentrations are also elevated in waters that received effluents from bleached kraft paper mills, which are widely distributed throughout North America (Kuehl et al. 1989; U.S. Environmental Protection Agency 1992).

Relatively small amounts of chlorinated dioxins and dibenzofurans occur in the environment as impurities and by-products of other substances. In contrast, large quantities of PCB's were manufactured for use in many applications (Table 1). First synthesized in 1881, some 635 million kilograms were produced in the United States alone from the beginning of commercial production in 1929 until the use, manufacture, and distribution of PCB's were discontinued in 1979 (U.S. Environmental Protection Agency 1979). Because of their longevity and widespread use in consumer products, contamination by PCB's is widespread, and concentrations tend to be elevated near all human population centers (Schmitt et al. 1990; U.S. Environmental Protection Agency 1992). Concentrations are generally highest near former point sources, primarily facilities that manufactured electrical and hydraulic equipment, paper mills that either produced or recycled carbonless copy paper, and metallurgical facilities, including foundries. Such point sources initially contaminated many waterways, including the Housatonic, Hudson, St. Lawrence, and Ohio rivers; New Bedford Harbor, Massachusetts; Waukeegan Harbor and Green Bay on Lake Michigan; Saginaw Bay on Lake Huron; and Lake Ontario.

Despite being manufactured and distributed since 1929, PCB's were not recognized as environmental contaminants until the 1960's, when they were discovered in fish and wildlife from the Baltic Sea (Jensen 1966). Soon after, PCB's were found to have accumulated in Lake Michigan coho salmon (Johnson and Pecor 1969), which caused birth defects and early kit mortality in ranch mink raised on salmon (Aulerich et al. 1971; Aulerich and Ringer 1977). Subsequently, PCB's and chlorinated dioxins have been among the most intensively and extensively investigated pollutants. Because some dioxins and PCB's are highly toxic and bioaccumulate, they are especially hazardous to predatory fishes and fish-eating birds and mammals. Significant ecological effects attributable to the reproductive toxicity of these and related

compounds have either been documented or are suspected to have occurred in fishes, reptiles, mammals, and birds, especially in the Great Lakes basin (Colborn 1991). Affected bird populations in the Great Lakes basin include the endangered Forster's terns of Green Bay, Wisconsin, in which reduced reproductive success and a high rate of deformities in hatchlings have been documented (Kubiak et al. 1989; Ankley et al. 1993); double-crested cormorants, in which hatching success is negatively correlated with dioxinlike activity of PCB's in eggs (Fig. 22); and bald eagles, in which coastal populations that eat fish with access to the Great Lakes reproduce less successfully than inland populations (Colborn 1991; also see chapter on Great Lakes). Reproductive impairment or population declines attributable to organochlorine chemicals—including PCB's and dioxins—have also been documented in Great Lakes populations of lake trout, coho and chinook salmon, snapping turtles, black-crowned night-herons, Caspian terns, common terns, herring gulls, ring-billed gulls, ospreys, mink, and river otters (Johnson and Pecor 1969; Mineau et al. 1984; Colborn 1991; Mac and Edsall 1991; Spitsbergen et al. 1991; Tillitt et al. 1991a,b, 1992; Wren 1991; Mac et al. 1993). The white whale population of the Saguenay–St. Lawrence estuary has also been affected (Colborn 1991). Elsewhere, PCB's were suspected of having caused a precipitous decline in the abundance of mink in the Upper Mississippi River corridor during the 1960's, from which the population has since partially recovered (Wiener et al. 1995). Dioxins and PCB's are suspected of inhibiting reproduction in the bald eagle population nesting along the Hood Canal, Washington (U.S. Fish and Wildlife Service, Division of Environmental Contaminants, unpublished data). Delayed egg maturation and reduced reproductive success in the starry flounder population of San Francisco Bay have also been attributed to PCB's (Spies and Rice 1988). Additionally, dioxins and PCB's are among the contaminants implicated in recent die-offs of bottlenose dolphins on the Atlantic and gulf coasts (Kuehl et al. 1991; Hutchinson and Simmonds 1994); the mid-Atlantic population has been declining over the last decade (Kuehl et al. 1991).

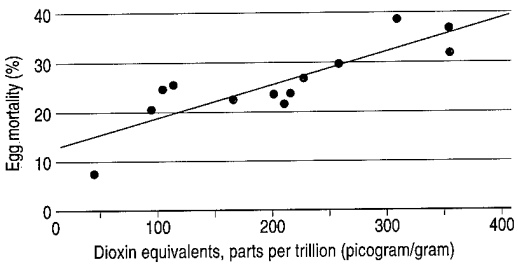

Fig. 22. Egg mortality in Great Lakes colonies of double-crested cormorants versus PCB's in eggs as dioxin-equivalent concentrations, 1987–1988 (Tillitt et al. 1991b); each point represents the mean for a colony. A similar relation between dioxin equivalents and hatching success has been demonstrated for United States bald eagles (D. E. Tillitt, U.S. Geological Survey, unpublished data; Tillitt et al. 1991a).

Restrictions on the sale and use of PCB's since the mid-1970's have resulted in reduced PCB concentrations in biota. Nationwide, PCB concentrations declined in freshwater fishes (Fig. 12) and European starlings through the mid-1980's (Bunck et al. 1987; Schmitt et al. 1990; Schmitt and Bunck 1995). Substantial declines occurred in heavily contaminated areas such as the Great Lakes and the Hudson and Ohio rivers (Mineau et al. 1984; St. Amant et al. 1984; Baumann and Whittle 1988; Hesselberg et al. 1990; Schmitt et al. 1990). Residues of PCB's nevertheless remain widespread because of their persistence and dispersion in water and air. Concentrations remain highest in the industrialized areas of the Northeast and Midwest (Fig. 23). The sediments of heavily contaminated waterways, which can be redistributed by natural processes as well as by human activities such as dredging and dredge spoil disposal, remain a significant and continuing source of PCB's, dioxins, and other contaminants to the environment, as do PCB's in consumer products either still in circulation or deposited in landfills. In addition, the toxicity of the PCB's, dioxins, and related compounds remaining in the environment may not be declining because the most toxic components among them may be selectively accumulated and resistant to degradation (for example, Kuehl et al. 1987; Tanabe et al. 1987; Kannan et al. 1989; Smith et al. 1990; Tillitt et al. 1992). Therefore, upper-level predators in marine and aquatic food chains—predatory fishes, fish-eating birds, and marine mammals—remain at risk. Because of the great difficulty and expense of analyzing dioxins or individual PCB's, there are no U.S. trend data for them.

Chlorofluorocarbons and Volatile Organic Compounds

Chlorofluorocarbons (CFC's) and volatile organic compounds (VOC's) are pollutants that are not generally perceived as directly toxic to plants or animals at environmental concentrations. Rather, CFC's and VOC's have the potential to affect biological diversity indirectly by altering the composition of the atmosphere. The VOC's have been used widely in industrial and

consumer applications (Table 1). Chloroform, one of the most widespread VOC's, can also be produced by chlorination of water and sewage. The VOC's are common groundwater pollutants, but concentrations in surface waters are generally low (Schwartzenbach and Giger 1985). The CFC's (Table 1) comprise widely used gases (Cumberland et al. 1982). In the troposphere (lower atmosphere), CFC's and VOC's contribute to the greenhouse effect and global warming. Through a complex series of chemical reactions, they also contribute to smog and ozone production, which damage vegetation.

Total CFC emissions have declined since the mid-1970's, primarily because of restrictions on their use in open-cell foams and as propellants; however, CFC releases from other applications, including refrigeration, continued to increase through the early 1990's (Boden et al. 1994). The long-term fate of CFC's and their breakdown products, which accumulate in the stratosphere (upper atmosphere), is unknown. In the stratosphere, CFC's, VOC's, and their degradation products contribute to ozone depletion, which enhances the penetration of damaging ultraviolet solar radiation (that is, UV-B). The DNA of plants and animals can be damaged by UV-B (van der Leun and de Gruijl 1993), which also interferes with the immune function in animals (Fabacher et al. 1994). The ecological risks associated with UV-B exposure vary for two primary reasons: because species differ in their sensitivity (for example, Little and Fabacher 1994), and because the distribution of UV-B is not geographically uniform (Madronich 1993). Aquatic and marine organisms that congregate near the water surface, as well as high-elevation plants and animals, are particularly vulnerable to UV-B. Among sensitive high-elevation organisms is the Lahontan cutthroat trout, a threatened species (Little and Fabacher 1994). Recent declines in California populations of western toads and Cascades frogs have been attributed to the inability of these species to repair UV-B-induced DNA damage (Blaustein et al. 1994).

Current stratospheric concentrations of CFC's and related compounds are the highest ever recorded (Anderson et al. 1991), and ozone depletion, formerly observed only over Antarctica, now also occurs periodically over North America (Kerr and McElroy 1993). The distribution and abundance of many organisms, including those most responsible for the primary and secondary productivity of the oceans, may currently be limited by UV-B irradiance (Calkins 1982; Häder 1993). If so, forecasts of UV-B increases in North America as a consequence of stratospheric ozone depletion will influence biological diversity over a wide area.

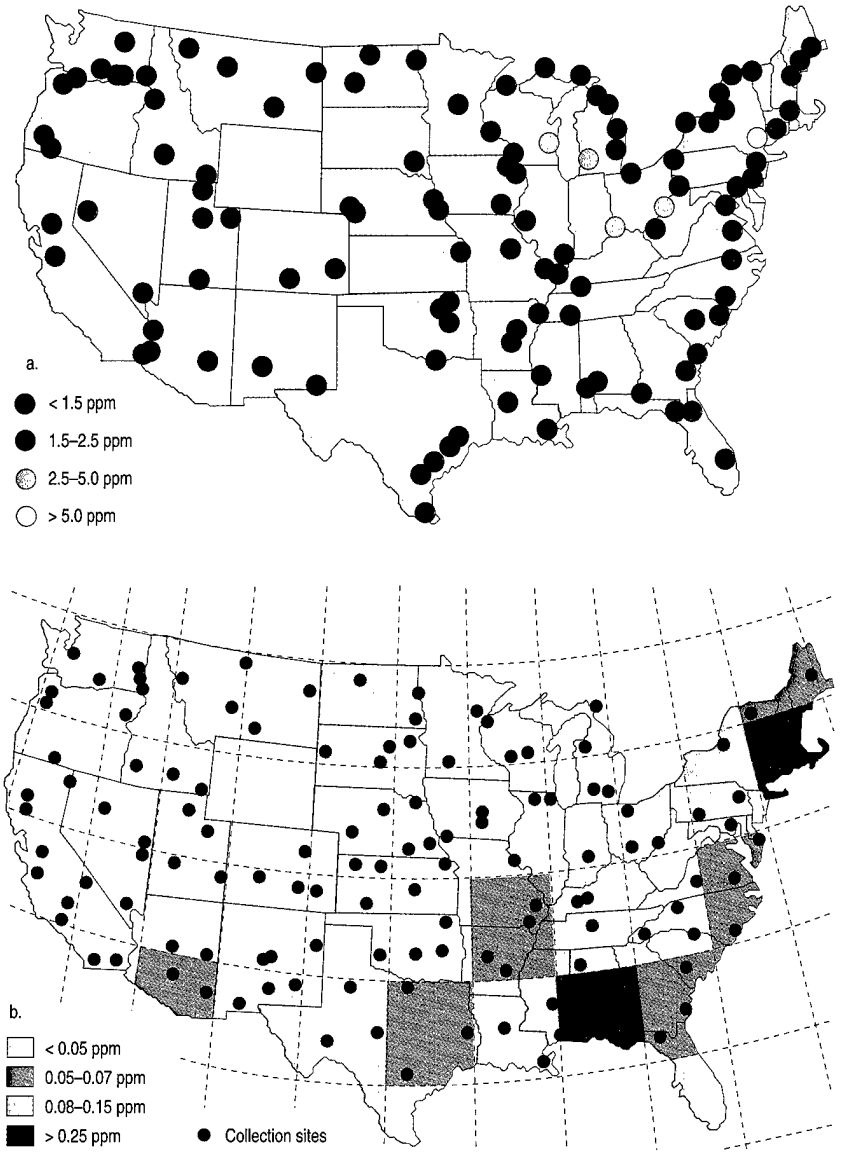

Fig. 23. Geographic distribution of PCB residues in the conterminous United States: a) in freshwater fishes collected in 1986 from the indicated sites and b) in European starlings collected in 1985 from the indicated sites. Also shown are boundaries of the 5-degree (latitude and longitude) sampling blocks (dashed lines) and collection sites (red dots; from Schmitt and Bunck 1995).

Summary, Conclusions, and Information Needs

Environmental contaminants are generally perceived as a twentieth-century problem. To the contrary, some of the most significant contaminants are biogenic (for example, petroleum), are natural constituents of the Earth's crust (arsenic, selenium, and metals), or result from the combustion of biogenic materials (PAH's). Accumulation to harmful concentrations may result naturally but occurs primarily when human activities such as agriculture, mining, logging, and dredging accelerate rates of natural processes. Once released into the environment, contaminants are distributed with water, air, soil, and sediment—the same

processes and media that govern the distribution of nutrients and other substances. Consequently, contaminants may affect biota long distances from their sources. Many of our most serious contaminant problems originated from the application of old-world mineral and energy extraction technologies at unprecedented rates. Subsequent problems developed as unforeseen consequences of accelerated energy and mineral extraction and of the industries, technologies, and human population centers they engendered. Many of these processes and problems predated environmental concerns and the technology and scientific knowledge base necessary to detect and interpret them, and their effects may have been masked by other natural and anthropogenic factors.

The comparatively recent regulation of toxic pollutants has lowered United States concentrations of many of these pollutants to the lowest levels since measurements began. Regulation of surface and subsurface mining and of direct discharges of pollutants to waterways and to the atmosphere, and the replacement of most bioaccumulative toxins with environmentally kinder alternatives have collectively reduced inputs of many pollutants to North American ecosystems. Concentrations of many toxins have declined accordingly. Reclamation has reduced the extent and magnitude of acid mine drainage from historically and actively mined lands, but whether effects on biota have been successfully mitigated has not been determined. Problems related to regulated contaminants persist, but they are primarily associated with historically contaminated sites, the atmospheric and waterborne redistribution of pollutants already released into the environment, and continuing use of these products outside North America. With the reductions in emissions, the sediments of industrialized waterways and the atmosphere have become important contaminant sources. The continuing discovery of potentially significant ecological effects attributable to regulated contaminants at environmental concentrations previously thought safe implies that further reductions may be warranted. With traditional contaminant sources regulated, future reductions in environmental concentrations will have to result from the control of more diffuse sources. These include agricultural soil erosion, urban runoff, and the atmospheric and waterborne transport of contaminants from artificial and natural sinks—industrial and mining waste disposal sites, landfills, and contaminated sediments.

In eastern North America, there is some evidence that recent restrictions on SO_2 emissions can reduce the acidity of surface waters (Lettenmaier et al. 1991; Clair and Ehrman 1995). Nevertheless, recent global increases in fossil fuel consumption increased atmospheric CO_2 concentrations by 12.8% from 1959 to 1992 (Boden et al. 1994), much of which was attributable to coal and oil combustion. Because fossil fuel combustion also releases mercury, selenium, and other elements into the atmosphere, it may be a source of the increasing concentrations of these elements observed in some parts of North America over the last decade. North American and worldwide electric power generation is expected to increase. Total emissions of toxic elements, PAH's, and SO_2 could increase correspondingly, offsetting anticipated future decreases at individual sources. Similarly, expected increases in petroleum consumption, especially in the transportation sector (Greene and Santini 1993), are expected to increase total pollutant emissions despite reductions from individual sources. Thus, increases in NO_x emissions from transportation sources could partly offset gains in rainfall pH made by reducing SO_2 emissions from stationary sources such as power plants. In addition, global economics determine the rate at which domestic energy supplies are exploited and, consequently, the rate at which energy-associated pollutants are released into North America. At present, U.S. oil demand is met largely by foreign sources. Should economic and political factors favor the large-scale exploitation of domestic energy sources such as oil shale and coal-based fuels, large quantities of toxins would be released. Mineral and energy exploitation effects would most likely occur in those parts of the West where biological diversity is already limited by water quality and quantity.

Environmental toxicology is a relatively new field that has focused primarily on the study of individual contaminants and on the distribution and abundance of toxins. Far less is known about the cumulative effects that the many chemicals released into the environment have had on biota, especially against the background of other human-induced perturbations. Although the need to link toxicology and population biology has been recognized (for example, Kendall and Lacher 1994), relatively few investigations of long-term effects of contaminants on populations have been undertaken. At the population level, evaluation of chemical or other effects requires information on the extent and magnitude of the stresses and losses to which populations are subjected and the size and status of the populations (for example, Pulliam 1994). This latter information is largely unknown for most species. Still more difficult to evaluate are sublethal effects on such aspects of species biology as reproductive and migratory behavior, which can be affected by pesticides and other contaminants at low concentrations. In addition, many new-generation pesticides are

short-lived and do not accumulate, making it difficult to document exposure. Collectively, these difficulties confound efforts to estimate the extent and population-level significance of losses from contaminants. The lack of this information is the greatest impediment to a full understanding of the significance of chemical exposure; that is, considerably more is known about chemicals and what they can do than about what they have actually done (Gilbertson and Schneider 1991). And finally, the advent of widespread contamination by synthetic chemicals is recent and unprecedented. These chemicals therefore represent a source of selective pressure to which long-lived organisms and ecosystems may not have adapted. Long-term study will be necessary to discriminate the effects of contaminants from those of other environmental stresses and natural variability if problems are to be foreseen and remedied before irreversible ecological harm occurs.

Acknowledgments

I thank R. Kendall and the graduate students of The Institute of Wildlife and Environmental Toxicology, Clemson University, and two anonymous reviewers for comments on an earlier version of the manuscript; E. Callahan, P. Greene, M. Laustrup, and J. Thomas for assistance with illustrations; and L. Jacobs for library and information services. I also thank P. Baumann, C. Brussard, D. Chapman, S. Finger, T. Haines, D. Hardesty, J. Layzer, G. Lear, D. Lemly, E. Little, B. McKinney, H. Ohlendorf, M. Saiki, D. Tillitt, and Normandeau Associates, Inc. for contributing maps, information, and photographs.

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Harvest

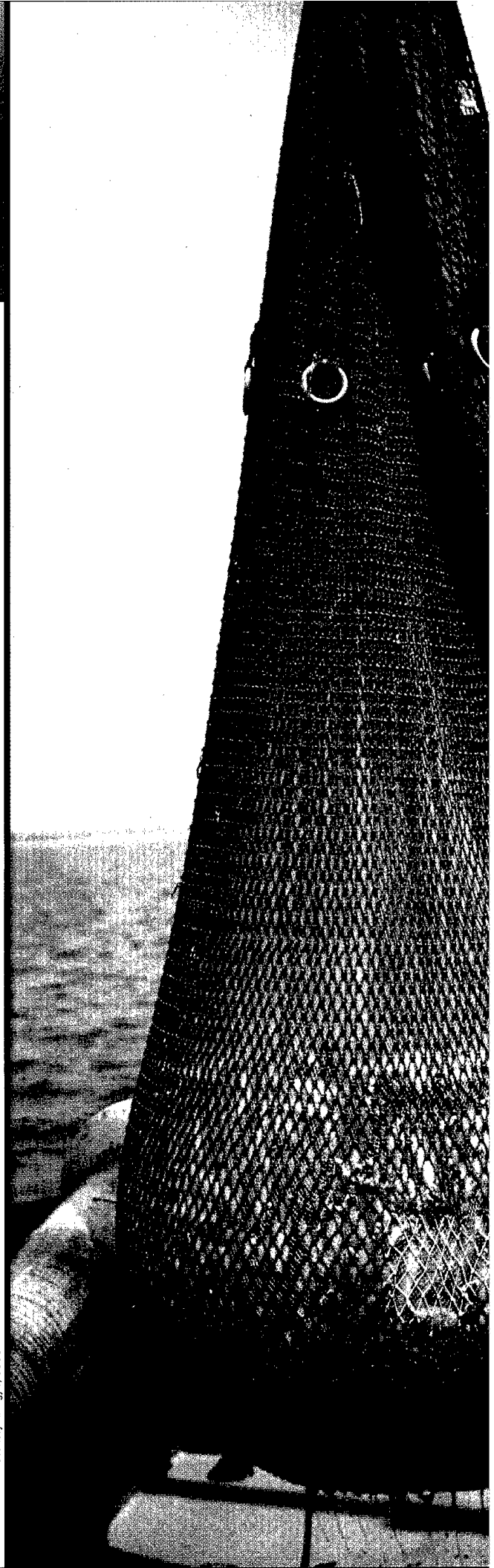
This volume contains a variety of chapters about the demonstrated and suspected effects of natural and human-related agents on biodiversity. The effects of human-related agents may be indirect (such as habitat or climate change) or inadvertent—perhaps even the result of well-intentioned efforts to preserve biodiversity, such as the isolation of nature preserves or the potential for disturbance caused by ecotourism. Although nonconsumptive use of wild species has increasingly become a focus for exploitation by humans, this chapter explores the direct effects of consumptive exploitation—harvest—on biodiversity.

Humans have long harvested, for commerce and for sport, many kinds of wild species from many different environments. Yet, as some human societies rethink their relations with other animal species (Scheffer 1976), the potential effects of harvest have become an increasingly contentious issue in the late twentieth century.

Much has been written about the effects of harvest, though the distinction between ethical and scientific arguments is frequently blurred (Decker et al. 1991). This chapter deals with some of the principal scientific arguments about the effects of harvest on biodiversity and skirts the ethical ones, if only because science, as a way of learning and improving the reliability of knowledge, might indirectly inform ethics, values, and therefore policies (Clark 1992; H. R. Pulliam, statement by the director, National Biological Service, before the House Appropriations Subcommittee on Interior and Related Agencies, 1995).

Historically, the scientific arguments about the effects of harvest on biodiversity revolved around how harvest affected the abundance or persistence of populations of single species, issues that still dominate the scientific literature and the day-to-day activities of many agencies charged with the management of natural resources. It is widely acknowledged, however, that we have little reliable information about the effects of harvest on wild populations. To improve our knowledge, we need a fundamentally new relation between the science and management of natural resources—namely, adaptive management (Walters 1992; Ludwig et al. 1993; Williams and Johnson 1995; Williams et al. 1996). By definition, biodiversity is exceedingly more complex than the most complex single population, so it follows that the potential effects of harvest on biodiversity must be exceedingly more complex. Because such complex issues cannot be dealt with in their entirety in this chapter, I focus on a few examples across several levels of biological structure from genes to populations and to ecosystems. I show that harvest exploitation *necessarily* alters some aspects of biodiversity. Thus, by extension, even nonconsumptive exploitation that indirectly, yet effectively, "removes" or prevents organisms from normal interactions in populations must also alter biodiversity. At the end of the chapter, I discuss the much more contentious issue about whether such change actually matters, to whom or what it matters, and how we might go about understanding these issues.

Much of the contention about the effects of harvest on individual populations exists, at least in part, because arguments frequently are rife with undefined terms. To help avoid similar problems and to erect a framework for the remainder of this chapter, I briefly define biodiversity and its relation to individual species and to populations (the traditional foci for studies of the effects of harvest exploitation). I then quickly review the concepts of sustainable use and sustainable yield management and how



Courtesy R. Argyle, USGS

harvest affects populations. Within this framework, I discuss the potential effects of harvest on biodiversity.

Biodiversity

Diversity is a state of variety, or variability, among objects in a collection; biodiversity refers to the state of variety among objects in collections of biological material. In popular and scientific literature, biodiversity frequently refers narrowly to the variety of species (sometimes called species richness) present at a particular place and time.

Species occupy just one of several levels in each of two intersecting hierarchies, or classification schemes, for biological structure: one taxonomic and the other functional (Fig. 1). Biodiversity refers to the entire variety that exists in biological material at the many levels of both the taxonomic and functional hierarchies (Trauger and Hall 1992).

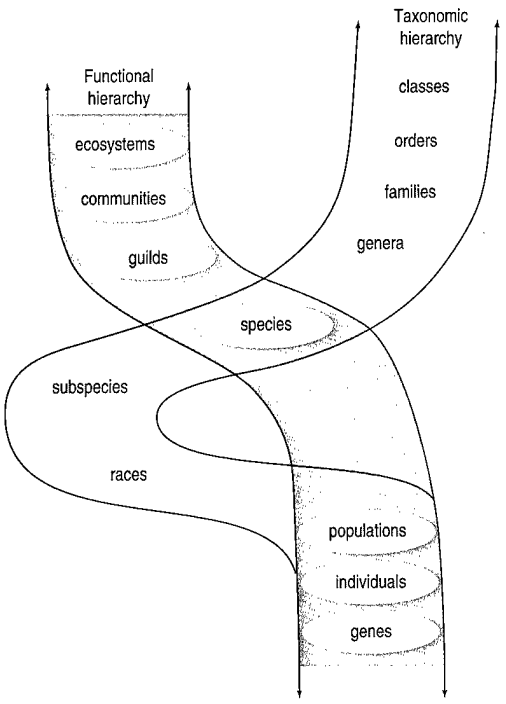


Fig. 1. Biological systems can be arranged in at least two nested hierarchies, one functional and the other taxonomic. The functional hierarchy reflects how researchers arrange biological material at various levels of interaction among the lower, component parts of a system. The taxonomic hierarchy provides a system for ordering and naming the diversity of life forms on Earth. To a great extent, it also reflects the suspected evolutionary relationships among the various taxa. The species concept is so important to biologists because species occur in both hierarchies. Thus, events that affect species have ramifications up and down both hierarchies.

Taxonomic Diversity

The state of variety in any collection (especially collections of species) is contingent on how many kinds of distinguishable objects are perceived. To varying degrees, in different circumstances and among different kinds of organisms (for example, insects versus birds), it is sometimes difficult to agree upon the diversity of a collection of species because exactly what defines a particular species is sometimes problematical, both for scientists (Dowling et al. 1992; Cronin 1993; Moritz 1994) and for policy makers (O'Brien and Mayr 1991; Geist 1992; Hill 1993). Unfortunately, the question of whether harvest affects diversity of species turns on the question of whether particular species exist as distinct entities and by whose definition.

Taxonomy provides a sort of great filing system to order the tremendous diversity of life forms for purposes of study, but it is not clear that the unique character and names assigned to individual species necessarily reflect anything unique about the particular functions of those species in ecosystems (Lawton 1991; Baskin 1994; Moffat 1996). Nor is it clear whether systematics and taxonomy as traditionally practiced are a necessary component of any agenda to conserve biodiversity (Renner and Ricklefs 1994a,b; Oliver and Beattie 1996), though it certainly seems so, given the amount of time and energy scientists spend arguing about the designation of species.

Major political and biological decisions often rest on the outcome of arguments about which names are preferred for groups of similar organisms. For example, the decision to further manage the harvest of American black ducks, a species that has declined over the past 30 years, depends, in one view (for example, Ankney et al. 1987), on whether black ducks will so freely hybridize with mallards that the species is doomed to extinction anyway. Similarly, because red wolves appear to be hybrids of gray wolves and coyotes, some researchers are concerned that the red wolf will be delisted from its endangered status (Brownlow 1996). Alabama sturgeon and shovelnose sturgeon present similar dilemmas.

The extreme difficulty is that, even though the term *species* has been used for centuries, there remains no standard, universally agreed-upon rule for delimiting each species (Fig. 2). There has been a flurry of recent attempts to deal with such criticisms and to delineate, objectively and fully, alternative groupings of similar organisms (such as evolutionarily significant units, recognizable taxonomic units, and morphospecies [for example, Moritz 1994]). These efforts correlated with the appearance of powerful molecular techniques for identifying fine differences in the genetic makeup of individual organisms (Brownlow 1996). Ultimately, all such classifications are still subjective, which causes further blurring between ethical and scientific judgments (Cronin 1993). Nevertheless, diversity clearly does exist at many levels in the taxonomic hierarchy, and the reasons for our concern about the state of biodiversity range from utilitarian (as-yet undiscovered drugs, genes, or other commercially viable products may exist in species residing in remnant natural ecosystems) to ethical (diversity has an intrinsic right to exist).

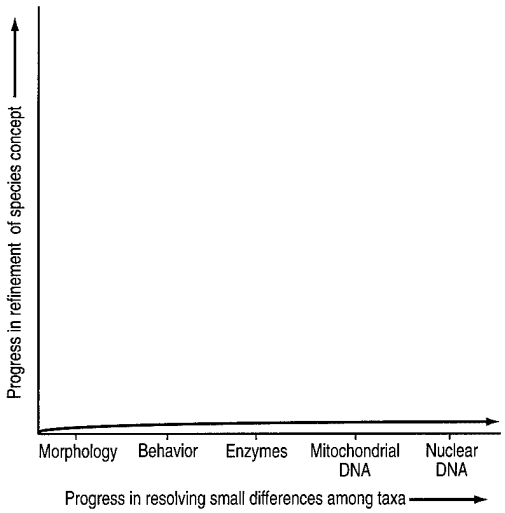


Fig. 2. Since the species concept appeared, scientists have greatly progressed in applying technologies to resolve finer and finer differences among organisms; this enables researchers to cluster organisms based on their degree of similarity. Because researchers have made much less progress in precisely defining a species, much argument exists about what the differences revealed at finer scales of resolution mean with respect to the designation of a species.

Functional Diversity

In this chapter, I emphasize the effects of harvest on diversity within and among levels of the functional, rather than the taxonomic, hierarchy. Within the functional hierarchy, variety is apparent at many levels—at the level of genes within and among individual organisms, of individuals within and among populations, of populations of different species within and among communities, and so forth. With the exception of individual organisms (except, perhaps, asexually reproducing species, for which even the identification of individuals may be difficult), scientists experience similar difficulties classifying within the functional hierarchy as in the taxonomic hierarchy. For instance, no universally agreed-upon boundaries exist for where one population ends and another begins nor where one community ends and another begins.

Within the very real constraint of the uncertainty associated with such classifications, I discuss the effects of harvesting—explicitly by humans, and, by extension, by other predators with whom humans share space in ecological food webs—on biodiversity at three levels of organization: genes within and among individuals, individuals within populations, and species within communities.

Harvest Effects on Populations

Sustainable Use and Sustainable Yield

Since the earliest references to sustainable harvest of renewable resources, some of which can be found in the Old Testament, the key idea has been to harvest in such a way that the removal of individuals from a population would not cause a decline in the ability of the population to replenish itself. Until fairly recently, though, the sciences of population ecology and those related to resource management evolved differently because they had fundamentally different questions and values about nature and populations of wildlife at their roots (Nudds 1979). Ecologists tended most often to focus on why populations fluctuate; wildlife, fisheries, and forestry scientists were concerned primarily with understanding how to sustain harvests from populations. To that extent, the science of resource management was rooted more firmly in agriculture than in ecology.

Indeed, utilitarianism, as fostered by Francis Bacon, gave rise in North America to a school of progressive agriculture, whose views then heavily influenced a school of progressive scientific conservation and a philosophy of "wise use" for forests and other wildlife, as espoused by Gifford Pinchot and Theodore Roosevelt (Worster 1977). In contrast, the environmental movement in North America (often linked more closely to ecology than to resource management) can be traced to the romantic tradition of Gilbert White and Henry David Thoreau, who strongly influenced John Muir and the protectionist school of conservation (Worster 1977). Wildlife biologist Aldo Leopold transcended these two schools during his career, first advocating Pinchot-like views for the scientific management of game resources and later espousing philosophies based on a broader appreciation of the ecology of natural systems (Kennedy 1984). Nevertheless, "barnyard management" philosophies still pervade many areas of natural resources management (Lavigne 1991; Dobb 1992) and, though the concept of sustainable use has a long history, the relatively new concept of sustainable development, when used in reference to harvests of renewable resources, actually has not evolved much from earlier notions of conservation as wise use (Lavigne et al. 1996).

By the mid-twentieth century, resource-management scientists had borrowed heavily from the science of population ecology,

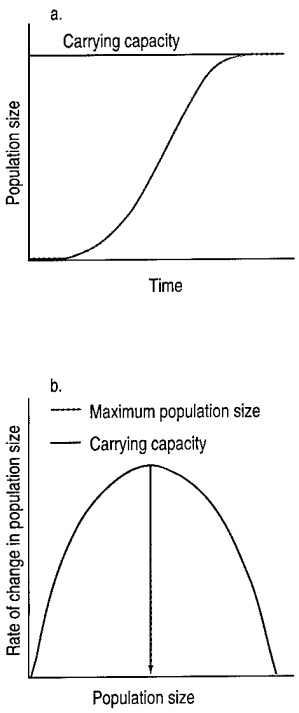


Fig. 3. Under a stringent set of conditions, which can probably only be approximated in nature, a) population size grows over time to its carrying capacity, which is when the rates of births and deaths exist in a dynamic equilibrium and the population grows no further. b) As a population grows, its rate of change in size increases, but at a decelerating rate. When the population size is half as large as the carrying capacity, the population's rate of change is at its maximum and declines thereafter, reaching zero when the population reaches carrying capacity. In theory, such a population could be continuously harvested to one-half of its carrying capacity, thereby producing a perpetual, maximum yield without compromising the ability of the population to be replenished. This is the kernel of the maximum sustained yield theory.

especially fisheries science. A specific and highly quantitative form of the sustainable use concept—maximum sustained yield theory (Fig. 3)—appeared, embued with the authority of mathematical equations of population dynamics developed many years earlier by theoretical ecologists (Hutchinson 1978). Unfortunately, the many simplifying assumptions of maximum sustained yield theory proved eventually to be its Achilles heel (Holt and Talbot 1978). This is especially true of the assumption that when harvesting the population of interest all other species in complex ecological food webs could be ignored, and of the assumption that nature is relatively constant and benign, enabling populations to persist at relatively constant sizes. In contrast, present-day natural resource management is evolving and becoming more firmly established on an ecological foundation as, indeed, is agriculture.

Compensation and Compensatory Mortality

To understand whether and how harvest exploitation might affect biodiversity, it is essential to understand how harvest might affect populations, particularly their size and composition, because effects at the level of populations can potentially range up and down the biological hierarchy (Fig. 1). The scientific literature on this subject is daunting, not only because of its sheer size (nothing generates discussion and analysis like controversies about the effects of hunting), but also because the terminology is inconsistent and confusing. For example, a harvest that removes even one individual from a population necessarily, but trivially, *limits* the population size, but it does not necessarily *regulate* it (Sinclair 1989). Regulating factors are a particular class of limiting factors that, depending on the biological characteristics of particular harvested species and the amount of time that passes after a harvest, may actually increase rather than decrease the number of individuals or the growth rate of the harvested population (Fig. 4).

Errington (1945) seems to have introduced the idea that if a harvest removed from a population the exact number of individuals that would die of natural causes anyway, the harvest (after a period of reproduction by the remaining individuals) would not change the population size from that which would occur in the absence of harvest. In other words, harvest mortality would merely be *compensatory* to, or substitute for, natural mortality. However, if the number of individuals that were harvested exceeded the number that would die naturally, then harvest mortality would be *additive*. This is different from *compensation* by the population for the removal of harvested individuals (Caughley 1985).

Whether a population exhibits compensation when it is harvested depends on whether and how the natural birth and death rates differ when population numbers change as a result of the harvest (Fig. 4). For many species, including many often assumed to respond positively to harvest, birth and death rates may be only weakly linked to population size, or at least lag behind changes in population size (Fryxell et al. 1991); these populations, then, only partially compensate (Caughley 1985) for the removal of harvested individuals.

The responses to harvest for many other species may be entirely independent of population size or may vary with changing environmental conditions (Berryman 1991). In these cases, long-term fluctuations of harvested populations may be chaotic, increasing the possibilities for population collapse (Fig. 4). Such a scenario may be true even for populations that have the potential for some kind of compensation, especially if harvest holds a population to a size where its birth and death rates are largely independent of the number of individuals in the population (Fig. 4).

I do not consider these complicated phenomena further, but this brief discussion illustrates a point I made earlier: that because the complexities involved in studying the effects of harvest on just a single population are numerous, so, too, must be any consideration of harvest effects on biodiversity. If compensatory harvest mortality is taken to mean *that which substitutes for natural mortality*, then unless we can somehow predict and exact a harvest that precisely mimics the mortalities that a population would experience through natural mortality, harvest will necessarily affect biodiversity. Consequently, we should be skeptical of claims that assert the feasibility of sustainable harvests that do not alter biodiversity. The critical issue is, however, whether altered biodiversity necessarily matters—and, if so, why it matters—at the genetic, individual, population, and community levels.

Much has been written about the importance of biodiversity and the need to conserve it, but from a scientific perspective many of these articles consist of hypotheses that need to be critically evaluated. Instead of concentrating here on the intrinsic ethical reasons to conserve biodiversity, I focus on what we think we know and do not know about whether changes in diversity that result from harvest actually matter with respect to the persistence of individuals, populations, and the higher-order systems (communities and ecosystems) in which individuals and populations live.

Harvest Effects at Three Levels of Biodiversity

Harvest and Genetic Diversity

Most biologists believe that populations are composed of individuals whose genetic makeup is suited, or adapted, to the particular environments they inhabit. Genes, sometimes in interaction with environmental factors, determine how individuals will grow and respond to environments. A diversity of genetic material exists within individual organisms and among individuals in populations. Biologists are concerned with the amount and distribution of this genetic diversity and how it changes when population size changes (Soulé 1987; Pimm 1991). Although biologists believe that small populations are particularly susceptible to extinction for many reasons, a great deal of their attention has focused on the fates of species with small populations and low levels of genetic diversity (Nunney and Campbell 1993). Too little genetic diversity, as might result from the inbreeding that occurs among close relatives in small populations, may disrupt the potential for a species or population to adapt to changing environments over the long-term, or it can lead directly to reduced ability for the population to survive and reproduce in the short term.

Historically, populations of many species were reduced substantially—some to extinction—by harvesting that was conducted primarily for commerce (Shaw 1985; Lavigne et al. 1996). When populations are severely reduced, a kind of genetic bottleneck occurs, the result of which is reduced genetic diversity in the population in subsequent generations. Even a population that recovers in size after a short time at a reduced size may be largely composed of genetically similar individuals. For example, even though present-day populations of northern elephant seals are substantially larger than they were after harvesting severely reduced their numbers in the last century, the populations still display a remarkably low level of genetic diversity compared with their counterparts in the Southern Hemisphere whose numbers were not as severely depleted.

The relation between population persistence and genetic diversity is, however, complicated and not well understood. For example, the population of northern elephant seals did grow despite low levels of genetic diversity, so if the viability of a population is assessed by its ability to grow, then the low level of genetic diversity presumed to have resulted from harvest did not affect viability. Similarly, natural populations on islands frequently start from few individuals and potentially suffer from founder effects (that is, a lot of inbreeding necessarily occurs, resulting in low levels of genetic diversity), yet grow and may persist. Also, populations of many introduced or invasive species begin from a few individuals. On the other hand, scientists believe that the reason the North Atlantic population of black right whales may not be growing, even though the population is protected, is because its reproductive success has been impaired by low genetic diversity caused by a severe reduction in population size from harvest.

Harvest may also result in genetic problems for natural populations in another, less direct way. For example, in areas where fisheries stocks have been depleted by harvest or other factors, it is common to augment stocks with individuals selected and reared in fish

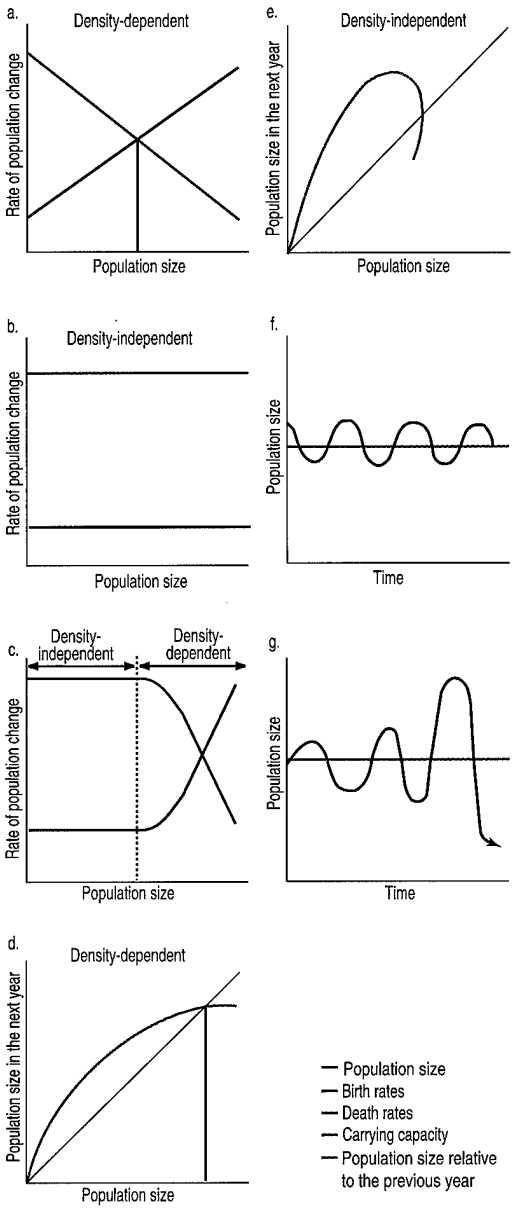


Fig. 4. a) The type of population growth to equilibrium (as shown in Figure 3) is obtained when rates of birth and death change linearly with an increase in population size. Specifically, the birth rate declines and the death rate increases until they are balanced at the population's carrying capacity; that is, the change in the rates *depends* on the size, or density, of the population. Another scenario b) is when the birth and death rates do *not depend* on density, but instead remain constant over a range of population sizes. In this instance, populations theoretically should continue to grow quickly and not show any deceleration of growth even at high numbers. More realistically, c) unbounded growth is not the rule in nature because environments are not limitless, although small populations may grow at rates not influenced by their density until the populations grow quite large, at which point effects of density on growth may suddenly appear. Real data from the kinds of large-bodied, long-lived species that humans frequently harvest (such as large mammals) often show this kind of relation between birth and death rates as population size changes. Harvesting can lower population sizes of such a mammal species to where the population might respond according to the approximations of maximum sustained yield and into a region where the assumptions of maximum sustained yield are violated. The relationship between the size of a population at one time (N_t) and its size at some later time after a harvest (N_{t+1}) is very different when birth and death rates are d) density-dependent or e) density-independent. The diagonal line connects values of N_t and N_{t+1} that are equal. The population's compensation for density reduction can cause an increase in population size at a later time, but the response is very different for a population at a size where the birth and death rates are not influenced by density. If birth and death rates are influenced by density, the population trajectory over time may f) fluctuate around an equilibrium size. If birth and death rates are density-independent, the fluctuations may g) be of increasing amplitude, suggestive of chaotic behavior. The fluctuations of increasing amplitude seen in g) increase the probability that the population could, by chance, become reduced to zero, which means, of course, extinction. Such cycles are observed in long-term data sets from marine fisheries and white-tailed deer.

hatcheries. In some fisheries, continued harvest may only be possible with the continual addition of hatchery-reared individuals (an aquatic analog to *put-and-take* hunting). Considerable debate exists about how the release of large numbers of genetically similar individuals affects the persistence of remnant wild populations (Ryman and Laikre 1991).

Harvest and the Diversity of Individuals

Organisms harvested by humans typically reproduce sexually, are long-lived, and are large-bodied when compared with almost all organisms in the animal and plant kingdoms. Within populations there is a diversity of individual organisms of different sexes and ages. The reason scientists and managers have spent so much time developing techniques to identify the sex and age of individuals (Bookhout 1994) is that, in theory and in practice, variability in sex and age composition of individuals affects the growth rate and size of the populations they compose (Beasom and Roberson 1985; Getz and Haight 1989). In fact, resource managers have long tried to manipulate population size by directing harvest mortality to individuals of particular ages or sexes (Giles 1978). For example, to decrease the size of a large population, a general guideline might be to reduce the proportion of females of reproductive age. To allow a small population to increase, mortality might be directed to males (particularly for species in which a few males mate with many females), thereby reducing competition for food with females and their offspring.

It follows, then, that harvest and the diversity of individuals of different sexes and ages within populations are inextricably linked. The fact that the diversity of individuals with respect to sex and age is another kind of biodiversity is less obvious and seldom appreciated. It is unclear, however, whether changes in sex and age diversity generally have beneficial or detrimental effects on populations. For instance, sex-selective harvests of male deer may, or may not, produce more "high-quality" males (Beasom and Roberson 1985). Harvests of males only have been reported to produce desired results for some populations, sometimes with unanticipated side effects such as increases in abundance of antlerless individuals, which can increase competition for food and reduce body condition and reproductive performance (Beasom and Roberson 1985). Similarly, a harvest intended to change the preponderance of one sex sometimes may result merely in compensatory, biased production of the rarer sex. Female white-tailed deer that do not conceive until late in estrous, as would occur when encounters with rare males are infrequent, more often produce sons than daughters (Verme and Ozoga 1981), leaving deer population managers no further ahead in their attempt to adjust the sex ratio of the population.

Scientists long assumed that the removal of nonbreeding individuals among species where the ratio of breeding males to females is skewed was beneficial and would not affect the population's reproductive potential (Giles 1978). Such species, though, usually possess highly organized, if not readily apparent, social systems that may undermine a sustainable harvest if disrupted by mortality directed to certain age and sex classes of individuals. For example, the selective removal of individuals from populations for trophy hunting or for obtaining breeding stock for game ranches often causes significant differences from natural mortality patterns (Fig. 5); these differences could potentially greatly reduce reproductive success and actually lead to population collapse (Ginsberg and Milner-Gulland 1994).

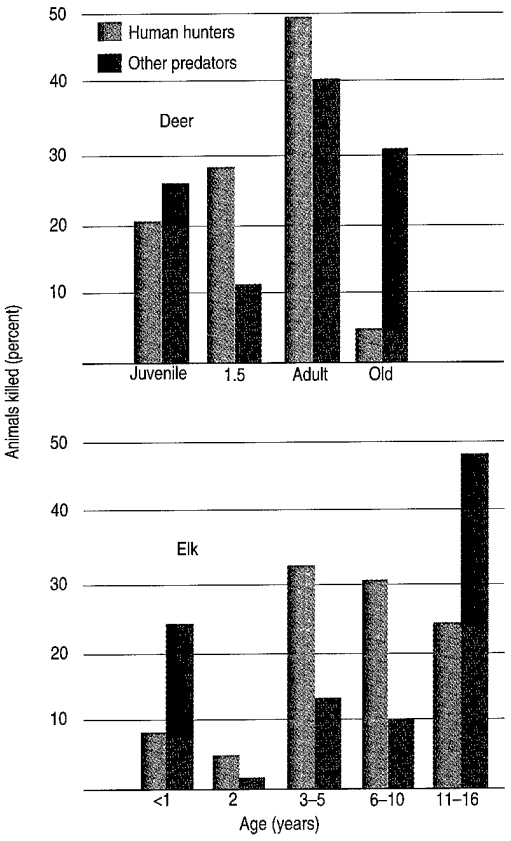


Fig. 5. Mountain lions in Idaho tended to kill more young and old deer, and wolves in Manitoba tended to kill more young and old elk, than they killed prey of prime breeding age. In contrast, humans hunting deer and elk nearby and at the same time tended to kill middle-aged individuals. Consequently, humans usually did not exact a harvest in which the mortality merely substituted for that which might occur naturally. Instead, humans altered the diversity of individuals of different ages within the prey populations differently than did the other predators.

Harvest and Species Diversity

Because harvest affects biodiversity at lower levels in biological hierarchies (Fig. 1), it follows that it must affect diversity at higher levels of organization, such as communities. A community, which is sometimes thought of as synonymous with a food web (Yodzis 1993), is the set of all species living together and interacting at a particular place and time. Interacting means, for example, that the species compete with one another, or one eats the other, but there is considerable ambiguity in actually measuring interaction (especially interactions less obvious and overt than predation) and its strength (Yodzis 1993). Nevertheless, how much interaction occurs among species has important theoretical implications for assessing the effects of disturbances such as harvest on the persistence and stability of communities (May et al. 1979; Yodzis 1994a,b). Space does not permit a thorough review of these ideas, though I will further discuss the general question about whether the persistence of a community is affected if the diversity of its constituent species is affected by harvesting some of those species.

Measurement of Species Diversity

The diversity of species in a community can be indexed quantitatively in many ways. The simplest index, and one frequently employed, is a count of the number of species, which is called species richness. As a measure of diversity, however, richness is heavily influenced by the presence of rare species in the community (Fig. 6). Consider, for example, two communities consisting of two species each and a total of 100 individuals. In one, the number of individuals is divided among the species in the ratio 99:1, and in the other, 50:50. Though species richness is equal, it is hard to be comfortable with the conclusion that the diversity of the two communities is the same. Clearly, were it not for the presence of just one individual in the one community, it would have just one species—only half the richness of the latter community.

Scientists have proposed alternative measures of species diversity that weigh the importance of each species in the calculation by its abundance relative to other species in the community. These various indexes, though, all convey essentially the same information about the variety in any collection of species and only differ in their sensitivity to the inclusion of rare species in the community on the calculated value of diversity (Hill 1973). But it is this very sensitivity to the inclusion of rare species that makes the use of different indexes problematical for assessing the effects of harvest on the diversity of species in a community: the answer might depend on the index used to quantify diversity.

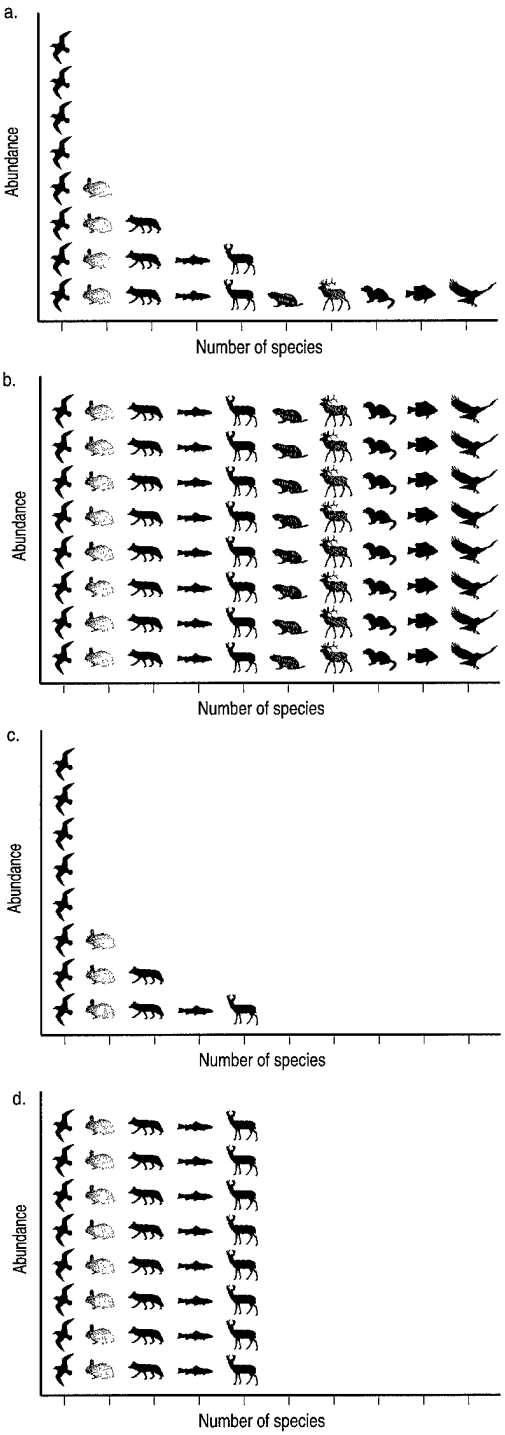


Fig. 6. As a measure of species diversity in a community, a species richness index is extremely influenced by the presence of rare species, as shown here in species-abundance diagrams for four hypothetical communities, two in which species richness (the actual number of species in a community) is 10 (a,b) and two in which species richness is five (c,d). Each community set has one community in which the relative abundances of species (or the evenness of the distribution) are equal (b,d) and one in which they are not (a,c). By the criterion of species richness, a) and b) have equal diversity and c) and d) have equal diversity, although b) and d) have much higher diversity by any index that takes into account the relative abundances of the species. A harvest that alters the abundance of a species must therefore alter diversity measured by any of those indices, but a similar harvest would not produce detectable change in diversity if diversity is measured simply as species richness.

Paradoxically, although richness is the index of diversity most sensitive to variation in the number of rare species, it will not detect changes in diversity brought about by a harvest of one or more species in the community unless the harvest is responsible for the complete eradication of one or more species. Conversely, any of the alternative diversity indexes that are less sensitive to variation in the number of rare species will necessarily detect a change in diversity caused by a harvest that alters the abundance of one or more species relative to the others.

Harvest Effects on Relative Abundance of Species

Whether harvest changes diversity of a community is clearly contingent on the kind of analysis performed, but what of the biological effects of altering the relative abundance of species? Assume, for example, that a harvest of a particular population of a species in a community affects the size of that population. This seems reasonable because, as noted previously, the stringent conditions under which a harvest would have no effect on population size hardly ever occur in the real world (Holt and Talbot 1978). Depending on whether the removal of individuals has a limiting or regulating (Sinclair 1989) effect on the population, the long-term effect of harvest might be either to increase or to decrease the population relative to the size it would be without harvest. By itself, this does not necessarily translate into a biological effect on the entire community in which the species population occurs, because changing the abundance of a particular species may not have far-reaching consequences for other species in the community, especially if the harvested species interacts only weakly with the other species in the community. Further, if harvest mortality substitutes for some kind of natural mortality, then to the extent that harvested organisms are not food for some other organisms in the community, it might be argued that harvest doesn't affect the population or the entire community. However, because it is difficult to imagine any organism in nature that is not food for some other (if not during its lifetime, then certainly after), it must follow that sooner or later a harvest necessarily alters the variety of species, with consequences for something somewhere in complex food webs.

Keystone Species

The logic and implications of various qualitative and quantitative definitions of diversity aside, ample evidence exists that harvests which alter the abundance of some species can directly and indirectly affect species diversity in the rest of the community, particularly if a harvest alters the abundance of a *keystone* species, which is an *organizing* species that has such particularly strong interactions with other species in a community that changes in its abundance cause significant changes in the abundances of other species. Paine (1966), who developed this concept based on a series of experiments in marine intertidal systems, removed the top predator, a sea star, from some areas and noticed that diversity of other intertidal species decreased. In addition, the removal of the starfish caused an increase in the populations of a few species that were able to outcompete others. Lubchenco (1978) extended this idea by showing that predator removal could decrease or increase species diversity of a community, depending on the kind of habitat from which the predators were removed and on whether the preferred prey of the predators were strong or weak competitors with other species. Today, examples of keystone species are recognized from a wide variety of systems: sea otters in coastal kelp beds, moose and beaver in boreal forests, and gopher tortoises in southeastern sandhills, among many others.

Humans are also keystone predators that can significantly alter the diversity of communities by harvest (or culls) of particular species, a fact long recognized, especially in fisheries literature (May et al. 1979). Some elegant new analyses of the effects of harvest by humans on multispecies fisheries (Yodzis 1994a), and the effects of a cull of South African fur seals (ostensibly to reduce competition with humans for fish) in the Benguela ecosystem (Yodzis 1994b), suggest complex and far-reaching effects of such harvests on the species composition (diversity) and the stability of entire communities.

Harvest and Habitat Fragmentation

Finally, harvest by humans can less directly affect the diversity of species by altering the habitats in which they live. Worldwide, habitat change through forest harvesting, as well as agricultural development and urbanization, may leave small, remnant patches of undisturbed habitat, but such residual natural areas (even some set aside to preserve the diversity of species in them, such as national parks) contain a much lower diversity of species than they would otherwise contain if they were still part of large, contiguous landscapes (Glenn and Nudds 1989; Nudds 1993).

Conclusion

I have argued that there are necessarily and obviously effects of harvest at each of several levels of a nested hierarchy of biological organization: at the level of genes within and among individuals, among individuals of different sexes and ages within populations, and among populations of different species within communities. My intent is not to insult by the simplicity of the arguments, but to take the opportunity afforded by this otherwise scant introduction to the topic of harvest effects to infuse a cautionary note into a literature becoming all too cluttered with ill-defined terms, illogical arguments, and glaring contradictions. None of this,

of course, will stop some claims that sustainable use of renewable resources does not affect biodiversity. However, to point out *only* that such statements are necessarily, at some level, false is about as helpful as trying to argue that they are true. Consequently, I want to make some general comments about whether the changes that occur as a result of harvest *matter*, and to whom or what. I conclude with some suggestions about how we might find out what changes matter, given that the ecological and evolutionary consequences of harvest are not well-understood.

Conservation of Biodiversity: What's the Goal?

What has been absent from discussions about conserving biodiversity is a clear definition and agreement about precisely what ought to be the objective for the management of biodiversity. This problem particularly plagues discussions about ecosystem health (Suter 1993; Steedman 1994) and integrity. The U.S. Environmental Protection Agency, however, borrowing from Karr's (1991:69) Index of Biological Integrity, defined ecosystem integrity as "diversity, composition and functional organization that is representative of natural habitats within a geographic region." It is important that this definition makes it explicit that integrity must be defined relative to a standard; in scientific terms, this means in relation to control areas (Solbrig 1991). Finally, Article 7 of The Convention on Biodiversity (Johnson 1993:85) charges the signatories to "identify... activities...likely to have significant adverse effects on the conservation...of biodiversity and monitor their effects..." Thus, it is important that sufficiently large natural areas be protected as baselines or controls (Sinclair 1983) against which to compare the diversity, composition, and function in ecosystems altered by humans, including those altered directly and indirectly by harvesting. Where typical scientific controls are not feasible, alternative means to assess the effects of harvest on biodiversity are possible. This approach, called adaptive management, explicitly links management actions, such as setting the sizes and timing of harvest quotas, to scientific analysis of the effects of harvest (for example, see Walters 1992; Williams and Johnson 1995; Williams et al. 1996).

Significant new information about the role of biodiversity, at least at the level of species in communities, suggests that its *purpose*, so to speak, may be to provide *redundancy*, which has a stabilizing effect on whole communities and ecosystems (Pimm 1993; Moffat 1996). In other words, in the face of significant environmental change, diversity may buffer ecosystems against collapse of ecological function. Experimental evidence suggests that some functions of ecosystems, such as trapping atmospheric gases, production, respiration, and water retention, decline when diversity declines (Naeem et al. 1994). Bethke (1993) and Bethke and Nudds (1993) showed that even though the abundances of individual species of waterfowl fluctuate widely in climatically variable environments, waterfowl communities are actually more persistent through time the more variable the environment—stability of the whole comes at the expense of the stability of the parts (Pimm 1993). Thus, biological integrity defined by function, as opposed to species composition or diversity per se, may be a more important policy objective (Angermeier and Karr 1994) for the management of harvest.

Acknowledgments

I appreciate the opportunity to present the opinions I've assembled here, and also the reviews of earlier versions of this paper by C. D. Ankney, A. Chek, S. Crawford, and D. M. Lavigne; discussions with P. Lundberg about the concepts in Figure 4; and help from C. MacLaughlin with the illustrations. There would not be any chapter at all, however, were it not for the many students of conservation biology and wildlife management over the years who keep asking the difficult questions.

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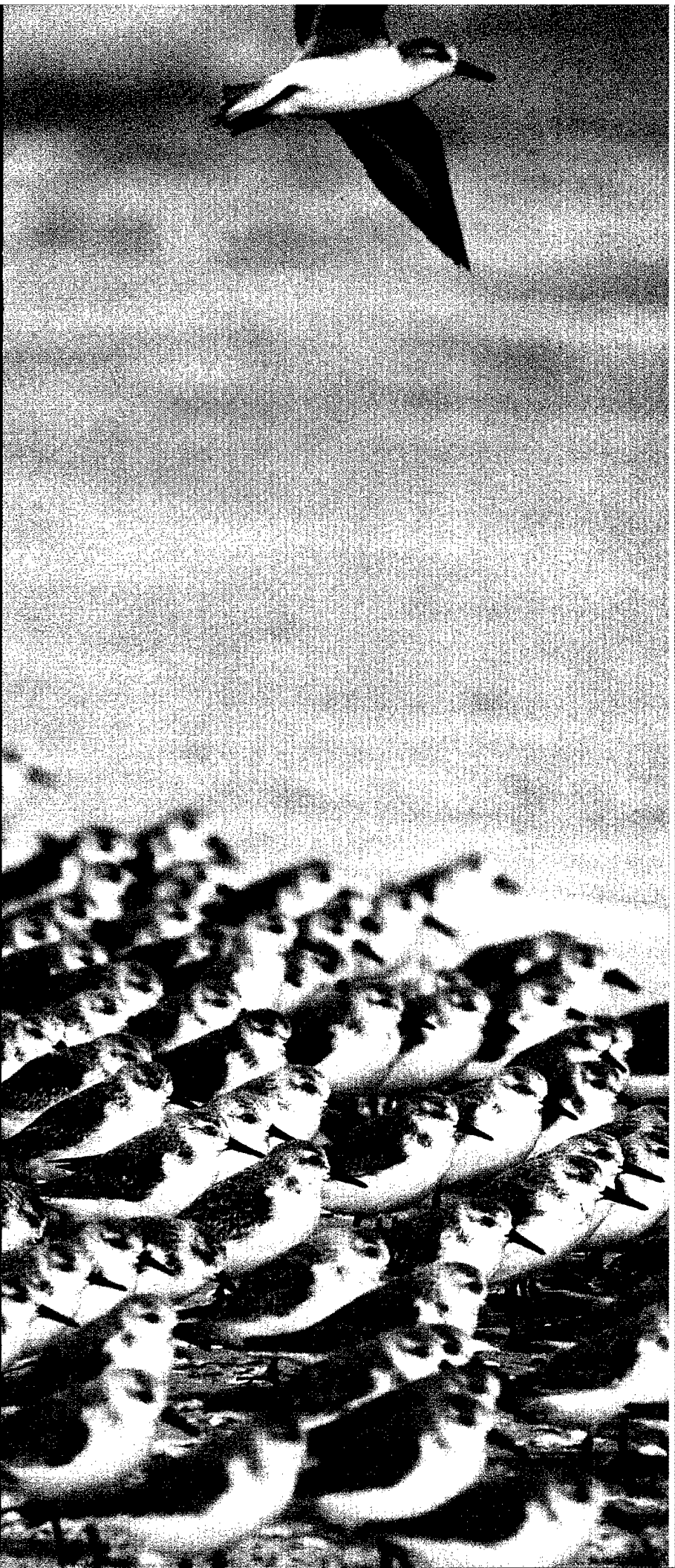

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Part 2
Regional Trends of Biological Resources

Northeast 181
Great Lakes 219
Southeast 255
Caribbean Islands 315
Mississippi River 351
Coastal Louisiana 385

Grasslands 437
Rocky Mountains 473
Great Basin–Mojave Desert Region 505
Southwest 543
California 593
Pacific Northwest 645
Alaska 707
Hawaii and the Pacific Islands ... 747
Marine Resources 775

Northeast

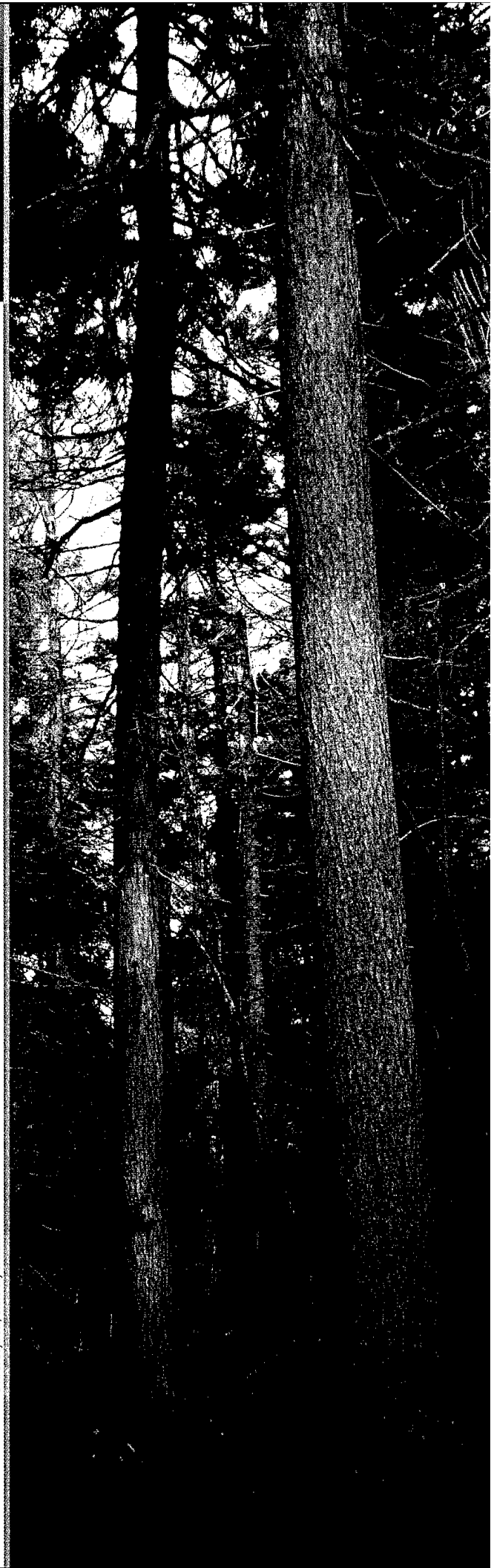
When European settlers arrived in the land that is now the northeastern United States, they found a vast forest with rich living resources. Stretching from the Coastal Plains to the Mississippi River was an environment shaped by trees. The climate, soils, and glacial history produced a forest that was unique in the world. In the 300 years since the arrival of Europeans, however, human activities have drastically changed this landscape. Still, as immense as the changes have been, they largely altered the appearance, but not the processes, of the ecosystems of the Northeast.

A comparison of pictures of the Northeast from the 1700's with the 1900's would reveal striking differences. Early Europeans encountered great forests of American beeches, maples, birches, eastern hemlocks, and spruces from New England to northern Pennsylvania, and oaks, hickories, American chestnuts, and pines from Maryland through Ohio. Inhabiting these great forests were many wildlife populations: white-tailed deer, beaver, wild turkey, passenger pigeon, common raven, elk, moose, black bear, gray wolf, mountain lion, lynx, and bobcat.

These hypothetical snapshots of the Northeast would show forests which had occupied 90% of the landscape in 1700 occupied less than 30% in 1900. The forests had been cleared for farmland and to feed a growing industrial base. What had been an uninterrupted forest became a mosaic of fields and woodlots. Many wildlife species, such as deer, beaver, and turkey, were nearly or completely destroyed by unregulated hunting for food, and species such as wolves and timber rattlesnake were heavily persecuted. As species that depended on the old-growth forests declined, species common to forest edges became more numerous. In addition, the Industrial Revolution had produced the first wave of urbanization and the introduction of many nonindigenous plants and animals, which exposed native species to a host of new influences (Whitney 1994).

Although these early effects of humans caused irreversible changes to the snapshot, they hardly changed the processes that shaped environments in the Northeast. Native species such as the passenger pigeon are extinct, and the American chestnut is nearly extinct. Nonindigenous species such as the European starling and the gypsy moth are well established. Although we may never know the full ecological significance of these changes, we do know that the landscape that was so greatly changed by the removal of the forest and by extensive creation of agricultural fields is today more than 60% forested. The essential elements of the physical environment persist: the water, soil, and climate. Only small portions of the original forest exist today, but regrown forests may eventually acquire many of the characteristics of the original forest. Vegetation changes and conservation have brought about the return of many wildlife species such as white-tailed deer, wild turkey, beaver, bald eagle, Canada goose, and wood duck.

In the past 30 years, the appearance of the northeastern landscape has continued to change. Today, the northeastern United States contains nearly half of the country's human inhabitants, although the large human population of the Northeast is still changing; it experienced only a 1% increase between 1970 and 1980 and will probably continue to grow at



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that rate in the near future (McCorkle and Halver 1982). Movement from the country into urban centers is now reversed—the human population is moving into the country. This movement has three significant effects: the loss of agricultural land to low-intensity human development, which creates a new type of patchwork of forest and open land; continued introduction and expansion of nonindigenous species, which change the character of natural environments; and increased conflict between humans and wildlife that may significantly shift society's values of wildlife and ecological processes.

Knowledge of the major components of the environments of the Northeast is extensive, but much remains to be learned. Knowledge of the species and ecological processes of natural environments has grown enormously since the birth of the science of ecology in the late 1800's, although the basic biology of organisms contains many mysteries, and understanding systems that are composed of thousands of species is exceedingly difficult. As a result, people face the great challenge of promoting the development of the region's economic base while protecting the ecological systems on which their lives depend. To paraphrase Frank Egler (1986), a prominent ecologist, the question is not whether the combination of economic and ecological systems is more complicated than conceived, but whether it is more complex than can be conceived.

Forests

Forest Types

Historically, the Northeast was a forested region unlike any other in the country. Indeed, the combination of mountains, lakes, and mixed hardwood forests is unique in the world (Fig. 1). If the land had not been disturbed and if there were no humans in the Northeast, the natural vegetation of this region would consist of 14 different types of forests, all named for their most common tree species (Küchler 1964). The ancient types are clearly evident in the second-growth forests of the present. Bailey (1978) described two dominant natural community types (also called provinces) in the northeastern United States: the Laurentian mixed forest and the eastern deciduous forest.

Laurentian Mixed Forest

The Laurentian mixed forest type occurs from northern Pennsylvania to Maine (excluding coastal areas) and in Connecticut, Rhode Island, and New York. In this region, glacial features are common, precipitation is moderate (600–1,150 millimeters per year), and the average annual temperature is 2°C–10°C; snow cover usually persists throughout winter. The vegetation consists of a mixture of American beech, maple, yellow birch, spruces, balsam fir, eastern white pine, and tamarack (Bailey 1978).

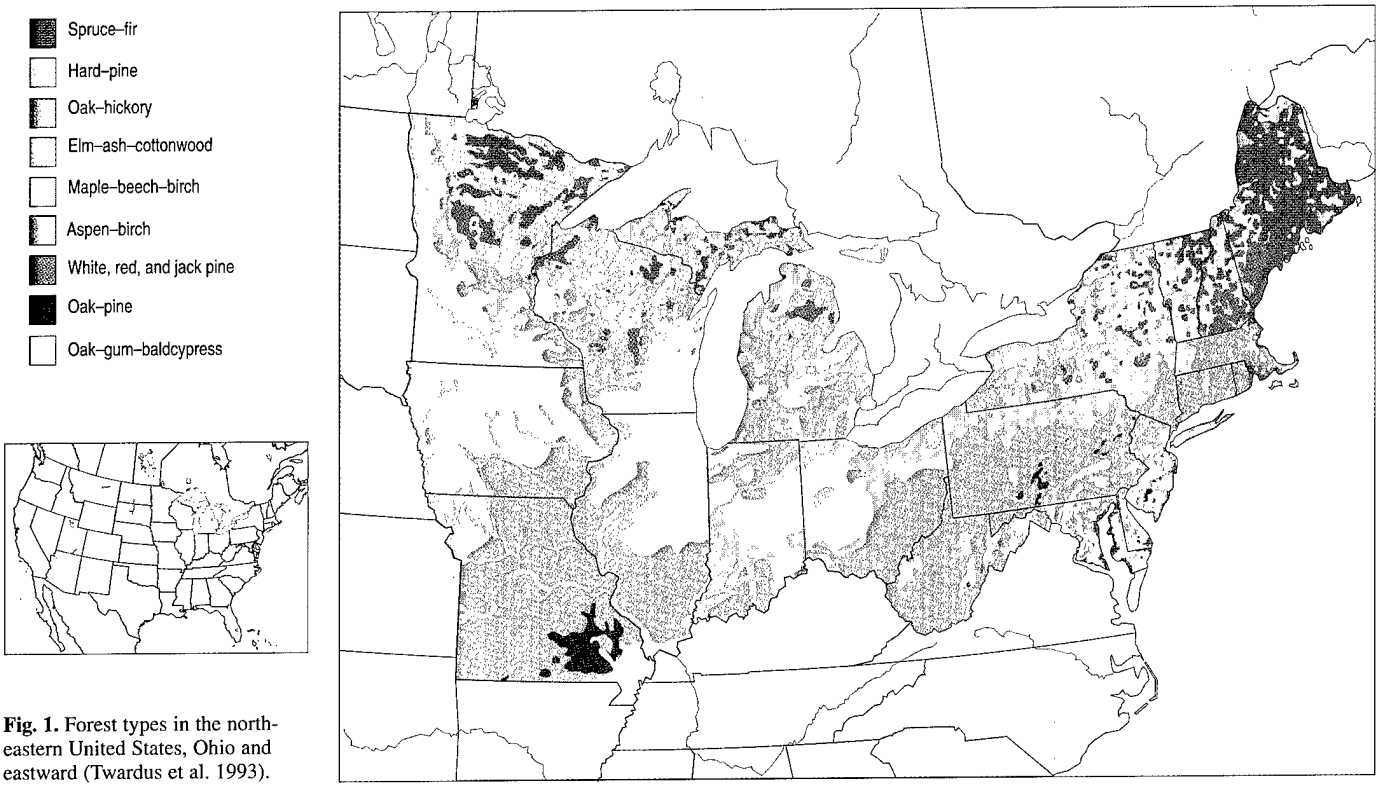


Fig. 1. Forest types in the northeastern United States, Ohio and eastward (Twardus et al. 1993).

Eastern Deciduous Forest

The eastern deciduous forest type occurs throughout most of Pennsylvania, West Virginia, Ohio, northern New Jersey, and coastal New England except in Maine. It is characterized by rolling hills, a precipitation regime that is equally distributed throughout the year and which averages 900–1,500 millimeters per year, and an average annual temperature of 4°C–15°C. The vegetation is primarily broad-leaved trees, such as American beech, oaks, hickories, and yellow-poplar (Bailey 1978).

Southeastern Mixed Forest

In addition to the two dominant forest types, southern New Jersey, Delaware, and most of Maryland also have characteristics of the southeastern mixed forest type. The southeastern mixed forest type consists of pines or a mix of broadleaf and needleleaf trees on uplands, and sweet gum and baldcypress swamps in lowlands and coastal marshes. Shrubs include dogwoods, viburnums, and haws (Bailey 1978).

Forest Changes

Although the Northeast contains some of the largest metropolitan areas in the country, the region is still dominated by forest (Table 1). Forests cover approximately 60% of the total land area, and in New England alone, the coverage is 80% (DeGraaf et al. 1989). Forest is least common in Ohio (30%) and most common in Maine (80%). New York has the greatest area of forested land with approximately 7.2 million hectares.

On average, forested area increased slightly (less than 5%) or remained stable during 1965–1990 and is expected to decrease approximately 3% in the Northeast (west to the Mississippi River) in the next 50 years. Losses of forested land in the 1980's were attributed to cropland conversions, but losses after 1990 are mainly due to urban expansion and reservoir construction (Flather and Hoekstra 1989).

Table 1. Land-use statistics (in thousands of hectares) by state in the northeastern United States (U.S. Forest Service, 1980–1981 unpublished data).

State	Forestland	Crop/pastureland	Total[a]
Maine	6,875.0	284.8	7,748.8
Vermont	1,775.0	346.5	2,318.2
New Hampshire	1,948.0	68.6	2,248.2
Massachusetts	1,259.8	103.9	1,956.1
Connecticut	713.3	87.9	1,217.9
Rhode Island	158.2	11.0	263.7
New York	7,227.0	2,627.0	11,810.5
New Jersey	784.0	340.2	1,867.0
Delaware	152.3	234.6	483.1
Pennsylvania	6,640.6	2,296.9	11,222.0
Maryland	1,055.9	846.9	2,459.2
Ohio	3,071.9	4,939.8	10,238.2
West Virginia	4,726.6	895.3	6,029.7
Total	36,387.6	13,083.4	59,862.6

[a]Numbers do not sum because these categories represent only two of many land-use categories.

Forest Composition

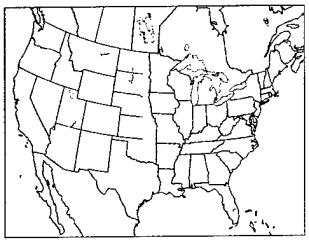
Forest composition is a product of the soils, climate, topography, and periodic natural and human disturbances. Soils and climate promote a natural sequence of tree species that occupy a given site for varying periods. The replacement of one set of species by another (called succession) generally follows a predictable sequence after a major disturbance (see chapter on Natural Processes). In northeastern forests, aspen, birch, ash, and pin cherry grow back first after a disturbance, but they are eventually replaced by sugar maple, eastern hemlock, and American beech. Today, most forests from New York northward consist of these latter species. South of New York, the species that grow back first are replaced primarily by oaks. Northern red oaks and yellow-poplars are especially prominent in the southern part of the region, and pitch pines and loblolly pines dominate the coastal regions of Delaware and New Jersey. Topography plays an indirect role in the revegetation of disturbed areas. More rugged areas were first abandoned by early farmers and now support the oldest regrown forests. The rolling, less-rocky ground to the west continues to be farmed.

Disease and Insect Effects

Introduced diseases and insects are shaping a forest that is very different from that encountered by the colonists. The American chestnut (see box on American Chestnut Blight in Nonindigenous Species chapter) once made up as much as 25% of the trees in some areas and was economically the most important hardwood in the eastern forests, but chestnut blight has almost completely wiped out the American chestnut. The blight, which is caused by a fungus, was introduced into the United States from the Far East around the turn of the century and killed as many as a billion trees in just a few decades. Although the forest lives on, the absence of the American chestnut may have caused the disappearance of at least five species of insects (Opler 1978) and eliminated a major food source for species such as chipmunk, deer, bear, and turkey. Research into the reestablishment of the American chestnut is pursuing three approaches: development of a virus that attacks the fungus (Chen et al. 1994), breeding hybrid chestnuts that resist the fungus (Burnham 1988), and genetic engineering to make chestnuts resistant to the fungus (Maynard 1994).

American beeches and American elms are other trees that dominate the forest overstory and are declining because of introduced non-indigenous species. The beech scale insect, which was introduced from Europe, allows a fungus to invade and kill beech trees. As the insect moved through the region, the fungus killed 85% of the trees that were greater than 35 centimeters in diameter and reduced beechnut production by 43%. The insect is now attacking smaller trees—the fungus has infected 97% of the trees with trunks that are more than 15 centimeters in diameter (R. Sage, State University of New York, Syracuse, personal communication). Elms are attacked by a combination of Dutch elm disease and elm phloem necrosis. Scientists successfully curbed Dutch elm disease by controlling the elm bark beetles that transmit the disease to the trees. Little is known about elm phloem necrosis, however, and researchers predict that it will eliminate elm trees from the Northeast (S. Teale, State University of New York, Syracuse, personal communication).

Many tree species have been affected by the gypsy moth, one of the most widespread and damaging pests in the Northeast (Fig. 2). The gypsy moth caterpillar, accidentally introduced from Europe around 1870, now occurs in every northeastern state and can completely defoliate forests (U.S. Congress, Office of Technology Assessment 1993). In 1971, it caused from 25% to 100% defoliation of more than 608,000 hectares of forest (Metcalf and Metcalf 1993). The cost of research, control, and lost trees probably makes the gypsy moth the most expensive pest in the Northeast. In 1981, when the loss was greatest, the U.S. Department of Agriculture estimated that $764 million worth of timber was destroyed (U.S. Congress, Office of Technology Assessment 1993). The most promising control is a combination of viruses, bacteria, and chemicals (Metcalf and Metcalf 1993; Fig. 3).



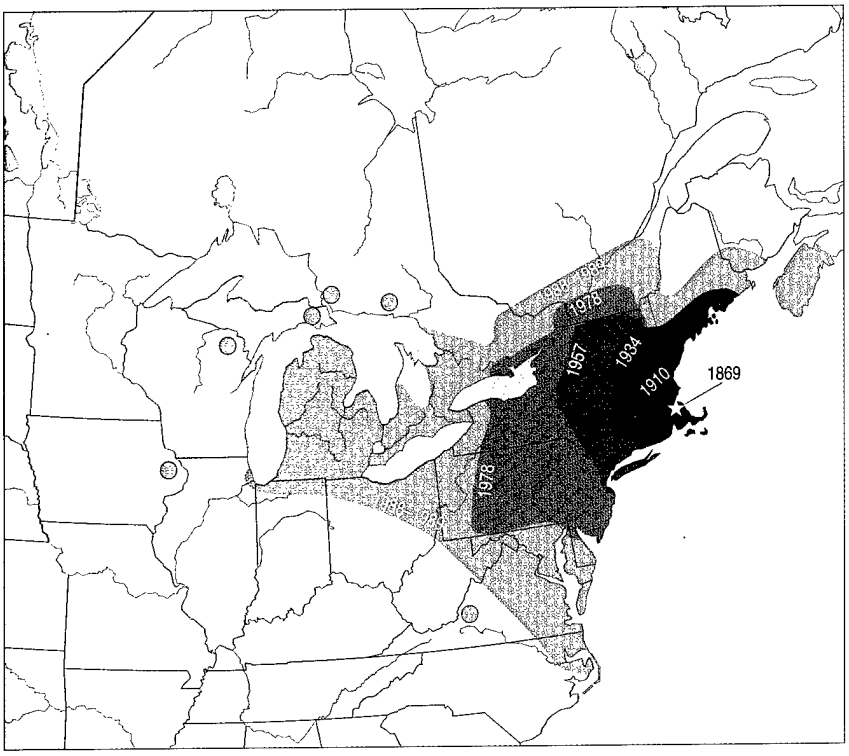


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Fig. 2. Historical spread of the introduced gypsy moth in the United States, 1990 (Nealis and Erb 1993).

Dogwood anthracnose is a disease that causes a severe decline in populations of the flowering dogwood throughout the eastern United States (see chapter on Southeast).

Acid Precipitation

Acid precipitation may change forests throughout the Northeast, especially at high elevations. More acid pollutants are deposited at high-elevation sites in the Northeast than anywhere else in North America. The most common pollutants, sulfur dioxide and nitrogen oxides, damage the leaves of trees and can also leach important nutrients like calcium and magnesium from the soils. Acid rain may be the cause for the decline of red spruce at high elevations in the Northeast, although the specific mechanisms through which damage occurs are not known. Studies revealed that pollutants in cloud water and rain can lower the tolerance of the trees to midwinter cold by 4°C–10°C. The lowered tolerance increases the trees' susceptibility to harsh winter conditions that are common in the mountainous Northeast. In addition, large deposits of nitrogen increase the leaching of nutrients from the soil and may make surface water acidic. Trends based on conditions in 1985 show that the proportion of acidic lakes in the Adirondacks could increase from 14% to 22% by 2034. A 40%–50% reduction of sulfur deposits would be needed to reduce the number of acidic lakes to 5% by 2034 (National Acid Precipitation Assessment Program 1993).

The Acid Deposition Control Program, which is Title IV of the Federal Clean Air Act, calls for reducing sulfur dioxide emissions by 40% from 1980 levels and nitrogen oxide emissions by 10% by 2010. Programs such as the Forest Health Monitoring Program and the North American Maple Project, a joint United States–Canadian effort, are monitoring long-term responses of forests to changing levels of ozone, acid rain, and other stressors. Data from the 1980's show that sulfate levels are decreasing at 49 of 53 sites in the Northeast, although nitrate levels are increasing at 27 of 53 sites (National Acid Precipitation Assessment Program 1993).

Old-Growth Forests

The changing composition of the dominant tree species is only one of the major trends in northeastern forests; changing age structure is another. The old-growth forests that were common before European settlement consisted of trees that could live as long as 300 years. Large stands of such trees are rare today and are becoming increasingly fragmented (Flather and Hoekstra 1989). No old-growth forests are left in Rhode Island, and only 40–80 hectares remain in Connecticut. Massachusetts, New Hampshire, and Vermont have a few hundred to a few thousand hectares, and Pennsylvania has 2,400–3,200 hectares in many sites of varying size. By far the largest area of old-growth forest is in New York; more than 81,000 hectares remain in the Adirondack Mountains and more than 24,000 hectares in the Catskill Mountains. Although a variety of old-growth forest types exist, these communities are typically dominated by eastern hemlock, American beech, sugar maple, eastern white pine, and yellow birch. Not all of these areas are untouched by humans; they are considered old-growth forests because their ages and species compositions reflect those of an undisturbed community.

Second-Growth Forests

Today's second-growth forests are not old enough to include trees of advanced age and the associated mix of trees of other ages that characterizes old-growth forests. Most trees in the Northeast are less than 100 years old. Stands often consist of trees that are of the same age because all the trees began growing in the same year, for example, after a fire, after a farm field was abandoned, or after a forest stand was logged. These stands can regain the qualities of old-growth forests if they are given enough time and the proper conditions (Dunwiddie et al. 1996). Concern over old-growth forests, however, persists because a variety of factors prevents most communities from acquiring the characteristics of their original state. Areas that were cut by humans probably have fewer eastern hemlocks, American beeches, and sugar maples and more black cherries, yellow birches, red maples, and black birches than undisturbed sites. Furthermore, clear-cutting and repeated logging probably favor short-lived species such as pin cherries, quaking aspens, and red maples. Eventually, the time span between successful reproduction of longer-lived species may be so great that the source of seeds for some species may be lost from the environment.

Loss of Forest Understory Plants

When most people think of forests, they think only of trees. Yet other species of plants are important components of many forest environments. The forest understory has been significantly affected by human activities, and hundreds of plant species are now rare, threatened, or endangered in the northeastern states. In fact, loss of plant species is higher in the Northeast than in any other part of the United States except Hawaii. Many states in the region are losing more than 5% of their native plants; the loss in Delaware is proportionally the highest at a rate of 15% (Guntenspergen 1995; Fig. 4; Table 2).

Two species, small-whorled pogonia and Robbins' cinquefoil, illustrate the variety of habitats and the modern causes of declines of species. The small-whorled pogonia is one of many endangered orchids; it occurs in second-growth forests in the Northeast, South, and Midwest. Reasons for its decline are not understood, but collection by people is believed an important factor (Mathews and Moseley 1990). The U.S. Fish and Wildlife Service drafted a recovery plan in 1992. Robbins' cinquefoil is an alpine plant, occurring above the treeline on shallow, sandy mountain soils. It now occurs in a single location in New Hampshire and in several places in Vermont. Hikers are a major problem for the plant because they climb to admire the views from mountain peaks and in the process disturb the fragile soils and trample plants (Mathews and Moseley 1990). Two methods by which this unique plant and its habitats are being protected are signs requesting that hikers stay on the trail and forest rangers stationed at the summits of mountains.

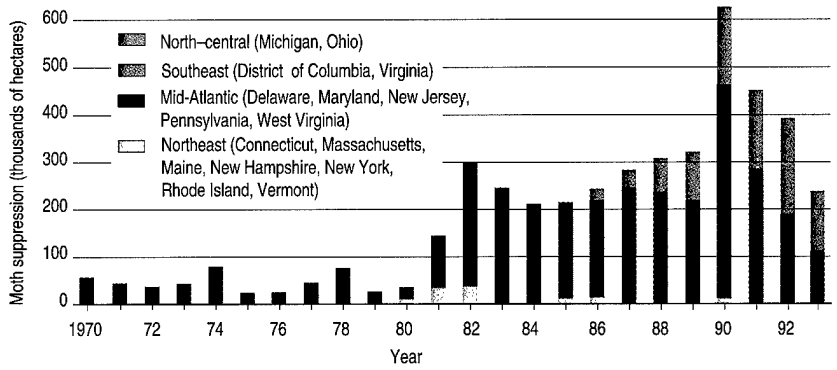

Fig. 3. History of gypsy moth suppression by federal or state cooperative suppression projects, 1970–1993 (Twardus 1994).

Table 2. Vascular plants that occur in the northeastern United States and are on the federal list of endangered species as of 20 August 1994 (U.S. Fish and Wildlife Service 1994).

Northern wild monkshood
Sensitive joint-vetch
Sandplain gerardia
Seabeach amaranth
Mead's milkweed
Jesup's milkvetch
Pitcher's thistle
Smooth coneflower
Swamp pink
Lakeside daisy
Small-whorled pogonia
Canby's dropwort
Furbish lousewort
Eastern prairie fringed orchid
Robbins' cinquefoil
Knieskern's beaked-rush
American chaffseed
Northeastern bulrush
Leedy's roseroot
Virginia spirea
Running buffalo clover
American hart's-tongue fern

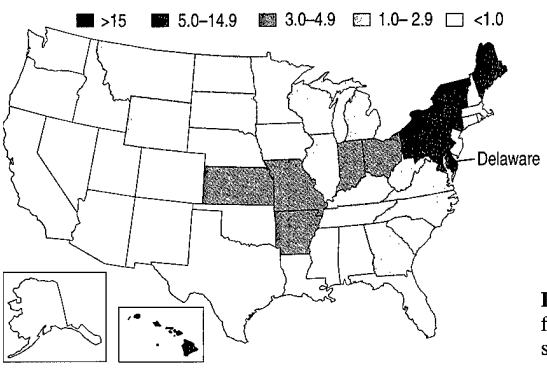

Fig. 4. The percentage of native flora potentially lost from each state (Morse et al. 1995).

The mosses may be among the smallest plants, but they also may be among the most politically potent plants. The famous surveyor VerPlanck Colvin used mosses to defend the need for a forest preserve in New York. He maintained that these species served as natural sponges that soak up moisture and release it slowly, thus keeping the canal system in New York state operating throughout the summer (Graham 1978). Although Colvin surely stretched the facts, his argument was sustained. In New York alone are 465 species of mosses, and new species are occasionally still discovered. The oldest list of rare nonflowering plants in the Northeast is probably from New York. In general, however, basic information on the occurrence and distribution of mosses is lacking in all states in the Northeast. This lack is troubling because many of these species are rare and some are already endangered. The principal threats to mosses in the Northeast are habitat destruction from suburban development, wetland alteration by humans and beavers, and fire suppression where fire formerly occurred naturally (Slack 1992).

Forest Vertebrate Animals

The forests of the Northeast are among the most important environments for the diversity of vertebrate species in North America. Nationwide estimates indicate that at least 90% of the total bird, amphibian, and fish species in the country and 80% of the mammal and reptile species rely on forests for at least part of their life requirements (Flather and Hoekstra 1989). Forests provide a three-dimensional structure that gives much more than simple shelter from weather and cover from predators. This structure also moderates temperature extremes, increases humidity and water retention in the community, and provides energy in the form of edible leaves, fruits, and nuts.

Forest Birds

Contaminant Effects on Forest Birds

Chemical contaminants, especially pesticides, have had substantial effects on birds. A good example is the pesticide that was used for the control of the eastern spruce budworm, an insect that is a favored food of many songbird species. Budworm populations follow a cycle of outbreak and dieback, and songbird densities increase and decrease according to the increasing or decreasing abundance of the budworm (Hill and Hagan 1991). The use of pesticides disrupted the cycles of the budworm populations and reduced the abundances of many bird species (see chapter on Contaminants).

Abundance Changes in Bird Populations

Many people are under the impression that the abundances of birds have substantially declined in the past 50 years, yet the abundance levels of a few species have shown extraordinary increases (Table 3), whereas many others are threatened (Table 4). A one-time candidate for the national symbol and a valued game species—the wild turkey—has thrived in the Northeast in the last few decades. From small populations in Pennsylvania in the 1950's, wild turkeys have spread to all northeastern states and number more than 280,000 (Kennamer and Kennamer 1990). The fragmented forest–agricultural environment provides the best habitat for these birds. Turkey populations were restored by transplanting birds to areas of their former range and by strengthening law enforcement against illegal hunting (Dickson 1992, 1995).

Human activities also provide new food sources for some species. The mourning dove, for example, has responded favorably to the modern landscape by increasing in numbers and by expanding its range, probably because of increased food from farming and residential feeders (Applegate 1993). Feeding in residential areas has also sustained species such as the house finch. Formerly western breeders, these small birds were released in western Long Island, New York, in 1940. The population growth of this species was exponential until about 1971 and has since been increasing more slowly. Concern has been expressed that the purple finch may be adversely affected by the invasion of the house finch, but recent findings suggest that the two species prefer different habitats and that competition between the purple finch and the house finch is probably minimal. The house finch does, however, compete directly with the house sparrow, and the outcome of this competition is unclear (Bosakowski 1986).

Forest Mammals

After birds, mammals are the most comprehensively studied taxonomic group. Two of the large predators, the gray wolf and the mountain lion, were extirpated from the Northeast. Interest continues in reintroducing the gray wolf to the Adirondack Mountains, where large tracts of wilderness still exist. Such a plan depends on public opinion, and restoration will be influenced by the current experience with the reintroduction of wolves in Idaho, Montana, and Wyoming. The eastern cougar, an endangered subspecies of the mountain lion, was also extirpated, and although individuals are periodically reported, self-sustaining populations probably do not exist (Cumberland and Dempsey 1994). The reintroduction of the eastern cougar to the Northeast is not believed feasible because human and road densities are too high, even in

Birds and Landscape Changes in Northeastern Forests

The past four centuries have brought to the landscape of the Northeast a series of changes of a magnitude and rapidity that has few precedents on Earth. Before European settlement, this region was a mosaic of open old-growth forests, shifting agriculture, and fire-maintained grasslands and savannahs. Following European contact, disease decimated Native American populations, and much of the unsettled interior became wooded. By the mid-1800's agriculture, the demand for wooden fencing, charcoal, tanning, and fuel for households, and iron and lime industries created a landscape that was devoid of all but scattered trees. This century has seen the return of forests throughout much of the region.

Such sweeping changes bring with them changes in bird communities. Clear preferences by many bird species for forested environments should mean that their populations wax and wane with changes in the composition, age, and distribution of forested lands. Given these predilections, it should be possible to use information on changes in bird populations as one gauge of the effects humans have had on the landscape.

Birds are connected to their environment in a direct and uncompromising manner. They have no buffer against regional changes in food, cover, predators, or landscapes. Marketing factors and government social welfare programs cannot compensate them if their environment deteriorates. If a site changes in such a way that the locale lacks what it takes to support their needs, they must leave or die. Consequently, the distribution, abundance, and changes in bird populations are a direct statement of the quality and suitability of a region to support birds.

Two large data sets are available for investigating changes in bird populations in the Northeast: the Christmas Bird Count, begun in 1900 (Butcher 1990), and the U.S. Geological Survey's North American Breeding Bird Survey, begun in 1966 (Peterjohn 1994; Price et al. 1995). Data from the early years of the Christmas Bird Count have not yet been converted to electronic format, but Christmas Bird Count data from 1959 to 1988 and Breeding Bird Survey data from 1966 to 1994 are available. Trends in bird populations from these data provide the means to examine the relative welfare of guilds of forest birds (Robbins et al. 1989).

The table presents a state-by-state breakdown of the numbers of bird species increasing and decreasing, organized by several

Table. Summary, by season, state, and guild, of increasing and decreasing numbers of species of birds based on data from the North American Breeding Bird Survey (1966–1994) and Christmas Bird Counts (1959–1988).

Breeding season

State	Mature forest		Scrub		Neotropical migrant		Permanent resident		Short-distance migrant	
	Decrease	Increase	Decrease	Increase	Decrease	Increase	Decrease	Increase	Decrease	Increase
Maine	11	19	9	6	6	12	1	2	4	5
New Hampshire	11	17	8	3	10	7	0	2	1	8
Vermont	11	8	9	3	6	4	2	1	3	3
Massachusetts	10	10	9	2	8	5	1	1	1	4
Connecticut	12	5	10	4	9	3	1	1	2	4
New York	14	20	7	6	11	7	0	3	3	0
Pennsylvania	14	17	11	4	7	10	3	2	4	9
New Jersey	9	4	13	2	7	2	1	0	1	4
Maryland	8	18	8	2	8	9	0	4	0	1
West Virginia	12	7	9	4	11	3	1	2	0	4
Virginia	12	13	9	1	9	7	1	4	1	3

Wintering season

State	Mature forest		Scrub		Permanent resident		Short-distance migrant	
	Decrease	Increase	Decrease	Increase	Decrease	Increase	Decrease	Increase
Maine	6	14	6	3	1	4	2	8
New Hampshire	5	10	3	2	1	3	2	6
Vermont	1	9	0	4	0	3	0	6
Massachusetts	10	15	7	8	2	3	5	9
Connecticut	10	13	6	6	2	3	7	7
New York	10	18	8	5	2	4	5	10
Pennsylvania	6	20	7	7	1	5	2	13
New Jersey	10	16	10	5	2	3	4	11
Maryland	7	13	9	3	0	3	6	9
West Virginia	0	15	9	3	3	2	3	12
Virginia	5	21	10	4	2	5	2	14

categories or guilds (Droege and Sauer 1989). Results for birds inhabiting mature forests show different patterns. Summer patterns present a mix of regions where increases and decreases predominate in different conditions, whereas winter populations show a pattern of uniform increases (Fig. 1a, b). Bird species composition shifts in forests with the seasons—some birds fly to the tropics, others shift farther south in the United States, and some are permanent residents.

If the overall results are broken down along lines of residency status, Neotropical migrants (Fig. 1c) are declining in more states than they are increasing. Short-distance migrants and permanent residents show the opposite pattern (Fig. 1d,e,f,g). Winter patterns for short-distance migrants and permanent residents both show increasing numbers of species in all states. Clearly the difference between the initial summer and winter results comes from the greater number of declines in Neotropical migrants.

The patterns and causes of changes in Neotropical migrants are a matter of much recent concern and speculation (James et al. 1996). The complexity of their migration, the diversity in their winter and summer life histories, and their great range in geographic and habitat locations in the winter make it difficult to separate out many competing hypotheses as to the causes of these patterns. Data (Table) indicate, though, that populations of Neotropical migrants, as a guild, are experiencing greater negative changes than their less-traveled, forest-dwelling neighbors.

Excluding the complex case of forest-dwelling Neotropical migrants, a clear pattern is evident of increases in forest-dwelling birds during the past 30 years. These patterns coincide with patterns of forest change revealed in the U.S. Forest Service Forest Inventory Program. Forest acreage, particularly of mature forests, has increased throughout the Northeast during this time, though increases in acreage have recently plateaued or declined slightly in some regions (Powell et al. 1994). There has also been a shift from pioneer plant species and those encouraged by regular fires, such as Virginia pine, black locust, and oaks, toward species that regenerate quickly following forest cutting, such as red maple, sugar maple, and yellow-poplar (U.S. Forest Service 1995).

Such patterns of forest change are the indirect result of the exploitation of rich prairie agricultural lands, the loss of local markets for agricultural goods through decreased transportation costs, and

subsequent declines in farming of the rocky uplands of much of the Northeast. Over the past 125 years these lands have slowly returned to forest cover. The fact that this process may have stabilized and that the rate of such change has declined is illustrated by the decline of bird species inhabiting early successional forests (scrub; see Table).

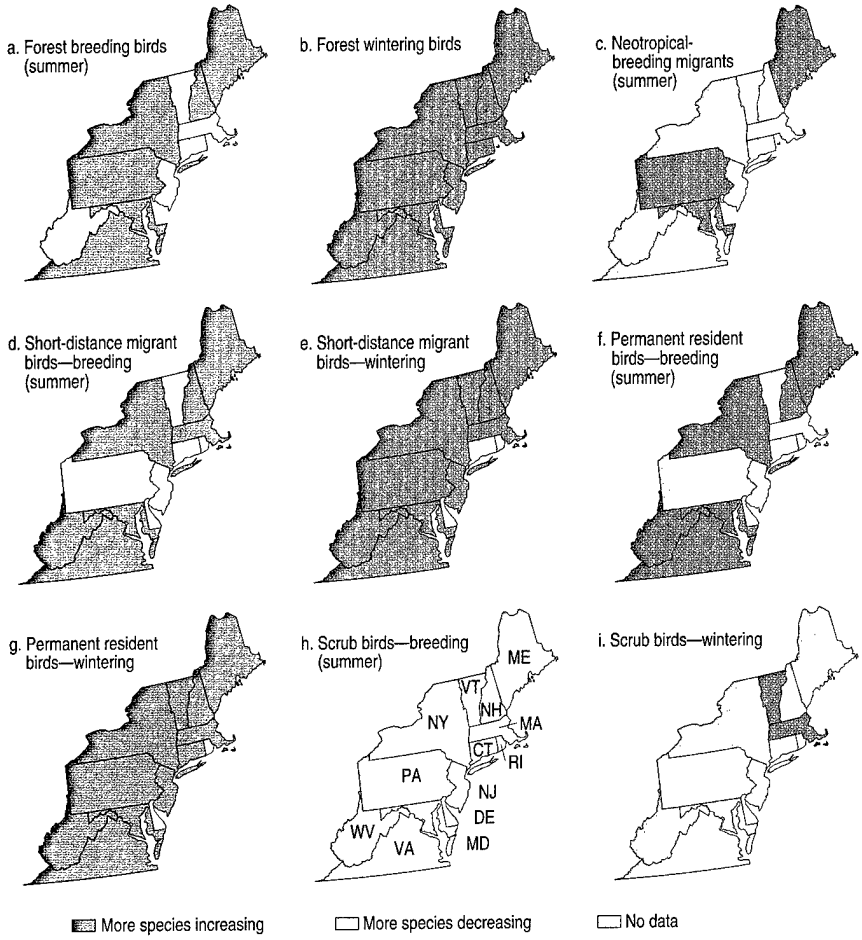

Fig. 1a–i. Regions of overall increase or decrease for wintering and breeding birds (by state). States colored yellow have more species declining. States colored blue have more species increasing. Breakdowns are given for a, b) the collective sum of all forest birds, c) Neotropical migrants (there are no wintering estimates), d, e) short-distance migrants, f, g) permanent residents, and h, i) scrub-inhabiting birds.

Both summer and winter data sets reveal that far greater numbers of scrub-nesting species are decreasing rather than increasing (Fig. 1h,i). Furthermore, the species showing most of the increases are species widely adapted to mechanized agriculture and suburban habitats, such as the mourning dove and the northern cardinal. Land-use patterns in the Northeast are likely to further decrease the number of successional habitats present. Already, Bewick's wren, Bachman's sparrow, and the lark sparrow, all inhabitants of sparsely wooded scrub areas and widely distributed until the middle of this century, have declined to the point that they are locally extirpated or that only a handful of individuals remain. Other species may soon follow.

Changing bird populations reflect the Northeast's changing landscape. Species differ in their responses to landscape change, each having unique preferences for the habitat architecture of their surroundings. By tracking changes in bird populations and other species, we can make statements and develop hypotheses regarding the health and future of our environment. Such measures cannot be found through inspection of our gross national product or consumer price indices. We must listen to what these changes tell us about our effects on the lands we share. By distancing ourselves from such information, we risk making the present round of changes irreversible.

See end of chapter for references

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sparsely settled areas. A low rate of reproduction, mortality on roads, and losses from illegal hunting would keep the eastern cougar from increasing its population (Brocke 1994).

Although most of the larger forest mammals have disappeared, several are showing stable or increasing population levels. Elk are confined to a small population in northern Pennsylvania. In spite of threats from habitat alteration and poaching, black bear populations are stable or increasing in all states in the Northeast. In fact, there are more than 40,000 bears in the northeastern forests; most are in Maine (20,000) and Pennsylvania (7,500), but populations that number from 150 to 5,000 are reported in every state except Connecticut, Ohio, and Rhode Island (Vaughan and Pelton 1995). The area's largest animal, the moose, was extirpated from the region in the mid-nineteenth century. Now, however, the moose is common in northern New England as a result of protection from unregulated hunting, expansion of the forest, and subsequent intensive tree harvest and regeneration. Some moose are even venturing into Connecticut, Massachusetts, and New York.

The two smaller cat species, bobcat and lynx, still occur in the Northeast. Bobcat and lynx prefer unbroken forests and are at risk from continuing human intrusion on forestlands. Bobcats are protected in Connecticut, Delaware, Maryland, New Jersey, Ohio, Pennsylvania, and Rhode Island. Bobcat populations seem to have declined since settlement; estimated densities are 2 to 6 cats per 100 square kilometers (Fox 1990). The bobcat will probably persist because of its high rate of

reproduction and its ability to adapt to varying landscapes (Koehler 1987). An effort to restore the lynx to Adirondack Park was made in 1985; the outcome of this project is still unclear (Brocke and Gustafson 1992).

Misunderstood Forest Wildlife

Because public pressure plays a major role in wildlife conservation, unpopular or feared animals are at a distinct disadvantage when their populations or habitats are threatened. This category of misunderstood wildlife includes bats and snakes. At least 10 species of bats occur in the Northeast. The Indiana bat is on the federal list of endangered animals; the small-footed myotis is on the state list of endangered animals in New Hampshire, on the state list of threatened animals in Vermont and Pennsylvania, and is of special concern in New York (Genoways 1985; New York, New Hampshire, Vermont, and Pennsylvania Natural Heritage Programs, unpublished data).

The status of an even more feared animal, the timber rattlesnake, is similarly precarious. The timber rattlesnake is extirpated in Maine and Rhode Island, endangered in Connecticut, Massachusetts, New Hampshire, New Jersey, and Vermont, and threatened in New York and Ohio. These snakes are still hunted in Pennsylvania, where populations are large but not necessarily secure (Breisch 1992). Populations of this snake are declining in all northeastern states, and a survey of den sites in northern New Jersey and New York revealed that den sites had decreased by an average of 60% since 1968 (Stechert 1992). The snake populations and their habitats are declining because of human development, various disturbances, and willful destruction (New York Natural Heritage Program, Latham, unpublished material).

Many different species that inhabit the forest floor are often overlooked because of their small sizes. These species include rodents, other small mammals, salamanders, insects, other arthropods, and many creatures that are too small to be seen with the naked eye. Animals that lack public appeal often get less attention from the scientific community and are therefore the least well known. The consequences of such a lack of knowledge are illustrated in the case of the American burying beetle, a forest insect that was widespread in the eastern forests before 1960. By 1970, though, the beetle was thought extinct but was then rediscovered in Rhode Island. No conservation measures were under way until 1983 (Wells et al. 1983); the beetle was placed on the federal list of endangered species in 1989 (U.S. Fish and Wildlife Service 1994).

Table 3. Number of species of Neotropical breeding birds in the Northeast with significant population trends and the number of these species that are short- and long-distance migrants[a] (Smith et al. 1993).

Wintering habitat	Upward	Downward	No trend
Short-distance	6	15	10
Long-distance	10	14	22
Total	16	29	32
Breeding habitat	**Upward**	**Downward**	**No trend**
Mature forest	7	7	16
Successional	9	22	3
Total	16	29	19
Breeding habitat	**Short-distance**	**Long-distance**	**Total**
Mature forest	11	41	52
Successional	32	42	74
Total	43	83	126

[a] Values are partitioned by habitat and migratory behavior.

Table 4. The status of birds that are endangered or extirpated in at least one of seven northeastern states in the United States (Vickery 1991). X = extirpated, E = endangered, T = threatened, S = special concern, • = occurs but not listed, N = does not occur.

Species	State status						
	Maine	New Hampshire	Massachusetts	Vermont	Rhode Island	Connecticut	New York
Common loon	•	T	S	E	N	S	S
Pied-billed grebe	•	S	T	S	X	E	•
Black-crowned night-heron	S	X	•	•	S	S	•
American bittern	•	•	S	•	E	E	•
Osprey	•	T	•	E	S	S	T
Bald eagle	E	E	E	E	E	E	E
Northern harrier	•	T	T	S	E	E	T
Sharp-shinned hawk	•	•	S	•	X	T	•
Peregrine falcon	E	E	E	E	E	E	E
Spruce grouse	•	•	N	E	N	N	T
Long-eared owl	•	S	S	S	S	E	•
Short-eared owl	N	S	E	S	N	T	S
Red-headed woodpecker	•	N	N	•	S	S	E
Sedge wren	E	S	E	T	N	E	T
Loggerhead shrike	X	X	E	E	N	N	E
Golden-winged warbler	•	N	S	E	•	X	S
Northern parula	•	•	T	•	X	•	•
Black-throated blue warbler	•	•	•	•	X	•	•
Yellow-breasted chat	N	N	N	N	E	E	•
Vesper sparrow	S	S	•	•	E	E	S
Grasshopper sparrow	E	S	S	S	T	E	S
Henslow's sparrow	N	S	E	E	N	X	S

Unique Forest Environments

Two forest systems in the Northeast deserve special mention because of their unique species and relative integrity—the Adirondack Park of New York and the Pine Barrens of New Jersey. Although these environments have experienced many disturbances by humans, both still include large parcels of land that are somewhat protected from development and disturbance and are functioning, largely intact, natural environments.

Adirondack Park

The Adirondack Park covers 2.3 million hectares in northern New York and is the largest park in the contiguous United States. Politically, the region is unique because it is a mosaic of public (45%) and private (55%) land that is under the stringent regulation of the Adirondack Park Agency. As part of the Lake

Champlain–Adirondack Biosphere Reserve, this region is involved in an experiment in the simultaneous development of human economy and protection of wilderness character. Although the park was historically exploited for timber and mineral resources, today it is dominated by second-growth forest. More than one million hectares of the park are designated as Adirondack Forest Preserve and held forever wild by an amendment to the New York State Constitution. Mining was a major portion of the economy as recently as the 1970's, and logging and tourism continue, but most of the species and environmental diversities of 300 years ago still exist (Davis 1988).

One inhabitant of the Adirondacks is the spruce grouse, a species that illustrates how subtle changes in the forest can isolate and ultimately eliminate species. The spruce grouse is slightly smaller than the more widespread ruffed grouse and inhabits spruce–fir forests throughout the Northeast and Canada and west into the Rocky Mountains. Populations in the Adirondacks have been declining since the late 1800's, primarily because logging changed the species composition of forests. Spruce and fir trees are critical habitat for spruce grouse, and these trees once composed 45% of the Adirondack forest. After logging, spruce and fir are replaced by other tree species. Today, only 10% to 25% of the Adirondack forest is spruce and fir, and these stands occur in isolated patches. The entire breeding population of spruce grouse in the Adirondack Park now consists of an estimated 175–315 individuals (Bouta 1991). Because of the small size and fragmented nature of this spruce grouse population and because of its need for mature spruce–fir forest, the long-term prognosis for the species is not favorable (R. Chambers, State University of New York, College of Environmental Science and Forestry, Syracuse, personal communication).

The mountainous terrain of the Adirondack Park includes hundreds of lakes. Unfortunately, because the park is downwind from metropolitan and industrial centers to the west, the Adirondack region has the highest percentage of acid waters in the United States. Nearly 20% of the Adirondack lakes have lost one or more fish populations to acidification. Brook trout and acid-sensitive minnow species suffer the most; however, no species seem in danger of extinction at present (Baker et al. 1993).

The decline of fish populations in acidified lakes also affects nesting common loons. Although common loons occur throughout North America, they have become a symbol of the northern wilderness in New England, New York, and the Great Lakes states. Loons show strong fidelity to specific nesting areas and continue to nest even on lakes that are acidic. Such acid lakes support few fishes, which are the primary food for the quickly growing young (Parker 1988). Loons are also at risk from a variety of human disturbances. Throughout New England, adult birds die from PCB and mercury poisoning and are easily disturbed by recreation and development. In fact, the leading cause of death for the species may be lead poisoning from anglers' lead sinkers (Pokras et al. 1991).

Pine Barrens

Although the Pine Barrens of New Jersey are not as large as the Adirondack Park, they are equally unusual. The Pine Barrens consist of 500,000 hectares of sandy soils in central New Jersey and are dominated by pitch pines and scrub oaks that are adapted to frequent fire. Pine barrens occur in all the coastal northeastern states, but nowhere in the world is the type as extensive and undisturbed as in New Jersey. Although the Pine Barrens are only a 2-hour drive from New York City and Philadelphia, they continue to have remarkable ecological integrity. Roads are relatively uncommon and large areas remain free from human disturbance (Kerlinger and Doremus 1981); some areas are farmed, mainly for blueberries and cranberries. Approximately 365,000 hectares of the Pine Barrens are preserved and managed under the New Jersey Pinelands Commission (Boyd 1991).

The New Jersey Pine Barrens provide habitat for 54 species of plants and 33 species of animals on the state list of threatened or endangered species. Two plants, the sand-myrtle and Pickering's morning-glory, occur nowhere else; Knieskern's beaked-rush and blazing star occur only in the barrens and in similar sites in Delaware. In addition, the environment's many bogs support more than 20 species of sphagnum moss. The low plant diversity and low nutrient conditions of the Pine Barrens support few birds, earthworms, or snails, but do support many butterflies, skippers, and moths, and some amphibians and reptiles (Table 5). The pine snake is a common inhabitant of the Pine Barrens but is threatened in New Jersey at large (Boyd 1991). Likewise, the Pine Barrens treefrog once was on the federal list of endangered species but is abundant in this region (U.S. Fish and Wildlife Service 1994).

Historically, the pine barrens habitat extended farther north and east, but today only portions persist. The portion near Albany, New York, is most notable. Commonly called the Pine Bush, this area is only 1,200 hectares (originally 104 square kilometers) and is so disturbed that continuous patches rarely exceed 300 hectares (Kerlinger and Doremus 1981). Heavy deer browsing, traffic, windbreaks made

Northeastern Spruce–Fir Forests

Forests dominated by red spruce and balsam fir cover 4.1 million hectares in the Northeast, principally in northern New England and eastern New York (Figure). Pollen records of past forests suggest that today's spruce–fir forests became prominent only around 1,000 years ago, corresponding to a decline in eastern hemlock and American beech abundance (Jacobson et al. 1987). Spruce–fir forests predominate on somewhat poorly drained, acidic soils of glacial origin. The region's cold climate and infertile soils have largely prevented the widespread conversion of natural spruce–fir forests to agriculture, as is common in more southerly regions.

The highly variable glaciated landscape creates many interesting habitat types. *Spruce flats* occur at low elevations on shallow glacial tills with impeded drainage. Red spruce and balsam fir mixtures dominate these sites, with minor components of paper birch and red maple. *Spruce swamps* support nearly pure stands of black spruce mixed with tamarack and Atlantic white-cedar on organic or poorly drained mineral soils. *Spruce slopes* occur on mountainsides above approximately 800 meters elevation on shallow, very rocky soils. Balsam fir and paper birch represented a minor component of the spruce slope type before human disturbance. On more fertile midslopes with well-drained soils, deciduous species—yellow birch, red maple, American beech, and sugar maple—mix with spruce and fir. Eastern hemlock and eastern white pine are also common associates (Westveld 1953).

Human Influences on Forests

Human disturbances have profoundly affected the current condition of the spruce–fir forest resource. Throughout the 1800's, virgin forests were logged repeatedly, first for scattered white pines, then for spruce, and finally for northern hardwoods. Since 1900 landownership has changed from the early lumber barons to pulp and paper companies. The largely unpopulated spruce–fir region of northern Maine comprises the largest contiguous industrial ownership in the United States, and commercial forestry continues to be the dominant land use.

Natural Disturbances

Natural disturbances, mainly wind storms and insect outbreaks, although frequent, have rarely killed stands over extensive areas before human exploitation. Large, stand-replacing wildfires were especially rare, averaging nearly 2,000 years between events. This presettlement regime of small spatial-scale disturbances maintained a landscape of multiaged stands dominated by long-lived trees as much as 300 years old (Lorimer 1977). The most prominent natural disturbance agent of spruce–fir forests is the eastern spruce budworm, a native insect that has reached outbreak status three times during the twentieth century (Irland et al. 1988). Balsam fir, a much shorter-lived species than red spruce, is the budworm's primary host, although spruce can also be killed in severe outbreaks. Widespread insecticide application during the 1972–1984 outbreak prevented the extensive mortality experienced during the very severe 1913–1919 outbreak. The spruce beetle was once a common cause of death of old, large-diameter red spruce (Hopkins 1901). The introduced insect, the balsam woolly adelgid, affects balsam fir in coastal regions but appears to be climatically limited and does not cause serious damage inland.

Although the current spruce–fir forest is, in many respects, quite natural in appearance, more than 150 years of human exploitation and forest management have significantly altered its age structure and species composition. Logging has always concentrated on the older, more valuable conifers, so late successional forests with old-growth structures have become quite rare, limited mainly to small stands in public and conservation ownerships. The second- and third-growth forests under management have much less age diversity than the presettlement forests. Although red spruce remains abundant, balsam fir has no doubt expanded greatly. Selective logging of conifers has also reduced tree species richness of formerly mixed stands that are now composed of pure northern hardwoods (Seymour 1992).

Future of Northeastern Spruce–Fir Forests

The future condition and sustainability of the spruce–fir forest will depend on how management practices of large landowners evolve to meet increasing demands for commodities while conserving biodiversity. One paradigm currently under wide discussion is a landscape *triad*, combining areas devoted to commodity production, unmanaged ecological reserves, and modified forestry practices (Seymour and Hunter 1992).

See end of chapter for references

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Figure. One of the finest remaining examples of an old-growth, low-elevation red spruce forest, a type of forest that once covered millions of hectares in northern Maine.

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Table 5. Number of species that occur in the New Jersey Pine Barrens, United States (Boyd 1991).

Taxon	Number of species
Algae	360
Fungi	>1,000
Lichens	275
Liverworts	78
Mosses	274
Horsetails and club-mosses	8
Ferns	21
Flowering plants	288
Insects	10,385
Fishes	36
Amphibians	24
Reptiles	19
Birds	73–144
Mammals	34
Total	13,000

by roads and buildings, development of open dunes, nonindigenous species, and fires at the wrong intervals have altered the environment. In the last century, 28 species of moths and butterflies have been lost from the Albany Pine Bush; the greatest decline occurred in the last two decades. Pine barrens regions are often home to insects that are not restricted to the environment but are on the edges of their ranges, which makes them more susceptible to local extinction. One species that depends heavily on pine barrens and the blue lupine plants that grow there is the Karner blue butterfly, which is on the federal list of endangered species. Its populations in the Albany Pine Bush have declined drastically since 1980, and its continued existence is doubtful (McCabe 1995).

The high human populations of the Northeast do not permit a complete restoration of pine barrens. The Nature Conservancy owns a large portion of what pine barrens remain in New York and together with state agencies is attempting to preserve them. A section of pine barrens on Long Island, New York, is 100,000 hectares but is much dissected by roads and development, and fire suppression has reduced the environment to less than 50% of its original size. The New Jersey barrens are somewhat more secure but are not isolated from development and pollution; fertilizers, pesticides, herbicides, and organic wastes have changed the water quality and have led to changes in the flora. This, in turn, crowds out species like the threatened Knieskern's beaked-rush, which inhabits areas of early regrowth (Moseley 1992).

Agricultural Lands

Although unforested lands occur naturally in the Northeast, the majority of open land in the region was created by humans for agriculture. Today, agricultural lands make up 22% of the total land area, or about 13.1 million hectares. This includes farmed land, fallow fields, and pastures. Agricultural land is most common in Delaware (49%) and in Ohio (48.3%); the greatest total area of farmland, 4.9 million hectares, is in Ohio (U.S. Forest Service, forest statistics for states, 1980–1991, unpublished data).

Cropland Trends

Total cropland in the Northeast and in the country has been declining since the 1930's. Exclusive of Ohio, the Northeast showed a net shift of 1.3 million hectares from cropland to other uses between 1967 and 1975. This trend was reversed somewhat in the 1980's because of an expanding export market but quickly tapered off. Further increase in cropland in the Northeast is not probable (McCorkle and Halver 1982). Continuing expansion of rural communities is converting significant amounts of agricultural land to housing and commercial developments. The consequences of this trend include a rise in agricultural land prices and more intensive farming of remaining land (McCorkle and Halver 1982). Economic forces continue to encourage the removal of hedgerows, field-border strips, wetlands, and woodlots, all of which are prime wildlife habitats (Flather and Hoekstra 1989).

Sustainable Use of Croplands

Agricultural land and its products are of such economic importance that legislation designed to encourage sustainable use continues to be developed. In the past decade, the Conservation Reserve Program, part of the Food Security Act of 1985, encouraged the removal of erosion-prone and marginal-soil lands from production for at least 10 years. As of 1989, 2 million hectares were under contract in the Northeast (west to the Mississippi; Flather and Hoekstra 1989). National legislation with so-called swampbuster clauses discouraged the conversion of 625,000 hectares of unprotected wetlands (6.1% of the nation's total) into croplands. In addition to protecting wetlands and reducing erosion, these programs produce prime habitat for a wide range of species that live in open land, as well as species that use both fields and forests. The preservation of agricultural land is beneficial to small game, nesting waterfowl, nongame animals, and fishes. If programs such as the Conservation Reserve Program are discontinued, many native species are expected to decline.

Wildlife Trends

Many wildlife species that inhabit open lands in the Northeast have declined in the past 20 years. Species such as the eastern and New England cottontails were plentiful in the 1960's but now seem to be declining across their ranges (DeGraaf et al. 1989). Grassland birds declined drastically in the Northeast during the last 100 years. Open habitats support many threatened and endangered bird species; nine species from grasslands are listed as threatened or endangered by five or more northeastern states (Vickery 1991). The populations of the long-eared owl declined between 1956 and 1986. Likewise, the northern bobwhite experienced a 40-year decline across its primary range, and although the rate of decline is less now than in recent history, populations are not expected to return to even the 1985 levels (Flather and Hoekstra 1989). Even

American Woodcock

The American woodcock is a shorebird that inhabits forested areas from Manitoba east to Newfoundland and Labrador and south to the Gulf of Mexico. It is known by a variety of colorful local names including timberdoodle, Labrador twister, brush snipe, woods snipe, and bog sucker. The woodcock is a popular game bird throughout eastern North America and is the object of an estimated 3.4 million days of recreational hunting annually (U.S. Department of the Interior 1990). Hunters in the United States harvest an estimated 1.1 million woodcock annually (Straw et al. 1994), making woodcock among the top ten species of migratory game birds harvested in the Atlantic and Mississippi flyways.

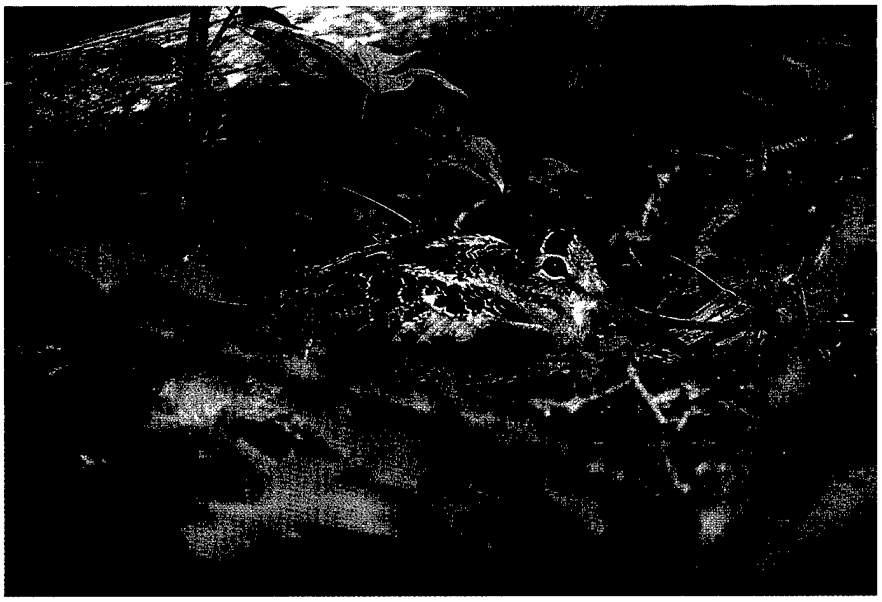
The most distinctive features of the woodcock are its long bill (60–75 millimeters), which is specialized for feeding on earthworms, and its large eyes, which are set far back for 360° vision (Keppie and Whiting 1994). Woodcock are cryptically colored and more compact than other shorebirds. Females are larger than males, with female weights ranging from 151 grams to 279 grams, and males from 116 grams to 219 grams (Mendall and Aldous 1943; Owen and Krohn 1973). Their plumage consists of a mottled pattern of browns, black, buff, and gray. Short powerful wings allow them excellent maneuverability when flying through the thickets and tangled brush where they live (Fig. 1).

The northeastern states are a major breeding area for woodcock. Most woodcock winter south of the region except for a small population along coastal Virginia. Cape May, New Jersey, and Cape Charles, Virginia, are major staging areas for woodcock during migration, especially in the fall. Birds arrive in the Northeast from wintering areas as early as February in some states, but the peak of the breeding season is in April and May. These birds are probably the earliest nesters among ground-nesting species in North America. Around dawn and dusk during the breeding season, males of this secretive species come out of hiding to perform a spectacular display. Courtship begins with a ground display during which the male turns and utters a nasal "peent" for about a minute. This is followed by a 45- to 60-second aerial display in which the male spirals 30 to 90 meters above the ground while creating a distinctive twittering sound with the outer three wing primaries. The display ends with a melodic warbling call during the descent. After the bird alights at the takeoff point, the sequence is repeated (Mendall and Aldous 1943; Straw et al. 1994). Courtship bouts last 25–45 minutes, depending on duration of twilight, but may continue throughout the night during periods of bright moonlight.

Habitat requirements of woodcock vary with activity, time of day, and season. Woodcock spend the daylight hours using their long bills to probe for earthworms, which make up nearly 80% of their diet (Sperry 1940; Keppie and Whiting 1994). They rely on their cryptic coloration and the dense vegetation to hide them from predators. At dawn and dusk they fly from the protection of their daytime cover to fields and openings to roost, feed, or mate. They are not restricted to specific plant assemblages (Keppie and Whiting 1994) as long as the habitat provides the necessary stem density and structure (Straw et al. 1994). The birds prefer early-successional habitats created by periodic disturbance of the forest; optimal habitat is provided by dense hardwood cover on good soils with an abundance of earthworms (Straw et al. 1994). Thus, young forests and abandoned farmland mixed with forested land are ideal woodcock habitat (Keppie and Whiting 1994).

Woodcock use forest openings, clearcuts, fields, roads, pastures, and abandoned farmland as display areas (singing grounds) for courtship (Mendall and Aldous 1943; Liscinsky 1972). Vegetative composition of the singing ground varies locally and throughout the range and is probably unimportant as a determinant of use (Dwyer et al. 1988; Sepik et al. 1993). More likely the quality of the adjacent habitat for nesting and brood-rearing determines use by males. Young aspen, birch, hawthorn, alder, and dogwood provide appropriate cover in the Northeast (Keppie and Whiting 1994; Straw et al. 1994). Nests and broods are found in young to mixed-age forests, but young, open, second-growth stands are preferred (Mendall and Aldous 1943). In areas where habitat is managed, woodcock select stands of young hardwood regeneration (Gregg and Hale 1977; McAuley et al. 1996). During summer, young hardwoods and mixed woods with shrubs, particularly alders less than 20 years old, provide daytime cover for feeding (Morgenweck 1977; Rabe 1977; Hudgins et al. 1985).

Woodcock are sometimes found in stands of mature forest, but only if there is a dense understory (Sheldon 1967; Rabe 1977). In the Northeast, woodcock rarely use conifer stands, except during drought when they may be critical for survival (Sepik et al. 1983). On summer nights, many birds roost in clearings, such as blueberry barrens, pastures, recently harvested woodlands, and plantations (Dunford and Owen 1973; Sepik et al. 1981; Sepik and Derleth 1993). Woodcock use many of these same fields as singing grounds in the spring. In the fall and during migration, woodcock spend the days in young, moist hardwoods with shrub understories (Keppie and Whiting 1994), whereas in winter they use a variety of habitats during the day, especially bottomland hardwoods, upland mixed



Courtesy D. McAuley, USGS

Fig. 1. A female American woodcock in typical habitat.

pine–hardwoods, and recently burned stands of longleaf pine (Glasgow 1958; Britt 1971; Dyer and Hamilton 1977).

Woodcock are managed on the basis of two regional populations, the eastern and the central (Owen et al. 1977); northeastern states are part of the eastern management unit. Analysis of band recovery data indicates that little crossover of birds occurs between the regions (Martin et al. 1969; Krohn et al. 1974). Furthermore, regional boundaries conform with the boundary between the Atlantic and Mississippi waterfowl flyways.

Reliable indices of population size, productivity, harvest size, and distribution of woodcock are difficult to obtain (Bruggink and Kendall 1995). Because of their small size, cryptic color, and preference for dense vegetation, woodcock cannot be censused. The status of the woodcock population is now monitored with a wing-collection survey and the singing-ground survey.

The wing-collection survey was developed in the 1960's to monitor productivity. Cooperating woodcock hunters and some waterfowl hunters who hunt woodcock provide wings from birds that they shoot (Bruggink and Kendall 1995). Hunters are also asked to record the effort and success of their hunts. Age and sex of the birds can be determined from plumage characteristics (Martin 1964), and the ratio of immature birds to adult females in the survey sample provides an index of recruitment. The recruitment index for woodcock in the eastern region for 1995 (1.4 immatures per adult female) was higher than in 1994 but was 17.6% less than the long-term average of 1.7 immatures per adult female (Bruggink and Kendall 1995; Fig. 2), indicating poor production of young in recent years, although these numbers should be interpreted with caution (see Owen et al. 1977 and Straw et al. 1994). A major problem of the wing-collection survey is that it is not random, because no comprehensive sampling frame exists for woodcock hunters. When the U.S. Fish and Wildlife Service's Harvest Information Program is implemented, this framework will be provided. Under this program, states will provide the U.S. Fish and Wildlife Service with a computerized address list of everyone who purchases a hunting license, allowing for a true random selection of hunters for the survey.

Researchers developed the singing-ground survey to count displaying males during the breeding season. Since 1968 randomly chosen roadside routes have been surveyed for "singing" male woodcock to provide an index of the population size. Routes were established along lightly traveled secondary roads in the central and northern portion of the breeding range. The survey consists of approximately 1,500 routes, each 5.8 kilometers long and consisting of 10 listening points. Recent (1985–1995) and long-term (1968–1994) trends in the singing-ground survey suggest that woodcock populations have declined at an annual rate of 2.0% recently and 2.4% long term in the eastern region (Fig. 3). Populations in the central region declined an average of 2.8% annually from 1985 to 1995 and an average of 1.4% per year from 1968 to 1994 (Bruggink and Kendall 1995). In every state in the Northeast except New Hampshire, the number of males heard on the singing-ground survey has declined (Bruggink and Kendall 1995).

The major causes of the long-term decline in woodcock populations are not known but probably result from degradation and loss of suitable habitat on both the breeding and the wintering grounds (Owen et al. 1977; Dwyer et al. 1983; Straw et al. 1994). Researchers have associated habitat loss with urbanization and forest succession on the northern breeding areas and with drainage and land-use conversion on the wintering grounds (Straw et al. 1994). Although forests cover 60%–90% of New England (Brooks and Birch 1988; Waddell et al. 1989) and northern New England is at least 75% forested (DeGraaf et al.1993), the forests of the Northeast are aging. New England forests are currently dominated by saw timber-sized trees, whereas the early successional seedling–sapling stands that woodcock require are becoming regionally scarce. As of 1988, young stands made up only 8% of the timberland in New England (Brooks and Birch 1988), a trend consistent throughout the Northeast (Fig. 4). The decline in young forest is the result of changing management objectives and techniques, changing attitudes of landowners, a decline in farm abandonment, increased fire suppression, and increased urbanization (Brooks and Birch 1988; U.S. Fish and Wildlife Service 1996). Thus, most changes in the timberland resources of this region have resulted from changes in forest structure and not from gains or losses in acreage. Most woodcock habitat in the Northeast is privately owned; timber companies control the next largest portion of this resource, and state and federal agencies control the smallest portion (U.S. Department of the Interior 1990). State and federal governments and private agencies need to determine ways to stimulate creation of woodcock habitat on private lands.

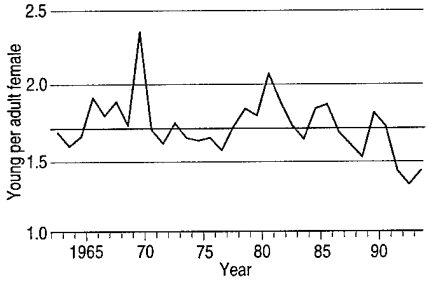


Fig. 2. Adjusted annual indices of recruitment, 1963–1994, determined from wings sent in to the annual woodcock wing-collection survey from states in the eastern region. Red line is the 1963–1993 average (Bruggink and Kendall 1995).

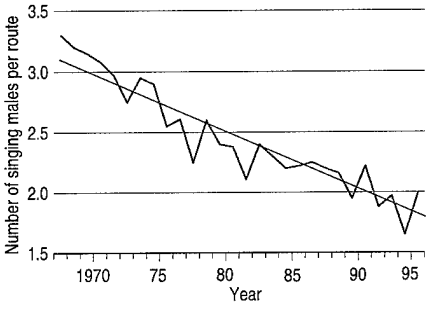


Fig. 3. Long-term trend and annual indices of the number of woodcock heard on the woodcock singing-ground survey in the eastern region, 1968–1995 (Bruggink and Kendall 1995).

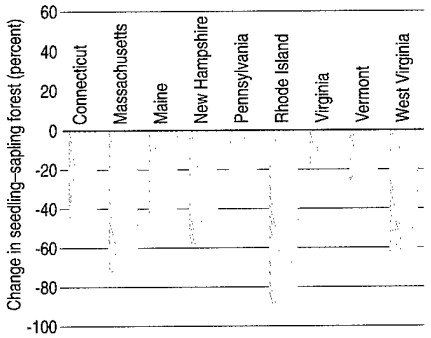


Fig. 4. Changes in the area of seedling–sapling forest in selected states in the Northeast, 1978–1996 (U.S. Fish and Wildlife Service 1996).

To increase the woodcock population, the U.S. Fish and Wildlife Service has developed an American Woodcock Management Plan (U.S. Department of the Interior 1990). In the Northeast, the management goal (U.S. Fish and Wildlife Service 1996) is to restore woodcock populations to 1985 levels by the year 2005. Conservation and management of woodcock habitat are critical to achieving these population objectives. Habitat management that promotes early successional forest types increases local breeding populations of woodcock and other wildlife. Crucial to this effort is encouraging commercial timber companies to incorporate woodcock habitat management into their timber-management activities and to inform private landowners of potential habitat-management opportunities on their lands. In addition, identification and management of woodcock wintering habitat are also necessary. Most importantly,

cooperation in habitat management among state, federal and nongovernment organizations, and private citizens will be necessary to reverse the downward trends of the woodcock population.

Although available data do not indicate that hunting has played a major role in woodcock population declines, proper management requires that we understand the relationship among hunting regulations, harvest, and woodcock populations, especially at the local level (Straw et al. 1994). Implementation of the Harvest Information Program will be the first step in determining this relationship. Research into the effects of hunting on local and regional populations is also necessary, but few studies are under way on woodcock in the Northeast. Likewise, research is needed to address the potential effects of new pesticides on woodcock, their habitat, and earthworms; such research has not been done for 15 years.

See end of chapter for references

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nonindigenous species such as the ring-necked pheasant have had drastic population-level declines.

Many losses of wildlife populations are attributed to changes in habitat as a result of current farming practices. During the past 20 years, use of row cropping and reduced field edges, use of herbicides and pesticides, widespread plowing under of crop residues in the fall, and abandonment of marginal fields to forest have increased. Many fields abandoned during the 1940's and 1950's were dominated by shrubs during the 1960's and early 1970's and were then taken over by trees. The combination of intensive cropping and maturing forest leaves little land in shrub and small sapling stages, reducing the habitat for many species that depend on these plant communities (Crawford 1987).

Some species have benefited from recent agricultural practices. Birds that find suitable habitat in row crops include the horned lark and the killdeer (Whitney 1994). The abundances of wild turkeys and Canada geese increased because of crop residues that are available throughout fall and winter. The practice of spreading liquid manure on fields in the winter also provides food in the form of undigested grain for turkeys, American crows, and many songbirds.

Some mammals benefited as well. Small seed-eating mammals thrive on the abundant grain waste on farms. Two species with increasing population levels because of row crops are the deer mouse and the house mouse (Whitney 1994). The predators of small mammals, such as birds of prey, snakes, foxes, and weasels, are also common. White-tailed deer, raccoons, coyotes, skunks, and Virginia opossums take advantage of residual corn and other crops, and their populations have grown more than tenfold across the region in the past 20 years.

Wetlands

Loss of Wetlands

Marshes, swamps, bogs, fens, ponds, lakes, and rivers are wetlands, a landscape class that is saturated with water at least part of the year. Wetlands are abundant in the Northeast and are rich in plant and animal life. Continuing human development, pollution, and use of water resources, however, threaten these environments, and loss of wetlands ranges from 9% in New Hampshire to 90% in Ohio (Table 6). Currently, small shallow pools and ponds are exempt from many permit requirements under the Clean Water Act unless the impact exceeds 0.4 hectares. Pollution and filling often threaten these important habitat islands, causing serious declines in many species of plants and animals (Table 7). Seasonally wet areas, known as vernal ponds, are important to amphibians and have been particularly affected in this region.

Declining Wetland Wildlife

Human alteration of the water regime of wetlands has caused serious repercussions for many species. Among the freshwater mollusks (snails, mussels, and clams), 13 northeastern species are on the federal list of endangered species (Table 8). Damming and channeling of rivers cause destruction of mussel and clam habitat because siltation and low oxygen levels are created above the dam, and fluctuating water temperatures and levels are created below the dam. Pollution of waterways, a common problem in this most densely populated part of the country, is also very detrimental to freshwater mollusks (Moseley 1992). Other invertebrates are also at risk; for example, three species of butterflies, moths, and dragonflies that occur in wetlands are extirpated from the Northeast (Opler 1993).

Table 6. Wetland loss by state in the Northeast between pre-Columbian settlement and the 1980's (Whitney 1994).

State	Percentage lost
Connecticut	74
Maine	20
Massachusetts	28
New Hampshire	9
Rhode Island	37
Vermont	35
Delaware	54
Maryland	73
New Jersey	39
New York	60
Pennsylvania	56
Ohio	90

Table 7. Percentage of hydrological basins in the northeastern United States affected by pollutants (McCorkle and Halver 1982).[a]

Type of pollutant	Percentage affected
Nutrients	63
Suspended solids	65
Dissolved solids	10
pH	18
Oil and grease	15
Toxics	33
Pesticides	18

[a] $N = 40$.

Table 8. Freshwater mollusk species in the northeastern United States that are on the federal list of endangered species (U.S. Fish and Wildlife Service 1994).

Dwarf wedgemussel
Ring pink
Winged mapleleaf
Orange-foot pimpleback
Pink mucket
Purple cat's-paw
White cat's-paw
Fat pocketbook
Northern riffleshell
Appalachian ambersnail
Cheat three-toothed snail
Clubshell
Fanshell

Invasion by Nonindigenous Species

Purple Loosestrife

Invasions by nonindigenous species also disrupt these environments, and purple loosestrife is one of the most rapidly expanding pest species in the country (Fig. 5). Introduced from Europe in the early 1800's, purple loosestrife spread throughout the Northeast, mostly because of the development of canal systems for transportation and the use of the plant by beekeepers and gardeners. Once purple loosestrife invades a wetland, it quickly crowds out cattails and other native plants and forms a one-plant habitat. Thus, the habitat suitability for songbirds, waterfowl, muskrats, and many other species declines (Thompson et al. 1987). The bog turtle, an endangered species in the Northeast, is also affected because purple loosestrife invades and covers its preferred habitat (Groombridge 1982; New York Natural Heritage Program, unpublished material). A variety of controls have been tested, including the herbicide glyphosphate (Rodeo™), water-level manipulation, and replacement with other species, but results have been mixed at best. At present, biological control by introducing European insects that destroy the plant shows the most promise (Thompson et al. 1987; Malecki 1995).

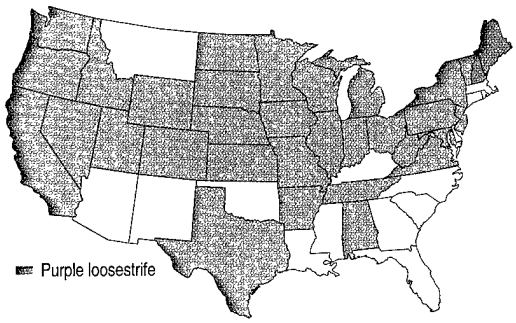

Fig. 5. Distribution of purple loosestrife in the United States, 1985 (U.S. Congress, Office of Technology Assessment 1993).

Invasion of Lakes by Nonindigenous Species

Introduction of nonindigenous species also affects lake environments. Lake Champlain and the Finger Lakes of New York illustrate important trends. Lake Champlain occupies a large shallow basin and drains to the St. Lawrence River. Plant and animal life include interior North American species and, because of the lake's proximity to the ocean, those of the North Atlantic. Landlocked Atlantic salmon and lake trout are abundant and economically important. As a result of the construction of a canal system the sea lamprey invaded Lake Champlain from the south and caused a major reduction in fish population levels throughout the 1970's and 1980's. Experimental management of sea lamprey was initiated in 1990 and has significantly reduced lamprey population levels (see box on Sea Lampreys in Great Lakes chapter). Consequently, abundance of fish populations has increased dramatically. The need for stocking of hatchery-produced Atlantic salmon, lake trout, brown trout, and steelhead has been reduced from 650,000 to 4,000 fish per year (C. Baron, U.S. Fish and Wildlife Service, Essex Junction, Vermont, personal communication).

Two nonindigenous plants, Eurasian watermilfoil and water chestnut, also invaded Lake Champlain from the south. Eurasian watermilfoil is a submersed plant with upper leaves that reach the surface. This species entered the lake in 1962, and because it spreads from plant fragments, mechanical removal is not effective; control with an herbicide is under consideration (Pullman 1994). Mechanical harvest, however, is effective for controlling water chestnut, and management has been aggressive until recently. Federal budget reductions preclude continued control, and water chestnut is expected to increase (H. Crossan, Vermont Department of Conservation, Waterbury, personal communication).

The most recent invader is the zebra mussel, first observed in the south end of the lake in 1993. Monitoring is under way, but no management is contemplated at present (Baron, personal communication).

The Finger Lakes are among the best-known lakes in the Northeast. These 11 lakes in central and western New York were formed as outlets to glacial Lake Iroquois and developed as deep canyons draining south. As glaciers receded to the north, these canyons were blocked by sediment at their southern ends and today drain north into Lake Ontario. Fish communities are primarily those associated with cold, clear waters such as trout and landlocked Atlantic salmon, but some lakes support warmwater fishes such as bass and sunfish.

Invasion by nonindigenous species began in the early 1800's when the Erie Canal was linked to many of the Finger Lakes (Schaffner and Oglesby 1978). Recent invasions include the alewife and the zebra mussel; both species are affecting the food chain (see chapter on Great Lakes). The alewife increases the forage base for larger fishes and thus supports species of economic importance. Because the zebra mussel is so prolific, however, it significantly reduces the amount of plankton, which are the foundation of the food chain in these lakes; thus, fish populations may eventually decline. As of July 1994, zebra mussels were in Canandaigua, Cayuga, Keuka, and Seneca lakes (New York Sea Grant 1994a,b).

Imperiled Fish Species

In the Northeast, 4.3% of the native freshwater fish species are imperiled (Johnson 1995). The number of different species in a state usually is related to the size of the state; the greatest number of species occurs in Pennsylvania (166), and the fewest number of species occurs in Rhode Island (43). Of New York's 155 species, 10 are endangered, threatened, or of special concern; at least 2 species of concern are in every state (Warren and Burr 1994; Table 9). In Pennsylvania alone, 27 species have been extirpated because of pollution and loss of marsh habitat; overfishing is often a contributing factor (Cooper 1985).

Table 9. Numbers of native freshwater fishes in the northeastern United States considered endangered, threatened, or of special concern by fisheries professionals (Warren and Burr 1994).

State	Number of species endangered, threatened, of special concern	Number of native fish species
Maine	4	49
New Hampshire	3	55
Vermont	2	88
Massachusetts	2	62
Rhode Island	2	43
Connecticut	2	55
New Jersey	2	77
Pennsylvania	8	166
Delaware	2	70
Maryland	4	99
West Virginia	9	148
Ohio	8	153

One of the most endangered fishes in the country is the Maryland darter. This species most likely occurs in only one stream in Maryland and has not been reported since 1988. The Maryland darter faces a host of threats, including silt, impoundments, pesticide and herbicide use, reduction of stream flow for consumption, and waste from sewage treatment plants (Ono et al. 1983).

Amphibian Declines

Amphibian population levels in the Northeast may be decreasing, although no documented evidence for a regionwide decline exists. A decline is predicted because of the acid precipitation problems in the Northeast; acid levels only slightly greater than normal can kill amphibian eggs and cause deformities in tadpoles. In addition, acidity can slow the development of tadpoles; consequently, the water in the temporary ponds where they are hatched dries up before they transform into adults (Milstein 1990). Although no amphibians from the region are on the federal list of endangered species, the eastern tiger salamander is listed as endangered in New York and New Jersey and is extirpated in Pennsylvania. Tiger salamander population levels and habitat sizes are listed as declining in New York. The reasons for the declines are pollution, introduction of predatory game fishes, illegal collection, and automobile-related mortality. With proper protection and management, the outlook for recovery is good (New York Natural Heritage Program, unpublished material).

Threats to Wetland Reptiles

Reptiles are also common wetland inhabitants and face many of the same threats as amphibians. Some reptiles that are generally considered too dangerous to be pets are often killed because of their perceived threat to human safety. Because of persecution, overcollection, and habitat destruction, the massasauga, a small rattlesnake, is of special concern in Ohio and is endangered in Pennsylvania and New York (Beltz 1993). Open wetlands—its preferred habitat—exist in relatively small isolated patches, which makes each population more vulnerable to extirpation because of local chance events. Only 2 confirmed populations still exist in New York (Johnson and Breisch 1993) and 8 populations exist in Pennsylvania, down from 19 (Reinert and Bushar 1993; G. Johnson, State University of New York, Syracuse, personal communication). Damming, highway construction, and forest succession harm the remaining habitat (Reinert and Bushar 1993).

Perhaps the rarest reptile in the Northeast is the Plymouth red-bellied turtle. This subspecies of the more common red-bellied turtle is restricted to a small portion of southeastern Massachusetts. The estimated total population size is 200, which makes the survival of the population vulnerable to chance events such as hurricanes. Added to this risk is the species' low rate of reproduction and its sensitivity to human disturbance. Management strategies, such as artificial incubation of eggs, may increase the population size from its critically low level (Groombridge 1982).

Hybridization and Decline of the American Black Duck

Introductions of nonindigenous species and habitat degradation are not always the main causes of a species' decline. For example, population levels of the American black duck have decreased by half in the past 40 years. Although habitat loss is partially responsible for the decline, acid rain, overharvest, and competition with the mallard are important contributing factors (Heusman 1991; Dwyer and Baldassarre

American Black Duck

The American black duck, with its brownish-black plumage and iridescent violet speculum, is one of the wariest of all the large dabbling ducks (Kortright 1942; Fig. 1). The black duck's distribution is confined to eastern North America but extends into Manitoba. The black duck breeds in a variety of habitat types, from the brackish coastal marshes of North Carolina to the open boreal forests of northern Quebec and Labrador (Bellrose 1976). In acidic bogs, beaver streams, and sluggish riverine and floodplain habitats of the boreal forest, the black duck's dark plumage (males and females have similar plumage) blends with the dark organic-stained waters of forested wetlands (Fig. 2).

After an intense courtship period in late March to May, depending on latitude, the female chooses a nest site, lays from 7 to 12 eggs, and incubates them for an average of 26 days (Fig. 3). She cares for her brood for about 60 days, after which time an average of 4 to 5 young fledge. Females then become flightless while molting to renew their worn primary wing feathers. Males, which leave after females have been incubating 2 weeks, fly north to isolated, traditionally used areas to molt (Bowman and Brown 1992).

In late summer and early fall, black ducks congregate on large freshwater river systems and coastal marshlands in the northern breeding areas. Depending on latitude, black ducks leave these staging areas in mid-November and migrate to the coastal marshes of the mid-Atlantic states (Maine to North Carolina), where more than 90% of the birds overwinter.

Determining the population status of the black duck has been difficult. The prehunting season black duck population in the 1950's was calculated as 3,738,000 (Geis et al. 1971) and averaged 804,000 during 1959-1961 (Bellrose 1976). Annual black duck status has been based mainly on the Midwinter Survey, which began in 1955 and is a survey by federal, state, and private agencies and individuals who attempt to count all waterfowl on the wintering areas during the first week of January. In 1955, in the Atlantic Flyway, 582,500 black ducks were counted (Serie 1994), whereas the preliminary count of black ducks in 1996 was 313,000 (Serie 1996).

Researchers began an experimental helicopter survey in 1990 for counting breeding black ducks and other waterfowl species in eastern Canada and Maine. During 1990–1994, the mean number of black ducks on 25 100-square kilometer plots in Maine ranged from 24.4 in 1994 to 36.9 in 1991. Similar aerial surveys were conducted in the Canadian provinces, where numbers of breeding black ducks seemed stable or increasing in the Maritime provinces (Prince Edward Island, Nova Scotia, New Brunswick), decreasing in Newfoundland, stable in Ontario, and decreasing in Quebec (Dickson 1995).

Courtesy U.S. Fish and Wildlife Service

Fig. 1. A male American black duck.

For waterfowlers in the Northeast, the black duck has historically been the "bread-and-butter duck," accounting for 40% to 60% of the annual harvest in many states (Martinson et al. 1968). Because it is such a prized game duck, more than 200,000 to 300,000 were harvested annually through 1981 in the Atlantic Flyway states alone (Serie 1994). As early as the mid-1930's, however, Wright (1947) recognized that black ducks were declining even before the dieback of eelgrass had occurred on the wintering grounds during the same decade (Cottam et al. 1944; Lincoln 1950). Gabrielson (1947:8), realizing the role of habitat loss, urged that marsh restoration programs be initiated and that they "be accompanied by restrictions on shooting limits sufficient to limit the kill to less than the annual number of ducks put on the wing."

Hunting seasons in the Atlantic Flyway ranged from 55 to 93 days throughout the 1950's and mid-1960's, and black duck bag limits varied from 5 to 8 in Canada and from 2 to 4 in the United States (Martinson et al. 1968). Munro (1968:81) noted the high recovery rate of bands from black ducks (mostly adult females and immatures) banded in southern Canada, and stated that this "strongly suggests that Canadians are equally responsible [as hunters in the United States] for the decrease in black ducks."

In 1968 waterfowl biologists and administrators reviewed the population status of the black duck (Barske 1968) and concluded that the population had declined to a critically low level and that restrictive regulations were required (Addy and Martinson 1968). By using methods and data available then, researchers agreed that to increase the black duck breeding population in the Atlantic Flyway by only 10%, the black duck kill would need to be reduced by about 40% from that of 1966. Because the Atlantic Flyway states could not meet their objective without substantial cooperation from

Courtesy J.R. Longcore, USGS

Fig. 2. Ginn Brook, Maine: typical brood habitat of American black ducks.

Courtesy J. R. Longcore, USGS

Fig. 3. A black duck nest on an upland site.

Canada, the recommended action was to negotiate with Canada to develop a unified management program.

Unfortunately, during the mid-1960's and 1970's, the black duck population continued to decline at an average rate of about 4% annually (Ringelman and Longcore 1980). The decline might have been prolonged by the adoption of "stabilized" regulations for black ducks, wherein the hunting regulations were the same from 1974 to 1977 (Grandy 1983) despite a declining population. At the same time, the development of modern band-recovery models allowed biologists to address the question of whether hunting resulted in an additive or compensatory effect relative to population size (Anderson and Burnham 1976; also see chapter on Harvest).

Mortality from hunting that merely replaces mortality from nonhunting causes is defined as compensatory. After levels of mortality reach some threshold, mortality from hunting that reaches or exceeds the threshold directly reduces the next year's breeding population and is considered additive. This threshold has never been determined and probably varies annually and geographically. The initial analysis of black duck band recovery data seemed to support the idea that hunting mortalities were mostly compensatory with other nonhunting kinds of death (Nichols et al. 1984).

From 1976 through 1981, the black duck population continued to decline, and Blandin (1982), after a thorough analysis of all the band recovery data for black ducks, recommended greater hunting restrictions on black ducks. Based on Grandy's (1983) review of the U.S. Fish and Wildlife Service's management of the black duck, the Humane Society of the United States brought a lawsuit against the U.S. Fish and Wildlife Service in 1982 requesting an injunction to keep the hunting season for black ducks closed. The result of this action was a compromise in which the 1982 season was allowed, but more restrictive regulations were started in 1983 to reduce the harvest of black ducks by 25% in each Atlantic Flyway state. Although effective restrictions were finally achieved in Canada sometime after 1986 (Boyd 1988), and retrieved kill in Canada started to decline in 1990, recovery rates of banded black ducks remain substantially higher in Quebec than anywhere else (Serie et al. 1997). Retrieved kill for black ducks declined considerably during 1983–1995 (Figs. 4 and 5).

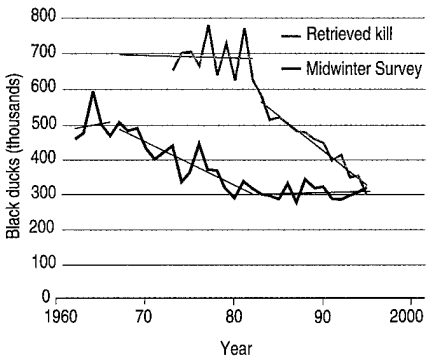

Fig. 4. Retrieved kill and Midwinter Survey counts of American black ducks for North America, 1962–1995. Two regression lines for black duck retrieved kill and three regression lines for the Midwinter Survey data represent the periods 1962–1966, when hunting regulations were most liberal; 1967–1982; and 1983–1995, when hunting regulations were most restrictive.

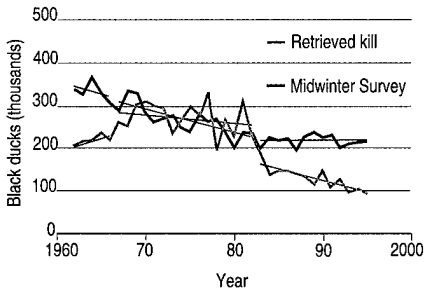

Fig. 5. Retrieved kill and Midwinter Survey counts of American black ducks for the Atlantic Flyway, 1962–1995. Three regression lines each, for black duck retrieved kill and the Midwinter Survey data, represent the periods 1962–1966, when hunting regulations were most liberal; 1967–1982; and 1983–1995, when hunting regulations were most restrictive.

Recently, the question of additive versus compensatory mortality for black ducks has been revisited. With larger data sets and improved statistical models for band recoveries, later analysis suggested more instances of additivity (Nichols 1993). Between the periods 1950–1966 and 1967–1982, mean survival rates of black ducks increased consistently with the model for total additivity of hunting mortality (C. M. Francis, Long Point Bird Observatory, Port Rowan, Ontario, Canada, unpublished manuscript). Between the periods 1967–1982 and 1983–1995, hunting mortality was additive for immature male black ducks, indicating that the long-term decline of the black duck population was related to excessive harvest.

Recent more stringent hunting regulations in the United States and Canada seem to have caused a decline in the retrieved harvest, and perhaps not coincidentally, the Midwinter Survey for black ducks in North America and for the Atlantic Flyway has stabilized (Figs. 4 and 5). Furthermore, in recent years the loss of intertidal and estuarine wetlands (Frayer 1991) has abated, at least in much of the mid-Atlantic region. Thus, some optimism seems justified that managers can achieve the goal of approximately 260,000 wintering black ducks for the Atlantic Flyway by the year 2000. The goal of attaining 385,000 wintering black ducks in the Midwinter Survey for North America will rely on increases in breeding populations in Mississippi Flyway states and Canadian provinces, where such increases might be a greater challenge because of the loss and conversion of habitat in southern Ontario (Snell 1987). Even achieving the population goal of 260,000 in the Atlantic Flyway will require discipline to reduce the continuing high harvest of young and adult females in Quebec, because most (Blandin 1982) of Quebec's black

ducks winter in the Atlantic Flyway. Overall, with continued vigilance on protecting and enhancing the numbers of breeding pairs on the vast breeding grounds of North America, we can expect the black duck population to increase.

Acknowledgments

We thank P. O. Corr, G. M. Haramis, H. W. Heusmann, J. R. Sauer, and J. R. Serie for reviewing and improving this manuscript. C. T. Moore performed the regression analysis and prepared the figures.

See end of chapter for references

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1994). Restrictions on black duck harvest started in the early 1980's but have had no effect (Merendino et al. 1993). Black ducks and mallards are closely related species, having diverged from a common ancestor about 40,000 years ago. Both species are native to the Northeast, inhabit the same areas, exhibit similar behavior, and hybridize (Baldassarre and Bolen 1994). In the Atlantic Flyway, hybridization is common and is exacerbated by state and private releases of mallards in winter when pair bonding occurs. Even when mallards and black ducks do not interbreed, mallards displace black ducks from high-quality wetlands. The mallard also causes problems when it breeds with the rouen barn duck, an imported domestic breed from Europe. The results of these crosses are nonmigratory mallards, which occupy prime nesting sites before wild black ducks, green-winged teal, and blue-winged teal return from winter habitat. Both teal species were once common and are now rare (Lazell 1989).

Recovery of the Wood Duck

In contrast, the wood duck has recovered from low abundances in the last century. Although no actual census figures at the turn of the century are known, the wood duck seemed endangered by overharvest. Closed seasons from 1918 to 1941 (under provisions of the Migratory Bird Treaty Act) and widespread establishment of nest boxes allowed numbers to rebound. Census figures during the past three decades indicated a steady increase in the number of wood ducks from 1959 to 1985 and a relatively constant population size since the mid-1980's (Bellrose and Heister 1987).

Creation of New Wetlands by Beavers

An important trend in the Northeast is the rapid creation of new wetlands by beavers. These mammals have been prized for their thick, luxurious pelts and were heavily trapped by Europeans throughout much of the past three centuries. Because of overtrapping, beavers were extirpated in much of the Northeast by the beginning of this century. The economic importance of the species led to its prompt reintroduction in the early 1900's, and populations were reestablished in most of the major watersheds by the 1950's.

Ponds and wet meadows created by beavers support more than 100 bird and more than 20 other mammal species (Grover 1993). In the past two decades, the demand for pelts has declined, and beaver populations have increased substantially. If trends continue, the beaver will probably become a widespread pest, flooding roads and blocking water-control structures (Distefano 1987). Beavers are now expanding into urban areas and will probably exacerbate conflicts between wildlife and humans in the future.

Urban Areas

Trends in Urban Landscapes

Urban landscapes are those in which human development and activities (except agriculture) have appreciably changed the character of the environment. The Northeast is the most densely populated part of the country, with an extensive megalopolis extending from Boston to Washington, D.C. The total area of urban land in the Northeast was 4.9 million hectares in 1987, a 53% increase from 1960 (Daugherty 1991). The pace of the shift in environment from rural to urban development in the Northeast was much slower than predicted: 859,000 hectares from 1960 to 1980 and slightly more than that from 1980 to 2000 (George 1982). Regardless of the precise numbers, urban land makes up a significant portion of the Northeast and is increasing.

Trends in the Chesapeake Bay Watershed Wetlands

The Chesapeake Bay watershed is a 163,170-square-kilometer drainage basin that encompasses portions of six northeastern states (Delaware, Maryland, New York, Pennsylvania, Virginia, and West Virginia; Fig. 1). Chesapeake Bay is the receiving body for surface water runoff from this basin. The watershed also includes parts of six major physiographic provinces (Lower Coastal Plain, Upper Coastal Plain, Piedmont, Blue Ridge, Valley and Ridge, and Appalachian Plateau). This diverse landscape, with its varied topography and surface geology, has profound effects on the abundance and types of wetlands throughout the watershed. Annual precipitation ranges from 89 to 114 centimeters across the region.

An estimated 2.1 million hectares of wetlands and deepwater habitats existed in the Chesapeake watershed in 1989 (Tiner et al. 1994). Wetlands accounted for roughly 690,000 hectares, covering about 4% of the watershed. This amounts to an area about 1.4 times the size of Delaware or about one-quarter the size of Maryland. Freshwater (palustrine) wetlands are the predominant type, occupying nearly 608,000 hectares, with forested wetlands alone representing 60% of the watershed's wetlands (Fig. 2). Estuarine marshes, palustrine shrub swamps, and palustrine nontidal marshes each make up about 10% of the watershed's wetland resources. Approximately two-thirds of the watershed's wetlands (Fig. 3) occur in Virginia (40%) and Maryland (27%).

Between 1982 and 1989, palustrine vegetated wetlands (freshwater marshes, wet meadows, swamps, and bogs) declined by 2%. A total of 14,580 hectares was converted to drylands and water bodies: 5,954 hectares of forested wetlands, about 4,293 hectares of emergent wetlands, and about 4,334 hectares of scrub–shrub wetlands. These collective losses equal an area about the size of the District of Columbia. In addition, about 7,290 hectares of palustrine forests were harvested for timber. This is not considered a loss, however, since these areas are still wetlands that in time will likely revert to forested wetlands.

Virginia had the greatest palustrine vegetated wetland losses of any state in the watershed, losing approximately 9,315 total hectares: about 1,620 hectares of emergent wetlands, more than 3,240 hectares of scrub–shrub wetlands, and nearly 4,455 hectares of forested wetlands during the study period. Maryland lost about 2,025 total hectares of the palustrine vegetated

Fig. 1. The Chesapeake Bay watershed.

Table. Changes in specific types of vegetated wetlands in the Chesapeake Bay watershed (1982–1989).

Vegetated wetland type	1982 hectares	1989 hectares	Hectares changed to other vegetated wetlands	Hectares gained from vegetated wetlands	Hectares destroyed	Hectares gained from other areas	Net change (hectares)
Palustrine forested wetlands[a]	406,517 *	400,682 *	10,390 *	9,054 **	5,954 **	1,456	-5,834 **
Palustrine scrub–shrub wetlands[b]	72,262 *	71,870 *	10,803 *	14,253 *	4,331	489 **	-391
Palustrine emergent wetlands[c]	69,457 *	67,722 *	7,788 *	5,667 *	4,310 *	4,696 **	-1,735
Estuarine intertidal emergent wetlands[d]	68,976 *	68,775 *	114 **	300	439 **	52 **	-201
Estuarine scrub–shrub wetlands[e]	1,309 *	1,496 *	79 **	239 **	0	28	+188 **
Estuarine forested wetlands[f]	9,633 **	9,280 **	529	190 **	25	11	-353

[a] Mostly nontidal freshwater wetlands dominated by woody plants 6 meters or taller, commonly called wooded swamps, river swamps, or bottomland swamps.

[b] Mostly nontidal freshwater wetlands dominated by woody plants less than 6 meters tall; includes shrub swamps and bogs.

[c] Mostly nontidal freshwater wetlands dominated by herbaceous species, commonly called marshes, wet meadows, and Carolina bays.

[d] Tidally influenced wetlands dominated by herbaceous plants, including areas commonly known as salt and brackish tidal marshes.

[e] Tidal wetlands dominated by woody plants less than 6 meters tall, including hightide bush and other halophytic shrubs.

[f] Low-lying hardwood, pine, or mixed Coastal Plain wooded swamps, originally nontidal, but now flooded by saltwater tides due to a combination of rising sea level and coastal subsidence.

* Reliable estimate (standard error is equal to or less than 20% of the estimated area).

**Less reliable estimate (standard error is less than 50% of the estimate, but greater than 20% of the estimated area). Estimates without an asterisk have higher standard errors and are not reliable, although they are the best available statistics.

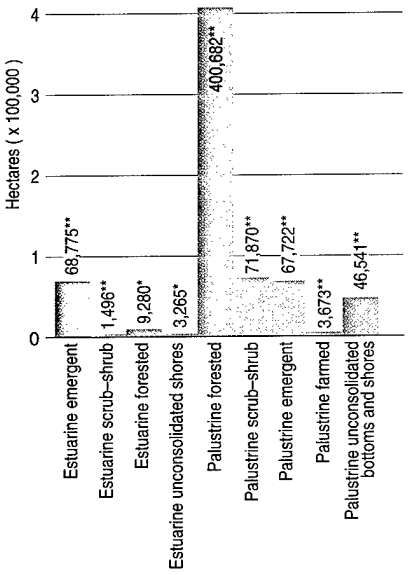


Fig. 2. Estimated 1989 wetland hectares for the Chesapeake Bay watershed. * = standard error is between 20% and 50% of the estimate and ** = standard error is 20% or less of the estimate.

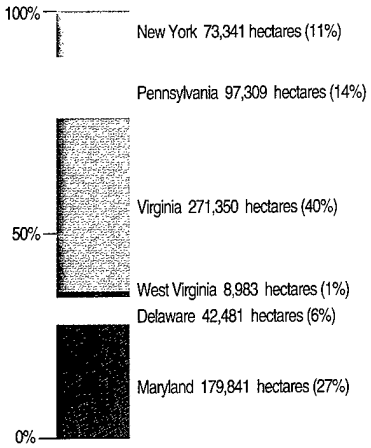


Fig. 3. Distribution of wetlands in the Chesapeake Bay watershed by state. Estimated hectares are also shown.

wetlands during this time, including about 972 hectares of emergent wetlands, about 203 hectares of scrub–shrub wetlands, and more than 1,013 hectares of palustrine forests. Pennsylvania lost almost 1,600 total hectares, mostly emergent wetlands (more than 810 hectares) and scrub–shrub wetlands (almost 689 hectares). The Table summarizes vegetated wetland trends for the watershed based on wetland type. Causes of palustrine vegetated wetland losses are presented in Figures 4, 5, and 6.

Overall, the status of estuarine wetlands (salt and brackish tidal marshes) has improved. Before the enactment of state coastal or tidal wetland laws and strengthened federal regulation under the Clean Water Act, these wetlands were dredged or filled at high rates. From the 1950's to 1980, for example, almost 203 hectares of estuarine marshes were lost annually, compared with an estimated 29-hectare annual loss from 1982 to 1989. Increased state and federal wetland regulations since the 1970's have improved the condition of these wetlands, which are no longer being wantonly destroyed. There is still pressure to convert these wetlands to alternative uses, but most landowners, developers, and the general public realize the values of these wet areas and are aware of government programs to protect them.

The situation for palustrine vegetated wetlands is quite different (Fig. 7). These wetlands continue to be destroyed at

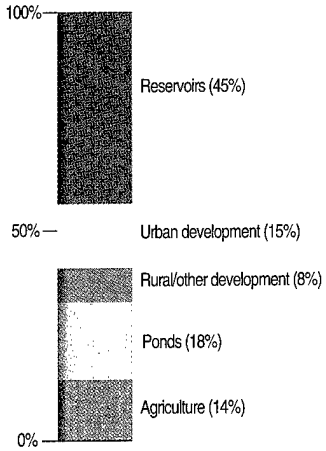


Fig. 4. Causes of palustrine forest destruction in the Chesapeake Bay watershed. (Note: excludes about 7,290 hectares that were harvested between 1982 and 1989.)

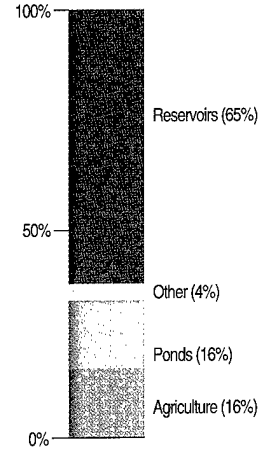


Fig. 5. Causes of palustrine scrub–shrub wetland destruction in the Chesapeake Bay watershed.

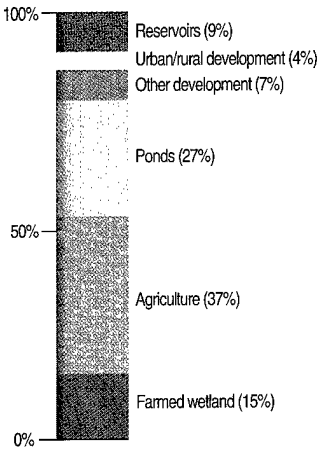
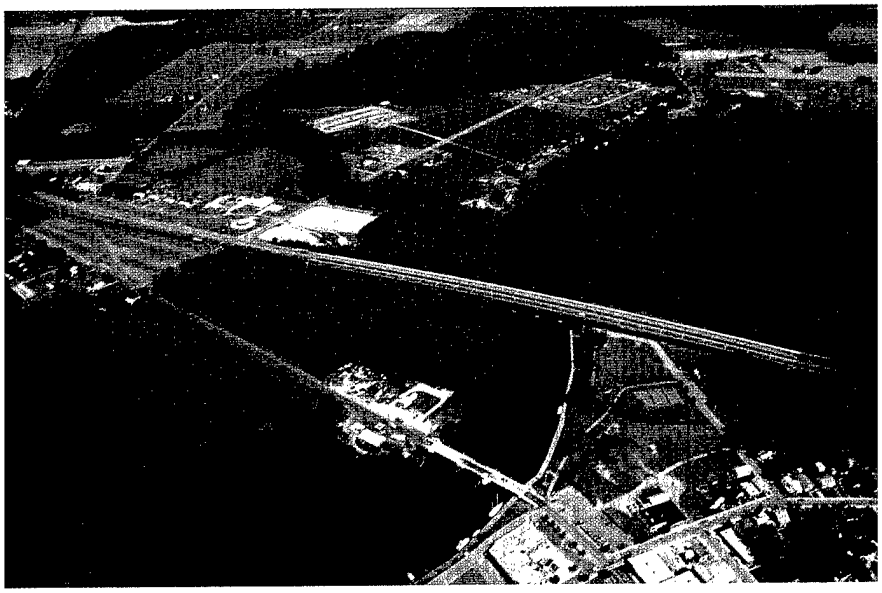


Fig. 6. Causes of palustrine emergent wetland destruction in the Chesapeake Bay watershed.



Courtesy R. Tiner, U.S. Fish and Wildlife Service

Fig. 7. Palustrine forested wetlands have been subjected to many changes, including conversion to farmland and filling for development and roads. Although forested wetlands are generally better protected today, some types are still threatened.

alarming rates. Despite the existence of federal regulations, nontidal freshwater wetlands continued to experience heavy losses from 1982 to 1989. Almost 6,075 hectares of palustrine forests were destroyed through conversion to drylands and to open waters such as reservoirs and ponds. In addition, another 8,505 hectares of vegetated wetland losses involved emergent and scrub–shrub wetlands. It is evident that wetland regulations must be improved if we are to protect our remaining freshwater wetlands. Many forested wetlands continue to be converted to alternative uses, particularly the wet flatwoods dominated by loblolly pine, which are currently unregulated because they fail to meet requirements of the 1987 delineation manual.

Seven areas were identified as hot spots where tremendous losses of certain wetland types occurred from 1982 to 1989: southeastern Virginia, the Piedmont region of Virginia, the Eastern Shore of Maryland, western Delaware, the upper Coastal Plain of Virginia, western Virginia (Blue Ridge and Appalachians), and northeastern Pennsylvania (Susquehanna, Bradford, and Tioga counties). These areas accounted for about 85% of the palustrine vegetated wetlands that were converted to drylands and open waters during the 7-year study period. Wetland protection efforts need to be strengthened in these regions.

See end of chapter for reference

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Structure of Urban Landscapes

Urban environments, from the concrete core of large cities to the lawns and gardens of suburbs, represent an extreme on the gradient of natural habitat conditions. Fragmentation reaches its maximum in urban landscapes because landownerships are relatively small and legal jurisdictions are divided (Zipperer et al. 1989). Soils are highly disturbed and ground vegetation and shrub layers reach minimum development in terms of abundance and species diversity. Furthermore, the structural form of ground cover, shrubs, and trees is often highly altered (for example, mowed lawns, trimmed hedges, and pruned trees). The spatial arrangement of shrubs and trees is often linear because their locations are determined by roads and property lines. Parks and green spaces occur in the heart of many urban areas, but these are isolated islands in the midst of a largely artificial environment. Even so, abandoned lots, parks, human structures, and even sewer systems provide a rich array of habitat conditions in the urban environment.

Urban Wildlife

Although wildlife diversity is lower in urban areas than in forests and wetlands, certain species thrive in these human-dominated habitats. Many of these species are not native, and not all were city dwellers in their native lands. Examples include the house mouse, Norway rat, German cockroach, house sparrow, European starling, and rock dove (Whitney 1994). In addition, native species like the house finch and raccoon increased because of an abundance of human structures and garbage that provide cover and food. Of native mammals, squirrels and raccoons are among the most successful, feeding on the fruits of native and ornamental trees, human handouts, and garbage. Urban raccoons have become a health threat in the past few years because they are unusually susceptible to a variant of the rabies virus. The high densities of urban raccoons and their proximity to humans have meant that the disease is quickly spread and that the potential exposure of humans or pets to this disease is high (Jenkins 1983). Although pets may be vaccinated and techniques for distributing the vaccine in the wild are in experimental phases, the feasibility of widespread vaccination of raccoons is low. Rabies was expected to reduce the population substantially in 1994, perhaps as much as 90% in many areas (L. VanDruff, State University of New York, Syracuse, personal communication). Raccoon rabies was spread from Florida to Virginia through translocation of animals to restock populations (Dein 1995).

Gray Squirrel

Gray squirrels are among the most visible mammals in urban areas, and although some people enjoy seeing and feeding these animals, others consider them pests that steal from bird feeders, damage ornamental plants, and den in attics. No widespread population surveys of squirrels are available in the Northeast, but the abundance of squirrels is influenced by vegetation (for example, broad-leafed trees with a diameter of more than 38 centimeters; Allen 1987) and by the amount of area that is covered by pavement and buildings. Densities range from 0.15 squirrels per hectare in highly urbanized areas to 1.08 squirrels per hectare in parks, college campuses, and cemeteries (Williamson 1983); more than 51.5 squirrels per hectare have been observed in Washington, D.C. Supplemental feeding is the primary cause of exceptionally high squirrel densities (Manski et al. 1981).

Peregrine Falcon

One of the most unusual success stories is that of the peregrine falcon, an endangered

Status of Living Resources in Chesapeake Bay

Chesapeake Bay is the largest estuary in the United States, covering 165,760 square kilometers and including parts of six states. Salinity gradations from fresh water, where the Susquehanna River empties into the bay, to near-ocean salinity at the bay's mouth contribute to high biological diversity. Around 2,700 plant and animal species inhabit the bay (White 1989); each year, 29 species of waterfowl rest or overwinter in the Chesapeake Bay watershed (Chesapeake Bay Program 1990). Wildlife, fish, and plant life compete for land and water resources with more than 14.7 million people (Chesapeake Bay Program Office 1995, Annapolis, Maryland, unpublished data).

Three centuries of human population growth have significantly affected the bay's water quality and its living resources. Toxic contaminants, excess nutrients, and suspended sediments compromise Chesapeake Bay water quality and threaten plants and animals. Recent evidence indicates that air pollution also adds contaminants to the bay (Appleton 1995). In addition, loss of forests and wetlands to suburban sprawl, agriculture, and commercial development jeopardizes the survival of many species.

Chesapeake Bay was the first estuary in the United States targeted for an integrated approach to watershed and ecosystem protection and restoration. The 1983 Chesapeake Bay Agreement initiated the Chesapeake Bay Program, which fosters cooperation among states, government agencies, and private organizations, with the goal of restoring Chesapeake Bay water quality and living resources (Chesapeake Bay Program 1983). In 1987 Chesapeake Bay Program partners set a goal to reduce by 40% the nitrogen and phosphorus entering the bay by the year 2000 (Chesapeake Bay Program 1987). By 1994 restoration efforts expanded to include nutrients in the tributaries, toxins, bay grasses, fish passages, and agricultural nonpoint source pollution (Chesapeake Bay Program 1994a).

Submerged Aquatic Vegetation

The total area of submerged aquatic vegetation (bay grasses) in the bay has increased by 72% since the low point of 15,390 hectares in 1984 (Fig. 1). By 1994 nearly 26,528 hectares of submerged aquatic vegetation existed in Chesapeake Bay (Orth et al. 1995). A decline in 1994 may have been caused by heavy precipitation in 1993 and 1994, which increased freshwater flow into the bay. Despite a baywide decline in 1994, substantial increases in submerged aquatic vegetation abundance occurred in the upper bay, even though previous increases had been concentrated in the lower bay (Orth et al. 1994). The density of many submerged aquatic vegetation stands also increased in 1994. At the current rate of recovery, the Chesapeake Bay Program expects 46,170 hectares of bay grasses to be restored by 2005 (Chesapeake Executive Council 1993.)

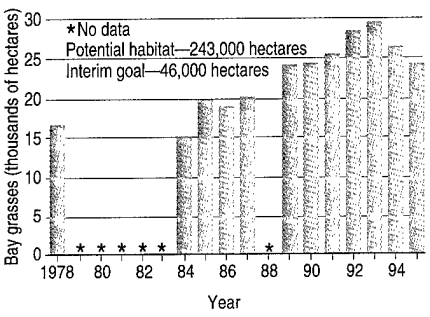

Fig. 1. Submerged aquatic vegetation produces oxygen in the water, provides food and shelter for a variety of animals, and traps sediments and absorbs nutrients such as phosphorus and nitrogen. After years of decline, the area of submerged aquatic vegetation has increased in recent years.

Forests

Forests originally covered as much as 95% of the Chesapeake Bay watershed. By 1900, though, less than 50% of the watershed was forested. Currently, about 16.7 million hectares, or about 59% of the watershed, are forested (Chesapeake Bay Program 1994b). Population growth and development constantly threaten the watershed's forests; for example, Maryland and Virginia lost as much as 5% of their forests to developed uses in just over a decade (Maryland Office of Planning 1991; Johnson 1992). Efforts to protect and restore forestland, especially streamside buffers, have begun throughout the watershed. Forest stewardship programs also help private landowners wisely manage their forest resources.

Striped Bass

Striped bass are a prized commercial and recreational fish in Chesapeake Bay. Fishing and habitat loss precipitated a decline in striped bass abundance, beginning in the mid-1970's. By the early 1980's, spawning stock (reproducing females) was at an all-time low (Chesapeake Bay Program 1989). In 1985 Maryland declared a moratorium on striped bass fishing; other northeastern coastal states followed with coordinated interjurisdictional management efforts. With careful management the striped bass population grew, as shown by increased catch-per-unit-effort and improved numbers and ages of spawners (Young-Dubovsky et al. 1993). The fishing mortality rate of striped bass in Chesapeake Bay (Chesapeake Bay Program 1995a) continues to be at or below the desired level, but the average size of captured striped bass has shifted upwards (Markham and Hornick 1994).

The Atlantic States Marine Fisheries Commission declared striped bass stocks restored as of 1 January 1995, when data showed that female striped bass spawning stock had reached the historical highs seen in the 1960's and early 1970's (Atlantic States Marine Fisheries Commission 1994; Fig. 2). A limited fishery opened in 1995, and the Atlantic States Marine Fisheries Commission will continue to conservatively manage striped bass.

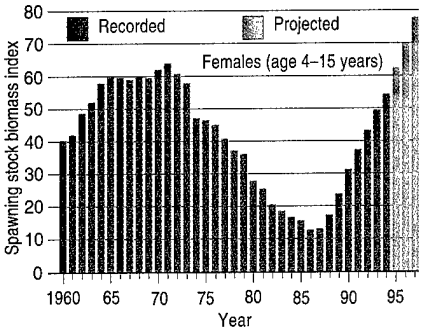

Fig. 2. Striped bass, an important commercial and recreational fish, which returns from the ocean to spawn in tributaries of Chesapeake Bay, has responded positively to decreased harvest pressure.

Shad

American shad and hickory shad are species that live at sea and spawn in freshwater tributaries (anadromous). Overharvest, habitat degradation, and stream blockages that prevent fish from reaching spawning grounds drastically reduced sport and commercial landings during the 1970's and 1980's (National Marine Fisheries Service, National Oceanic and

Atmospheric Administration, Annapolis, Maryland, unpublished data). To help restore shad populations, Maryland initiated a moratorium on shad fishing in Chesapeake Bay in 1980 and Virginia in 1994 (Chesapeake Bay Program 1995b). Pennsylvania, Maryland, and Virginia committed to providing fish passages at dams and to removing other stream blockages. By the end of 1995, watershed states had opened nearly 483 kilometers of river. Before the turn of the century, another 1,434 kilometers will be opened when the 30 projects under design or construction in the watershed are completed (Fish Passage Workgroup, Chesapeake Bay Program, Annapolis, personal communication; Fig. 3).

Maryland, Virginia, and Pennsylvania are restocking bay tributaries with hatchery-raised shad. Stocking efforts, combined with harvest restrictions and blockage removal, are succeeding—the shad population in the upper bay and Susquehanna River increased from fewer than 10,000 in 1980 to well over 300,000 shad in 1995 (Maryland Department of Natural Resources, Annapolis, unpublished data). However, the effects of ocean fisheries, which catch shad before they spawn, remain a concern.

Crabs

The blue crab population is declining in Chesapeake Bay. Although no accurate numbers of the bay's blue crab population exist, four different surveys indicate population declines. The Chesapeake Bay Winter Dredge Survey, conducted throughout Maryland and Virginia, shows a 34% decline in overall blue crab abundance since 1990 and an even greater decline in adult females (Vølstad et al. 1994). The Maryland Trawl Survey, conducted during summer and fall, suggests adult female abundance has been low since 1988 (Davis et al. 1995). The Virginia Trawl Survey, conducted in fall, shows decreasing abundance of all age classes of crabs since 1990 (Bonzek et al. 1995). In addition, Maryland commercial catch-per-unit-effort data indicate that the weight of crabs caught per pot has steadily declined since 1985 (Maryland Department of Natural Resources, unpublished data).

In late 1994 and 1995, Virginia implemented regulations that expanded crab sanctuaries and imposed limits on commercial and recreational fishing times and harvests. Maryland enacted emergency regulations with the goal of reducing the harvest of female crabs by 20%. In 1996 both states implemented additional restrictions on both recreational and commercial crabbers.

Eastern Oysters

Estimates suggest that a century ago billions of eastern oysters filtered the entire bay in around 4 days. Today, the bay's depleted oyster population requires more than a year to complete filtering (Newell 1988). Commercial landings of oysters declined from over 6 million bushels in the 1950's to fewer than 200,000 bushels in 1993 (Virginia Marine Resources Commission, Newport News, and Maryland Department of Natural Resources, unpublished data). The decline has resulted from harvest pressure, habitat destruction, water pollution, and diseases. MSX, a parasitic disease introduced to the bay in the 1950's, kills oysters within their first 2 years. Another parasitic disease, Dermo, has always been in the bay but did not begin killing significant numbers of oysters until the late 1950's. Nearly 100% of oyster beds in Maryland and Virginia are infected with the parasites (Chesapeake Bay Program 1994c). Maryland stock surveys find moderate numbers of juvenile oysters, but adult oysters are often killed before reaching market size (Maryland Department of Natural Resources, and Virginia Marine Resources Commission, unpublished data).

Harvesting techniques have removed oyster shell from the bay's oyster bars, leaving formerly three-dimensional oyster reefs reduced to flat beds. Oysters living on the bottom, without the benefit of shell reefs, can be killed by sedimentation. Artificial oyster reefs are being created by using recycled construction materials, old oyster shells, and other materials; by the end of 1995, 12 reefs were completed (Chesapeake Bay Program 1994d). The success of reef restoration is demonstrated by the colonization of natural oyster bars within a 1.6-kilometer radius of one of the first reef projects (J. Wesson, Virginia Marine Resources Commission, Newport News, personal communication).

Ducks

More than a million waterfowl migrate through or overwinter in Chesapeake Bay (Midwinter Waterfowl Survey, U.S. Fish and Wildlife Service, Arlington, Virginia, and Seaduck Survey, Chesapeake Bay Field Office, Annapolis, Maryland, unpublished data). Almost 40 years of Midwinter Waterfowl Survey counts reveal decreasing numbers of ducks in the bay, beginning in the early 1970's. Waterfowl management programs, however, are helping spur increases in Chesapeake Bay winter duck populations.

American black ducks compete with mallards for food and nesting sites. Although bay mallard populations have remained relatively stable over several decades, black duck numbers have declined (see box on American Black Ducks). In the late 1950's, around 95,000 black ducks were counted on the bay, but populations plummeted to around 32,000 by the mid-1970's, and numbers have remained fairly low since then (Midwinter Waterfowl Survey, unpublished data). Chesapeake Bay Program biologists hope to see the population reach 39,800 by the year 2000 as habitat restoration progresses (Chesapeake Bay Program 1990).

Diving ducks, such as redheads, are good indicators of water quality because they feed on bottom-dwelling plants and animals that depend on good water quality.

Courtesy U.S. Fish and Wildlife Service

Fig. 3. A fish passage (on the left) allows shad to migrate upstream.

Redheads, which feed on submerged aquatic vegetation, have experienced population declines that roughly correspond with losses of submerged aquatic vegetation. Bay redhead populations dropped to around 1,500 in the early 1990's, down from 38,000 redheads recorded in the late 1950's. Scientists hope that current increases in the bay's submerged aquatic vegetation will help support more redheads. The Chesapeake Bay Program set a goal of 8,200 redheads by the year 2000 (Chesapeake Bay Program 1990).

Canvasbacks (Fig. 4) also feed on submerged aquatic vegetation but adjust their diet to include clams when such vegetation is not available. Chesapeake Bay canvasback populations dropped during the 1970's and 1980's, but in the mid-1990's numbers climbed to those seen in the late 1950's—around 62,000 to 63,000 birds, thus meeting the Chesapeake Bay Program goal of 62,000 birds; the total diving duck goal of 162,600 ducks was also reached (Chesapeake Bay Program 1990).

Canada Geese

In the 1970's, the Canada goose population in Chesapeake Bay reached well over half a million geese. Chesapeake Bay goose populations, which include both migratory Atlantic Flyway geese and nonmigratory geese, dropped below 300,000 in 1995 (Midwinter Waterfowl Survey, unpublished data). Although nonmigratory goose numbers remain healthy, breeding pairs in the entire Atlantic Flyway population have declined by 75% since 1988 (Maryland Department of Natural Resources 1995). Overharvest and poor weather in northern Canada during the breeding season have contributed to the alarming decline in Atlantic Flyway geese. International efforts to protect Canada goose populations resulted in a ban on migratory goose hunting for the 1995–1996 season throughout the Atlantic Flyway, including Chesapeake Bay. The hunting ban should help restore the Chesapeake Bay migratory Canada goose population.

Bald Eagles

At one time, as many as 3,000 pairs of bald eagles inhabited the Chesapeake Bay watershed. The effects of DDT, however, reduced the Virginia and Maryland bald eagle population to only 80–90 pairs by 1970 (Fraser et al. 1991), but after the 1972 ban on DDT use, populations increased (Fig. 5). Recently, both the national and Chesapeake Bay bald eagle populations crossed the threshold for downlisting from endangered to threatened. The Chesapeake Bay threshold was 175–250 nesting pairs in the basin, producing at least 1.1 eaglets per active nest. The number of nests in the Chesapeake Bay basin soared from 72 in 1977 to 332 in 1995. More than 500 young were produced in 1995, up from only 63 young in 1977 (Maryland Department of Natural Resources, Annapolis; Virginia Department of Game and Inland Fisheries, Richmond; and Pennsylvania Game Commission, Harrisburg; unpublished data). Continued success of the bald eagle depends on preservation of shoreline forests with suitable large trees for nesting.

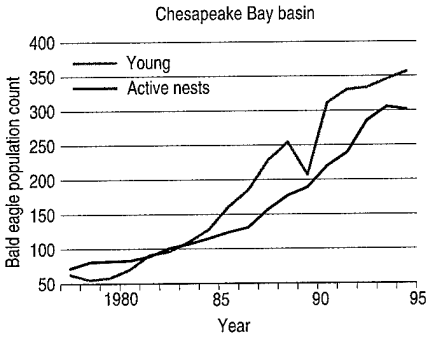

Fig. 5. Bald eagle populations have rebounded since the ban on DDT in 1972.

Living resources in Chesapeake Bay are still in jeopardy because of intensive human use of the bay and because of increasing human populations. Aggressive management and cooperation between federal and state agencies, though, have produced several successes in restoring habitat such as submerged aquatic vegetation and wildlife populations such as American black ducks and striped bass. Protection and restoration of the watershed and ecosystems of Chesapeake Bay continue under the guidance of the Chesapeake Bay Program.

Courtesy U.S. Fish and Wildlife Service

Fig. 4. Canvasbacks on Chesapeake Bay.

See end of chapter for references

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Coastal Maine: Island Habitats and Fauna

Maine's coastal islands, most of which can be reached only by boat, were once a series of mountains located many miles inland. As the last glacier receded 11,000 years ago and sea level began to rise, former mountaintops became isolated islands and former valleys were submerged to become bays and estuaries. Different bedrock types along the newly exposed mainland coast underwent thousands of years of weathering and erosion to become the complex shoreline seen today. Maine's coast stretches for more than 5,600 kilometers, ranging from sandy beaches and salt marshes in the south to cliffs and rocky shores at the Canadian border. In addition to a variety of shoreline habitats, the Maine coast contains more than 3,000 islands and thousands of intertidal ledges (Fig. 1). This multitude of habitats supports a rich assemblage of wildlife that has changed, and continues to change, through time.

Maine's present-day island biota is the result of thousands of years of human influence as well as geologic and climatic factors. The Red Paint people, who lived in Maine about 4,000 years ago, were among the first humans known to have used the coast's abundant natural resources. Probably the first seagoing fishermen in Maine, these Native Americans left their island camps to harvest large swordfish, Atlantic cod, and other fish from ocean waters 300 meters deep or more (Caldwell 1981). Like most of the tribes that followed, these people mostly lived inland but camped on the coast in summer. Their affinity for shellfish is evident from the massive shell mounds unearthed along the coast; these mounds consist primarily of oysters, which no longer occur naturally in Maine. In addition, Native Americans frequently hunted seals and seabirds and harvested seabird eggs for food. Even so, their management of coastal wildlife resources appears to have been one of sustainable use; some tribes were known to limit their hunting of seabirds to specific islands, harvesting from a given colony only once every three years (Conkling 1981). Although the Native Americans living on the islands and along the coast occasionally burned land for crops, the landscape remained largely forested.

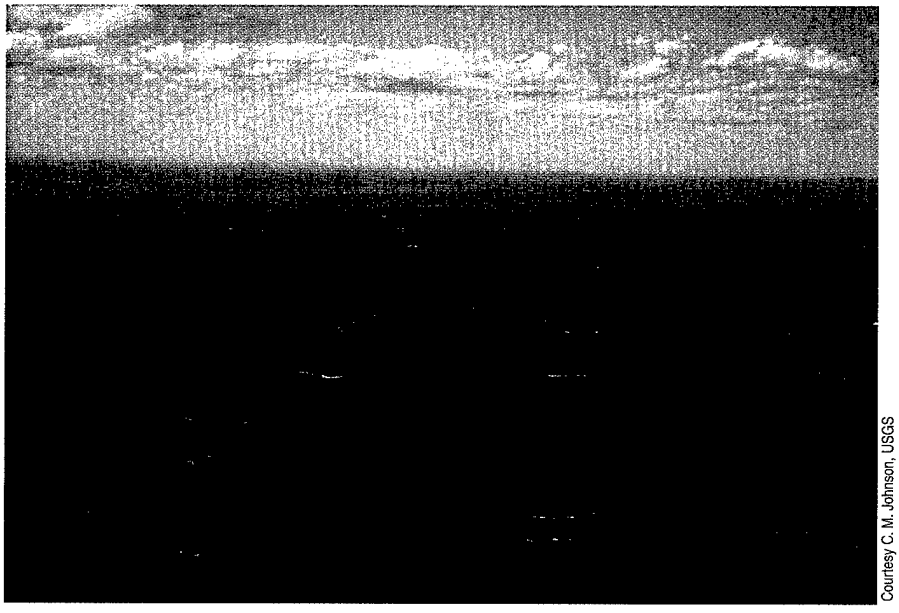
Thus, when the Europeans first saw the Maine coast, they saw a land that appeared to support a limitless abundance of natural resources. Although spruce dominated the forests on Maine islands even in the 1600's, visitors to this region also commented on the abundance of commercially important tree species. Large hardwoods and white pines commonly occurred in the more complex island forests that were present before European colonization. During the following century, as Maine became the shipbuilding capital of the world, the islands' supplies of oak and other valuable timber trees were rapidly depleted (Conkling 1981). As each stand of timber was cut, the shipyards relocated to harvest new areas that still supported preferred species. Cut areas generally were cleared and used for agriculture; land that was not converted to crops or pasture reverted to the near monocultures of spruce seen on most forested islands today. Unforested islands often were used to graze livestock, especially sheep, which remain on some of the islands today.

Human colonization of the islands affected native wildlife both through habitat destruction and through the introduction of domesticated animals and other nonindigenous species. Far more devastating to many species, however, was the intensive harvest of both aquatic and insular wildlife. Huge cod and other large predatory fish, once found in abundance along the Maine coast, were harvested intensely throughout the nineteenth century, resulting in their virtual extirpation from coastal habitats (Steneck 1995). The loss of these predators may have precipitated a major change in the composition of the nearshore aquatic community by removing the principal predators on adult American lobsters, crabs, and sea urchins (Steneck 1995). This aquatic community continues to change even today, as harvesting of large invertebrates intensifies and new markets open for species such as urchins, seaweeds, and snails, which had been ignored by commercial fishing industries until recently.

Insular wildlife communities also have changed drastically over the past few centuries. Some species, such as the giant sea mink, were hunted to extinction, whereas others were extirpated from islands. Perhaps the most obvious effect of the Europeans on wildlife populations was on seabirds. Virtually every seabird species was hunted for food or feathers, so that Maine's coastal breeding colonies were in danger of total extirpation by the beginning of the twentieth century (Norton 1907).

The first European colonists relied heavily on the dense concentrations of nesting seabirds and the huge rafts of wintering birds for food. Many birds were sought for their feathers, down, and oil as well as for their meat. Thousands of birds, such as the common eider, were shot or killed in huge *drives* during their flightless summer molting stage (Conkling 1981). Because these colonists made no attempt to manage this resource for the future, they decimated local populations by overharvesting.

The decline in bird populations in the Gulf of Maine by the end of the 1800's was dramatic. The great auk, once so plentiful that islanders filled their boats with the birds



Courtesy C. M. Johnson, USGS

Fig. 1. An overview of a few of Maine's more than 3,000 coastal islands.

"as if they had been stones," was driven to extinction by 1842 (Conkling 1981). Those less palatable species that continued to nest in fairly large numbers were nearly eliminated by two campaigns of shooting for the millinery trade (Drury 1973). The few seabird colonies left on the Maine coast in 1900 nested on remote, difficult-to-reach islands. Double-crested cormorants continued to nest only on one large rock until 1896, when only two nests were found (Knight 1897)—the last record of cormorants nesting in New England for more than 30 years (Mendall 1936). Atlantic puffins also had stopped nesting in Maine by the beginning of the twentieth century, and only one colony each of laughing gulls and common eiders remained. Leach's storm-petrels, black guillemots, herring gulls, and terns managed to remain relatively abundant on a few isolated islands. These species, too, might have been extirpated from the state if not for legal protection offered seabirds on their breeding grounds in 1901 (Norton 1907).

Human populations declined rapidly on the islands after 1910, largely because of the development of inland transportation and the depletion of coastal resources. As a result of this shift of people to the mainland, and the legal protection provided seabirds, many species began to recolonize the islands. Cormorants, eiders, and herring gulls made an immediate and dramatic comeback (Fig. 2). By 1931, only 6 years after they began to nest again in the state, over 1,700 pairs of cormorants were observed (Norton and Allen 1931). Cormorants are opportunistic feeders, foraging mainly on small- to medium-sized benthic fish and other species as they become seasonally available (Mendall 1936; Blackwell et al. 1995). Although the effect of cormorants on commercially important fish species was questionable, the dramatic increase in cormorants was considered by many fishermen to be a partial cause for the fisheries decline; these fishermen pressured the government to institute a cormorant and herring gull control program in 1944 (Erwin 1979; Krohn et al. 1995). Despite this brief setback, cormorants continued to increase in numbers at least until the 1980's; herring gulls may have reached a peak in the 1970's, while great black-backed gulls continue to increase (Fig. 2).

Most other seabirds also prospered following protection and have continued to increase in numbers to the present (Korschgen 1979; Krohn et al. 1992; Maine Department of Inland Fisheries and Wildlife, Augusta, unpublished data). However, good fortune for species such as the herring and great black-backed gull may have spelled disaster for others. Laughing gulls and terns began to recolonize many Maine islands early in the century, but because these colonies proved highly susceptible to predation and interference by the larger gulls, the laughing gulls and terns were driven from many islands by the late 1940's (Nisbet 1971). As a result, only a few islands now support colonies of laughing gulls, although intensive control of large gulls on those islands managed for terns has allowed both tern and laughing gull populations to increase (Fig. 2).

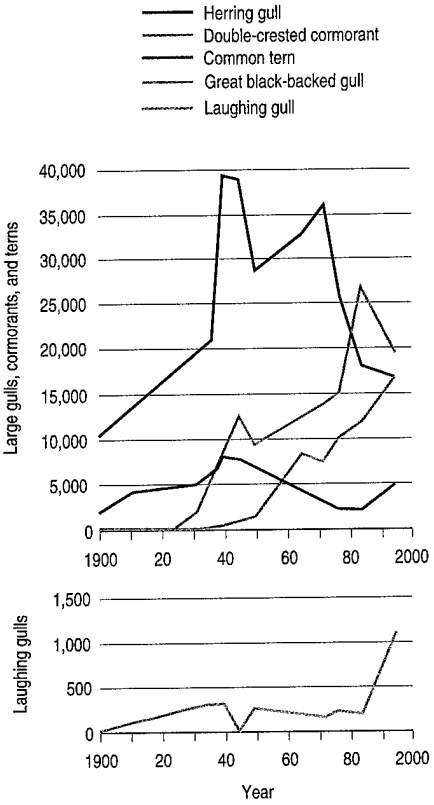


Fig. 2. Trends in the numbers of nesting pairs of five species of colonial seabirds nesting in Maine, 1900–1995. (Data from Norton and Allen 1931; Nisbet 1971; Drury 1973; and B. Allen, Maine Department of Inland Fisheries and Wildlife, unpublished data.)

As of 1990, there were over 120,000 pairs of seabirds and waterfowl nesting on about 355 islands in Maine (Maine Department of Inland Fisheries and Wildlife, unpublished data). In a sense, we have come full circle during the twentieth century, so that large numbers of seabirds are once again characteristic of Maine's coastal landscape. It is now widely recognized that seabirds represent an intrinsic part of the ecology of Maine islands, yet their continued prosperity is again threatened as the demand for waterfront property rises and human use of the islands and adjacent waters for commercial and recreational purposes increases. Fortunately, through concentrated efforts to protect the most valuable seabird islands, many of these islands are owned by public or private conservation groups, including the islands that harbor most of the largest seabird colonies. Many other seabird islands, though, are privately owned and so are susceptible to development, and even protected islands are vulnerable to disturbances in adjacent aquatic habitats. As in the case of gull control, human intervention may be necessary again, this time in the form of conservation of important nesting habitats, to preserve the current status of seabird populations in Maine. However, conservation efforts directed at seabird nesting habitats alone may not be enough. Maine's seabirds depend on a variety of other habitats and wildlife communities for survival. Adult eiders, for example, feed heavily on mussels, sea urchins, and other coastal invertebrates, whereas their ducklings rely on snails and amphipods as critical food sources during their first few months of life (Cantin et al. 1974; Krohn et al. 1992). The effects of increased human pressure on these invertebrate resources could have unanticipated ecological consequences for these birds and other coastal wildlife species.

We hope we have learned enough from the historical trends of Maine's coastal resources to understand that effects upon any part of this complex system may be far-reaching. Although we have no control over the many environmental events that can dramatically affect local wildlife populations (for example, hurricanes and rising sea levels), we can attempt to minimize human impacts. Careful management of our coastal resources today is critical to the survival of this ecosystem, but regardless of our best efforts to understand it, the coast will remain dynamic and unpredictable. It is this unpredictability that makes the island habitats of coastal Maine such mysterious and special places.

See end of chapter for references

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species. Peregrine falcons have been raised in captivity and released into the wild by the U.S. Fish and Wildlife Service. Some of these falcons have been observed nesting in urban centers, where an abundance of rock doves provides a consistent food source for urban peregrine populations. Large suspension bridges that exist in most northeastern cities may be especially important nesting sites for peregrine falcons because they offer isolation and a clear view for the birds. In fact, nesting peregrine falcons have already been observed on the Throgs Neck and Verrazano Narrows bridges in New York City. Because of this adaptation to a changing landscape, the expected trend of the peregrine population size is upward (Cade and Barclay 1984).

Canada Goose

Canada geese have also learned to use urban and suburban landscapes and have become so successful that they are considered a nuisance in many areas. Beginning in 1948, Canada geese densities increased sharply and have doubled approximately every 20 years (Trost and Malecki 1985). Grazing geese congregate in large numbers on short grass; golf courses provide excellent habitat. Densities on golf courses are greater than 30 geese per course in New England and 250 geese per course in the mid-Atlantic states. In the coastal states from Maryland to Massachusetts, more than 50% of the respondents to a poll classified the geese as a nuisance, and all Northeast states except Maine reported some nuisance problems. Most complaints about the geese focus on their droppings, which kill grass, are unsightly, and are perceived as a health threat (Conover and Chasko 1985).

Status of Other Urban Wildlife

Comparatively little research has been done on the wildlife and communities of the growing cities of the Northeast. Little attention has been given to reptiles and amphibians (herptiles) in urban areas, even though destruction, fragmentation, isolation, and alteration of habitats have caused a low abundance of herptile species in these settings (VanDruff et al. 1994). A 1987 survey of North American colleges and universities revealed that only 5% of wildlife research during the 1983–1984 school year was devoted to urban wildlife, and only 2% of the schools' wildlife research budgets was devoted to urban species (Adams and Dove 1989). This effort was greater than that of state and federal agencies during the same period, and, in fact, the U.S. Fish and Wildlife Service assigned only one person to urban wildlife study during the 1970's and 1980's (VanDruff et al. 1994). Research priorities include the species-specific extinction or colonization rates typical of urban parks of varying sizes. In addition, more research is needed on the effectiveness of wildlife habitat corridors (Adams and Dove 1989).

Urban areas are especially important environments for biotic resources because they bring many species into close contact with humans. For good or ill, the contact of humans with plants and wildlife in urban habitats shapes societal values about our biotic resources and influences the political process. Perhaps the best example today is the white-tailed deer, a species that is causing significant upheaval in societal values, as discussed previously.

Fragmented Landscapes

Human Activities

The first Europeans in the Northeast sought to break up the vast forest into farmlands and settlements. This trend continues today, and the landscape is becoming an increasingly complex mosaic of forest, city, farmland, and wetland. Fragmentation occurs when a block of one vegetation type is divided into two or more smaller parcels. Fragmented habitats are now so widespread and support such a characteristic array of wildlife that they deserve recognition as a major habitat type in the Northeast.

Fragmentation Favors Invasive Species

Fragmentation caused by human activities variously alters the landscape and its biotic components. Disturbance of an existing environment can give aggressive invaders a competitive advantage. Nonindigenous plants and animals invade more rapidly because trucks inadvertently carry seeds from one part of the country to another and canals link previously separated watersheds. A 1950 survey revealed that 20% of the plant species in the Northeast were nonindigenous (Guntenspergen 1995). In the state of New York alone, more than 200 species of nonindigenous plants have been recorded in the past 20 years. In West Virginia, 400 plant species (19% of total) are nonindigenous, and in New England, 821 (29%) of the plant species are considered nonindigenous. This trend is probably increasing for plants and vertebrates, but figures on nonindigenous species are not available in many states (U.S. Congress, Office of Technology Assessment 1993; Table 10).

Change in Distribution of Native Species

Fragmentation also changes the distribution of native species. In the Northeast, the Delmarva peninsula fox squirrel is one of only two extant mammals on the federal list of

Table 10. Loss of native vertebrates and introduction of nonindigenous vertebrates in Massachusetts, Pennsylvania, and Ohio (Whitney 1994).

Class State	Number of nonindigenous	Number of extinct natives	Percent of native species now extinct
Mammals			
Massachusetts	5	8	14
Pennsylvania	2	8	11
Ohio	2	13	20
Birds			
Massachusetts	5	3	2
Pennsylvania	6	8	4
Ohio	6	8	4
Fish			
Massachusetts	27	1	2
Pennsylvania	7	28	15
Ohio	15	9	6

endangered species (the other is the Indiana bat). This is a subspecies of the fox squirrel that historically ranged over parts of Delaware, Maryland, New Jersey, and Pennsylvania. Today it is restricted to the Delmarva peninsula and prefers ecotones where forest grades into scrub or grass. The clearing of woodlots for more intensive agriculture and for residential development not only changed its habitat but also allowed a competitor, the gray squirrel, to expand (Mathews and Moseley 1990). The gray squirrel is more adaptable than the Delmarva peninsula fox squirrel, and competition between the two species may have led to the decline of the Delmarva peninsula fox squirrels. A recovery plan has been completed, and reestablishment of this squirrel is possible (Thornback and Jenkins 1982).

Highways are an important component of fragmentation because they make traveling easier for some species. Highways also provide food in the form of animals that are killed by cars (Lazell 1989). The coyote may be taking advantage of this food source, because it is the only large predator with a significant range expansion in the past 30 years. This species has expanded its range eastward from the central plains and now occurs throughout the Northeast, except in Delaware and in the Philadelphia urban areas (Chambers 1987). The coyote is broadly adapted to forest, agricultural, and suburban environments. The highest densities of coyotes occur in Maine (22 per 100 square kilometers). The coyote is the largest predator in many parts of the Northeast, and its presence raises many concerns by the public because of perceived threats to deer, livestock, humans, and pets (Chambers 1987). As coyotes become more common, management and education will be important for mitigating conflicts between this species and humans.

As in the urban landscape, no species is as visible or as controversial in the fragmented landscape as the white-tailed deer. Deer populations in Virginia, Maryland, New Jersey, Pennsylvania, New York, Connecticut, and Massachusetts have increased significantly during the last few decades, and today the estimated population size in this region is 3 million animals (Storm and Palmer 1995). Densities as high as 70 deer per square kilometer occur in Pennsylvania (Storm et al. 1989).

Some people find deer in urban areas attractive and others view them a nuisance. Each year, as many as one million deer are killed on the highways of the Northeast (Decker et al. 1990); deer also cause more than $10 million in damage to orchards and other vegetation (Connelly et al. 1987). Concerns for effects on park areas (Porter et al. 1994; Underwood et al. 1994) are heightened by the possibility that deer play a role in the incidence of Lyme disease, which can cause serious health problems in humans (Anderson 1988). The conflict is leading to new technology for managing deer in these environments (for example, remote-delivery contraceptives), expanded education programs (for example, ecology of wildlife), and debate of societal values (for example, animal rights), all of which may influence how deer are managed in rural and urban landscapes.

Gaps in Knowledge and Directions for the Future

Uneven Knowledge of Resources

The knowledge of biological resources is uneven. More is known about the larger and more obvious plants and animals. Although many people believe that biologists have a thorough understanding of most species, this is still far from true. Significant gaps occur in the basic inventory of existing species, availability of long-term data describing population change, and knowledge of how species interact. Biologists have a rudimentary understanding of the basic biology of many organisms, but little is known about most species, and much of the microflora and microfauna may be undescribed. Perhaps more importantly, biologists have only a preliminary grasp of how these species interact to produce the various characteristics of northeastern environments.

Small Species

Small mammals, amphibians, reptiles, insects, and other invertebrates are largely unrepresented in many state and federal inventories (Flather and Hoekstra 1989). These same groups are also underrepresented in the wildlife literature. Insects are an enormous group for which status and trend data are lacking. Of the northeastern states, only New York has an all-insect list, and this dates from 1926. In addition, surveys of butterflies and moths of Maine,

New York, New Jersey, and Pennsylvania exist, and surveys are in progress in Maryland, West Virginia, and Ohio (Hodges 1995). Population information on pest species is sometimes available, but the typical unobtrusive insect of the forest or suburb is relatively unknown. A good resource for endangered insects and invertebrates in general is the *IUCN Invertebrate Red Data Book* (Wells et al. 1983), which summarizes most information about many endangered invertebrates.

Most gaps in information about a group exist not only in the Northeast but also usually across the country. This is particularly true of amphibians, which are experiencing national and perhaps worldwide declines. Although declines are not thought to be as drastic or widespread in the Northeast as they are in the West, basic information on the status and health of amphibians is nearly nonexistent. Efforts to monitor amphibian populations are just starting.

Inconsistent Record Keeping

Surprisingly, gaps in our knowledge occur even about some of the more popular mammal and bird species. Many state agencies monitor populations of game species through harvest reports of hunters. Properly analyzed, such records can be good indicators of population size trends, especially when linked with data on the intensity of hunting. Record keeping, however, is inconsistent and data are poorly stored and difficult to access. This is unfortunate because reporting by hunters is one of the most economical and extensive methods for collecting information. Where populations of special concern are monitored by formal surveys, good statistical design is lacking, and the ability to detect changes in species abundance of less than 30% is therefore rare.

Fungi and Lichens

Trees, rare plants, and species of economic importance are reasonably well studied, but much information is lacking on two groups in particular, fungi (molds, rusts, mildews, smuts, and mushrooms) and lichens (plants that consist of an algae and a fungus). Biological information on these groups is so incomplete that determination of whether a species is threatened, endangered, or has disappeared cannot be made. Checklists of North American fungi or comprehensive regional treatments of the species do not exist. European studies suggest a relation between forest health and successful reproduction of fungi, and although this may be an important phenomenon in the Northeast, no rigorous study has been conducted (Mueller 1995).

Lichens are similarly ignored. Of the northeastern states, only Connecticut and New York have lichen checklists, and these are incomplete. Although lichens have become scarce or have disappeared in parts of Connecticut, Pennsylvania, and Ohio because of acid rain or air pollution, the effects of the pollutants are poorly studied. On the whole, research on lichens is not encouraged at universities, in part because of poor funding (Bennett 1995). A lack of attention to these sensitive environmental indicators, though, may mean a missed opportunity for early warnings of environmental problems, or even the disappearance of species before they are ever described.

Conclusions

Reports such as those of the U.S. Geological Survey's GAP program are beginning to provide summaries of what is and what is not known about the nation's biological resources (Edwards 1995; Scott et al. 1995). Other federal programs, such as the U.S. Environmental Protection Agency's Environmental Monitoring and Assessment Program, are designed to collect extensive data on the current state of species. A partnership between a private organization, The Nature Conservancy, and state natural resource agencies created the Natural Heritage Program, a state-by-state database of information on native species. Although somewhat decentralized, this program has one of the most promising summaries of the status of our biological resources.

The development of a strong scientific foundation for management requires techniques for the early recognition of environmental degradation, a determination of the ability of northeastern environments to recover from repeated human disturbance, and an understanding of the means to maintain biological diversity. The complexity of the environment poses extraordinary challenges for the scientific community and seems to require a shift from the study of individual species to investigations of systems of interacting species.

Recent planning and thinking are providing a foundation for a new approach to the science and management of biotic resources. Just as F. E. Clements' *Plant Succession* (1916) and Aldo Leopold's *Game Management* (1933) shaped the early notions about the degree to which changes in populations or communities are discernable, predictable, and ultimately controllable, new ideas are initiating a rapid evolution of the way we think. Works such as Daniel Botkin's *Discordant Harmonies* (1990), Stuart Pimm's *Balance of Nature* (1991), and Carl Walters' *Adaptive Management* (1986)

are central to this new way of thinking. Examples that illustrate the integration of this new thinking into research are plans such as the Sustainable Biosphere Initiative of the Ecological Society of America (Lubchenco et al. 1991) and the National Research Council reports on science in the national parks and national forests (Gordon 1990; Risser 1992).

Recent reports and publications have noted common threads that can be seen as major gaps in knowledge for confronting the challenges of the next 20–30 years, including:

- In the absence of frequent disturbance, a few species or groups of species control environmental change. Some environments are limited by plant production and others are limited by consumers. Still other environments seem able to switch back and forth between limitations. Evidence suggests that biodiversity in an environment is one key to understanding the behavior of environments and to predicting their abilities to cope with disturbance. Researchers should focus on the effects of how the loss of species or drastic increases in the relative abundance of species affect other species in the system. The ways in which interactions among species shape environmental change must be determined.
- Past researchers focused almost exclusively on single, specific disturbances. Increasingly, we are aware that the frequency of the disturbance is crucial. For instance, the character of eastern forests is often determined by the time elapsed since the last hurricane. To predict and manage the response of various components of an ecological system requires an understanding of the frequency of disturbance, the type of disturbance, and its geographic extent. The influence of the frequency, geographic extent, and quality of disturbance on the dynamics of populations, communities, and environments must be determined.
- Because fluctuation may be normal and disturbance is common, scientists must determine the existence and identity of thresholds to major shifts in the bounds of fluctuation. The first signs of environmental stress are probably evident at the population level, and their timely detection requires the study of long-term population data sets. Characteristics of stressors that are great enough to cause drastic and potentially irreversible changes in environments must be identified.
- The protection of species diversity and ecological systems from varying anthropogenic impacts requires the identification of a viable reserve or cluster of reserves for maintaining a genetic pool, species, or environment type. The importance of shape and size of reserves and corridors for determining long-term environmental behavior must be recognized. Researchers must examine the direct and indirect influences of the surrounding landscape in areas of concern. The goal must be the identification of factors that convey increased resistance to invasion by nonindigenous species, decreased risk of extinction, and the benefit to cost ratio of restoring native species. The value of seminatural environments as biotic reserves relative to natural environments must be defined.
- Although the complexity of any one of these areas is still beyond comprehension, the scientific community must begin to learn more about the interactions among these units because they are the context within which sustainable use must operate. Researchers must define the relationships among societal values, land-use policies, and socioeconomic conditions with the intent of establishing management that encompasses a broader environment. The linkages among economic, social, and ecological systems must be identified.

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Acknowledgments

We thank the following people for their kind assistance on this report: D. Allen, G. Baldassarre, R. Burgess, R. Brocke, R. Fewster, D. Leopold, S. McNulty, M. Pike, R. Raynal, C. Smith, and R. Werner.

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Great Lakes

"If we could first know where we are and whither we are tending, we could better judge what we do and how to do it..."

Abraham Lincoln

The Great Lakes region, as defined here, includes the Great Lakes and their drainage basins in Minnesota, Wisconsin, Illinois, Indiana, Ohio, Pennsylvania, and New York. The region also includes the portions of Minnesota, Wisconsin, and the 21 northernmost counties of Illinois that lie in the Mississippi River drainage basin, outside the floodplain of the river. The region spans about 9° of latitude and 20° of longitude and lies roughly halfway between the equator and the North Pole in a lowland corridor that extends from the Gulf of Mexico to the Arctic Ocean.

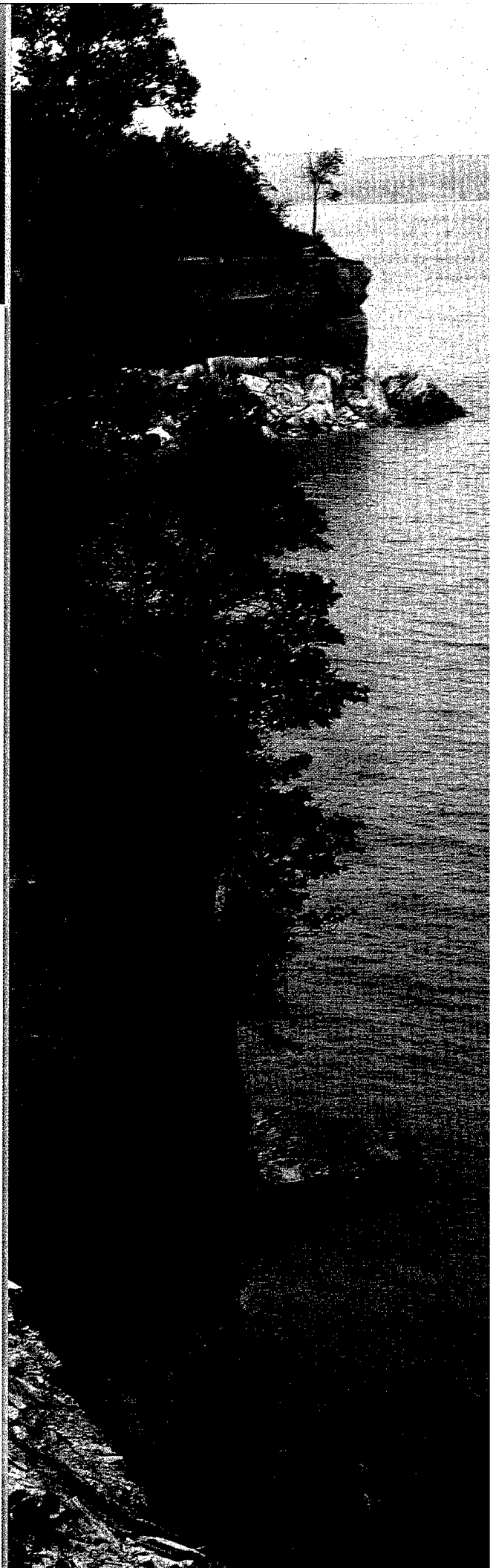
The Great Lakes are the most prominent natural feature of the region (Fig. 1). They have a combined surface area of about 245,000 square kilometers and are among the largest, deepest lakes in the world. They are the largest single aggregation of fresh water on the planet (excluding the polar ice caps) and are the only glacial feature on Earth visible from the surface of the moon (The Nature Conservancy 1994a).

The Great Lakes moderate the region's climate, which presently ranges from subarctic in the north to humid continental warm in the south (Fig. 2), reflecting the movement of major weather masses from the north and south (U.S. Department of the Interior 1970; Eichenlaub 1979). The lakes act as heat sinks in summer and heat sources in winter and are major reservoirs that help humidify much of the region. They also create local precipitation belts in areas where air masses are pushed across the lakes by prevailing winds, pick up moisture from the lake surface, and then drop that moisture over land on the other side of the lake. The mean annual frost-free period—a general measure of the growing-season length for plants and some cold-blooded animals—varies from 60 days at higher elevations in the north to 160 days in lakeshore areas in the south. The climate influences the general distribution of wild plants and animals in the region and also influences the activities and distribution of the human population.

The wild plants and animals and the natural systems that support them in the Great Lakes region are valuable resources of considerable local, regional, and national interest. They are also, in part, transboundary resources that we share with our Canadian neighbors to the north. The way these resources are changing over time is inadequately known and is a cause for concern for resource users and for those charged with managing and protecting these unique and valuable resources. This chapter describes the wild plants and animals and the systems that support them in the Great Lakes region; addresses their condition; and points out the gaps in our knowledge about them that, if filled, would aid in their conservation and appropriate use.

Regional Setting

Geology and climate are the major physical factors that influence the distribution and abundance of native plants and animals on a broad scale across the Great Lakes region. Much of the Great Lakes watershed lies in the Michigan Basin, an area centered in the Lower Peninsula of Michigan where an ancient, massive sinking of the surface of the Earth occurred



Courtesy M. Mac, USGS

Fig. 1. The Great Lakes are a major physical feature of the North American continent.

Courtesy National Oceanic and Atmospheric Administration, Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan

(Hough 1958). In the center of this basin, Precambrian rocks more than half a billion years old are overlain to a depth of 3,000 meters with Paleozoic rock 185–520 million years old and also with newer sedimentary and glacial deposits (Dorr and Eschman 1970). The Precambrian rocks slope upward to form the Canadian Shield, which lies north of the Great Lakes and extends into Minnesota, Wisconsin, and the western portion of the Upper Peninsula of Michigan. These rocks, which are generally hard and dense, underlie Lake Superior and form much of its shoreline. They also underlie and form much of the shoreline of Georgian Bay on the northeastern side of Lake Huron. The softer Paleozoic rocks, which include limestones, dolomites, shales, and sandstones, were laid down in the Michigan Basin 185–520 million years ago when the area was covered with a shallow sea. These are the rocks that were most deeply eroded to form major surface features, including the basins of the four lower Great Lakes.

During most of the last million years, the climate in the region favored the formation of glaciers. These glaciers reshaped the Earth's surface in the region, creating a low-relief surface, with elevations ranging from 700 meters above mean sea level in the Minnesota highlands north of Lake Superior to about 220 meters below mean sea level at the bottom of Lake Superior.

The last Ice Age, which ended about 12,000 years ago, produced an ice sheet that pushed enormous amounts of glacial till across the surface of the land. This till ranged from boulders several meters in diameter to fine silt and lake clays with particle diameters of a fraction of a millimeter. The ice smoothed the landscape in some areas, grinding down bedrock highs and depositing till in valleys and other depressions

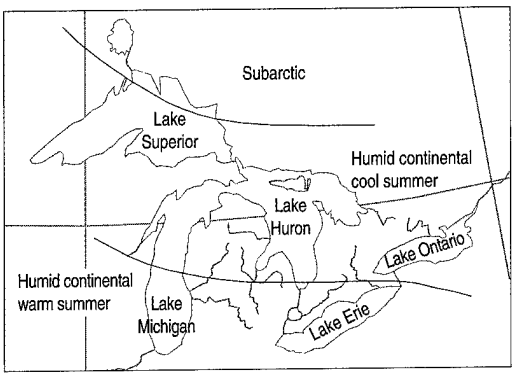


Fig. 2. Climate of the Great Lakes region.

between high areas of resistant bedrock. In other areas, including parts of the present basins occupied by the Great Lakes, the advancing ice sheet gouged the surface more deeply instead of filling and smoothing it. As the climate changed, the ice sheet stopped advancing and began to melt, and the till being transported by the ice was deposited in a variety of distinctively shaped ridges, hills, terraces, plains, and other landforms that provide much of the varied topography in the region. These landforms reflect both the thrust of the ice and the subsequent eroding action of the water that flowed out of the melting ice sheet.

The various tills or parent soils distributed broadly across the region by the ice sheet (Fig. 3) weathered differently to produce soils of varying fertility and water-holding capacity. The calcareous soils derived from limestone and related sedimentary bedrock were generally more suitable for colonization by plants than the sandy soils that were produced from sandstone and the harder crystalline bedrock from the northern part of the region. As the glacier retreated, water levels in the Great Lakes fell tens of meters and areas of former lake bed with sandy, silty, and clayey sediments became available to terrestrial plants and animals. Wind also redistributed the finer till, creating the silt-rich loess deposits in the southwestern portion of the region. The postglacial bedrock formations, elevation, local topography, precipitation patterns,

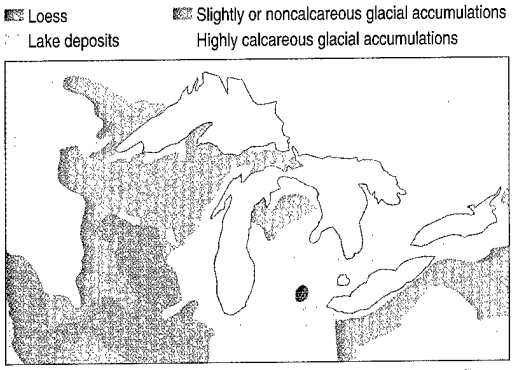


Fig. 3. Distribution of parent soils (glacial till) in the Great Lakes region (after Whitney 1994).

and soils also influenced the distribution of surface water, creating streams, lakes, and wetlands, which in turn influenced the local distribution of native plants and animals.

The plants and animals that colonized the area after the ice sheet retreated were from ice-free areas to the east, west, and south. Tundra vegetation was established in the northern portion of the region at least 10,000 years ago. As the climate moderated, tundra was replaced by a succession of larger plants, including coniferous and hardwood tree species typical of a warming environment. The forests were typically spruce and fir in the north, and beech, maple, oak, and other hardwoods in the south. Prairie grasslands developed at the region's drier western end and along its southwestern edge. Farther east, these prairie grasslands graded into savannah grasslands with sparse tree cover. Prairies and savannahs reached their greatest sizes in the region during the warmer, drier period that ended about 7,000 years ago (Barnes and Wagner 1981).

Animal communities became established in the area soon after the ice sheet retreated; their composition changed with the changing vegetation and climate. The muskox was an early inhabitant that lived near the ice front and moved north out of the region as the ice sheet retreated. A number of other large, now-extinct Ice Age mammals were also recorded in the region. Moose and caribou occupied the northern areas, elk occurred in some areas, and white-tailed deer were common in the south. Some coldwater aquatic species, including the whitefishes and the small mysid shrimp eaten by whitefishes, became established as the ice retreated. These relict glacial species are abundant today in the Great Lakes.

Archaeological evidence indicates that humans occupied portions of the region shortly after the last ice sheet retreated. Human occupation in the Saint Marys River valley at the north end of the region dates back 11,000 years (Conway 1977, 1980). These early people were hunters who moved frequently in search of food; they did not establish permanent villages (Cleland 1982). As these people's fishing implements improved and their spears and gorges (a primitive fishhook) were replaced with nets, fish became a more important food for them. Seasonal or permanent villages were established at sites containing concentrations of catchable fish. One such site in the Saint Marys River valley was occupied continuously by humans for about 2,000 years preceding the arrival of the first European explorers in the early 1600's.

About 1,000 years ago, four subsistence patterns based on domesticated plants, fishing, hunting, and wildrice had evolved in the region, and some people may have systematically exploited all of these resources in different seasons (Tanner 1986). In the south, where the growing season was longer and agriculture was an important contribution to subsistence, more permanent villages developed. The first introductions of nonindigenous species in the region, including domesticated forms of maize and beans from Central and South America, are attributed to these early cultures.

There is scholarly debate about the role of early humans in the extinction of some of the large Ice Age animals. Similar debate exists about the effects of the more recent and populous American Indian cultures on plants and animals, and their ecosystems. The local scarcity or extirpation of some food types and the deliberate use of fire to maintain some natural plant community types—particularly the prairie and savannah ecosystems in the western and southern portions of the region—have been attributed to these more recent Indian cultures.

Settlement of the region by the new Americans of European descent began in the late 1700's on the south shores of Lakes Ontario and Erie. Settlement spread rapidly westward, and by 1820 all of the drainage basin was settled from the south shore of Lake Ontario and Lake Erie and the west shore of Lake Erie to Detroit, Michigan. In 1835 settlements extended across southern Michigan, northern Ohio, Indiana, and Illinois, and into southern Wisconsin. By 1890 the entire region was settled except for the portion of Minnesota east of a line from Duluth to Lake of the Woods on the Canadian border.

Settlement brought about major changes in the landscape. Forest cover was removed to permit farming and for lumber and fuel (see chapter on Land Use), and streams were dammed to provide waterpower for mills and other industries (see chapter on Water Use). The vast eastern white pine forests in the lower peninsula of Michigan and northern Wisconsin were clearcut for lumber from 1850 to 1890. Large forest fires occurred in northern Michigan and Wisconsin during that same period, and the accumulation of branches and treetops discarded during logging contributed to intense, widespread fires that burned with such heat that they destroyed much of the humus in the sandy northern soils. The combined effect of the fires and logging led to the replacement of the pine forests with hardwood or mixed hardwood and pine forests. In the southern part of the region, nonforest areas—including grasslands, savannahs, and large wetlands in the lake plains—were also among the first lands converted to agriculture.

Settlement also affected the native animals, restricting their distribution and abundance and

causing the extinction of a number of notable species. The extinction of the Atlantic salmon in the Lake Ontario drainage took place in the 1800's and was attributed to overfishing during spawning, the construction of mill dams that prevented fish from reaching their spawning grounds, and forest removal that reduced streamflow, increased stream temperatures, and made streams unsuitable nursery areas for young salmon (Smith 1972; Webster 1982). The arctic grayling, which had been abundant in streams in northern Michigan, became extinct in the early 1900's, probably through the combined effects of forest-cover removal, overfishing, and the introduction of trout into its habitat. The passenger pigeon, which had nested in aggregations of as many as several million birds in northern Michigan and portions of Wisconsin, was hunted intensively during its nesting season and suffered major population declines in the late 1800's. The species became extinct at about the turn of the century. Hunting for commercial markets and the conversion of wetland habitat to farming sharply reduced the number of waterfowl that nested in the region or migrated through it. Bison, which had inhabited the savannahs in the southwestern part of the region, disappeared with settlement. Likewise, white-tailed deer and wild turkeys had been common in the forests and savannahs of southern Michigan at the time of settlement, but by the late 1800's uncontrolled hunting had eliminated the turkeys and most of the deer in the southern part of the state. In northern Michigan, the last caribou was seen on an island in the lower Saint Marys River around 1900 (Bayliss and Bayliss 1955). Self-sustaining populations of elk, gray wolf, fisher, and marten in the region were lost because of hunting and trapping.

Settlement also brought into the region many nonindigenous species from various parts of the world. Many of these were domesticated species that were intensively cultured. Other introductions were often wild European species that were accidentally or deliberately introduced. Some of these introductions were beneficial and filled habitats that would no longer support extirpated native species, but many had substantial undesirable effects on native animals and plants.

The human population in the region increased markedly after 1850, when most of the region had been settled. In Illinois, for example, the population increased almost linearly from slightly less than 1 million people in 1850 to more than 9 million by 1970 (Illinois Department of Energy and Natural Resources and The Nature of Illinois Foundation 1994). About 95% of the population of Illinois lived in rural areas in 1850, but by 1970 about 85% of the population lived in urban areas. Similar rapid growth and urbanization occurred in other parts of the region, with the highest population density occurring in a band across the southern portion of the region. In Michigan, the inhabitant-to-land density in the 1970's exceeded that in China at the beginning of the twentieth century. The population of Michigan now exceeds that of about 170 nations in the world (Santer 1993). A similar demographic situation exists in the Canadian portion of the Great Lakes basin, which supports a population greater than half of the nations in the world. In 1990 the Great Lakes basin in the United States and Canada contained more than 95 metropolitan-sized communities of at least 50,000 inhabitants each. The U.S. population in the eight states bordering the Great Lakes was about 77 million, of which about 34 million resided in the Great Lakes region (U.S. Bureau of the Census 1994).

This brief description and history of the region is intended to provide a context in which the status and trends of the present plant and animal species, natural communities, and ecosystems of the region could be examined. The changes in the region, particularly those that have occurred since settlement, are reasonably well documented. Detailed knowledge of the processes that brought about these changes continues to elude us, but it is clear that dramatic change occurred in the plants and animals and their ecosystems during the first 10,000 years of human occupation and that humans contributed to this change. It is also clear that climate was the major instrument of change and that the change occurred extremely slowly when compared with the change that occurred during European settlement in the late 1700's–1800's and in the years between then and the present. It is evident that the change during and following settlement was the consequence of resource use patterns and species introductions that deliberately or incidentally resulted in the alteration or destruction of most preexisting natural ecosystems. The detailed and intriguing account by Whitney (1994) of resource use and its effects on natural systems in the region is recommended to the serious reader.

Regional Ecosystems

The Nature Conservancy (1994a) identified six major ecosystems that supported significant elements of biological diversity in the Great Lakes basin. Although the original classification was intended to describe only the ecosystems in the Great Lakes basin, the categories are broad enough to also include the major ecosystems in the portion of the region in Illinois,

Minnesota, and Wisconsin that lies outside the Great Lakes basin. To aid presentation, the ecosystem designations and the grouping of ecosystem elements within each major category presented here were changed slightly from those given by The Nature Conservancy (1994a).

This discussion addresses in general, nonquantitative terms the status or health of each of the six major ecosystems in the Great Lakes region. The process of defining ecosystem health has just begun, and a more detailed assessment of the health of the ecosystems of the region will have to be delayed until an accepted procedure for doing so is developed. The International Joint Commission (1991) presents a condensed discussion of ecosystem health and proposes a useful framework for identifying physical, chemical, and biological indicators that could be used to measure ecosystem health in the Great Lakes region. Constanza et al. (1992) also present useful guidance for defining and measuring the region's ecosystem health.

Open Lake and Connecting Channels

All of the open lake and connecting channel ecosystems of the Great Lakes have been altered and stressed to some degree by human activities in the last 200 years. Lake Superior is the least altered water body in the system, whereas the large embayments and certain basins and harbors of the other lakes and the connecting channels are the most altered and stressed.

Commercial fishing and the introduction of nonindigenous aquatic plants and animals have permanently altered these ecosystems. Fishery management plans and goals are being developed to help assure that these interjurisdictional resources are managed as a sustainable resource supported largely by wild stocks of native fish species. Stocking of native and nonindigenous trout and salmon to support intensively managed recreational fisheries will probably continue indefinitely in all of the lakes, however. No practical way exists to control or eradicate most of the undesirable nonindigenous species that have become established in the Great Lakes; thus, most will probably become permanent members of the aquatic community. Efforts to control the sea lamprey, though, will continue as long as salmon, trout, and whitefish are managed to support major recreational and commercial fisheries. Control of rainbow smelt and alewife populations can probably be achieved in many areas by enhancement of the trout and salmon populations that prey on them. The zebra mussel may be impossible to control and may cause major changes, some of which may be beneficial. Western Lake Erie and Saginaw Bay of Lake Huron—once clear waters—became artificially enriched and plagued with high turbidity caused by runoff from agricultural lands. The filtering action of the zebra mussels in these areas may reduce turbidity and restore water clarity to historical levels, thus benefiting native fishes adapted to clear water. More comprehensive efforts by the United States and Canada will be needed to prevent further accidental or deliberate introductions of nonindigenous species into the Great Lakes region (International Joint Commission and Great Lakes Fishery Commission 1990).

Physical alteration of the Great Lakes and their connecting channels has had profound effects on the waters and their biota. The installation of dams and locks at the outlet of Lakes Superior and Ontario regulates the levels of those lakes and has significantly reduced the natural, seasonal, and between-year fluctuation in levels and interlake flows that sustain the pulsed stability of wetlands in the system (Jaworski and Raphael 1979). These dams have also fragmented the system by cutting off historical fish migrations between parts of the system. The commercial extraction of sand and gravel at the head of the Saint Clair River in 1908–1925 and dredging there in 1933–1962 to increase the depth of the navigation channel permanently lowered the levels of Lakes Huron and Michigan by 0.3 meters (Derecki 1985). The effect of this change on the coastal wetlands in those lakes is unmeasured but undoubtedly substantial and adverse.

Channel dredging and shoreline modification have permanently destroyed many coastal wetlands and large amounts of fish spawning habitat throughout the Great Lakes system, but particularly in the connecting channels. It is unlikely that such alterations of the system would be permitted now or in the future. Recent proposals to further regulate levels and flows in the system (to benefit navigation and hydropower interests and to reduce flooding and shoreline erosion in residential areas during high-water years) have been rejected. The decision to not further regulate the system expressly recognizes the ecological importance of retaining the natural fluctuations in levels and flows in the system.

Pollution has severely degraded portions of the Great Lakes system. Surface drainage from agricultural areas has added large amounts of silt to Lake Erie and to Saginaw Bay in Lake Huron. Herbicides and pesticides have also entered the system in large quantities from agricultural areas bordering Lake Michigan and Lake Saint Clair. Legal discharges of municipal and industrial wastes have overly enriched and

polluted major embayments and other portions of the system. These discharges, together with spills of pollutants and frequent discharges of raw sewage into storm drains that flush directly into the Great Lakes system, are still problems in many municipal areas. Aerial inputs of some contaminants are also significant. Organochlorine compounds have reached high levels in Lakes Michigan and Ontario. These and other industrial pollutants, including oils and metals, occur at high levels in sediments in some areas of the connecting channels and in certain harbors throughout the system. The International Joint Commission has identified more than 40 such areas of concern in the Great Lakes system where the beneficial uses of the system have been substantially degraded by pollution. Remedial Action Plans are being developed to reduce the amount of incoming pollutants and to restore the affected areas to good ecological health.

Water withdrawals and out-of-basin diversions are subjects of major concern for the Great Lakes system. Most of the water withdrawals are made to provide cooling water for steam-electric power plants on the shoreline of the Great Lakes or the connecting channels. In some areas these withdrawals may approach 1% per day of the nearshore waters of Lake Michigan and western Lake Erie and 5% per day of the total flow in the connecting channels between Lakes Huron and Erie (T. Edsall, U.S. Geological Survey, Great Lakes Science Center, Ann Arbor, Michigan, unpublished information). Fishes and invertebrates in the withdrawn water are killed by a combination of stresses, including physical collisions in the cooling system, elevated temperatures, and biocides used to clean the cooling system surfaces and to aid heat in exchange. Most steam-electric power plants built on the Great Lakes and connecting channel shorelines through the early 1970's operated with once-through cooling, a process that withdraws large volumes of water from the lake or channel, heats it 10°C–20°C, and then returns it to the water source. Steam-electric plants constructed after the early 1970's use closed-cycle cooling and are not a major threat to the aquatic resources of the Great Lakes system. Fish losses continue at the older plants, but these losses will eventually end when the older plants are retired from service and are replaced with plants using closed-cycle cooling.

Water withdrawals are also made for hydropower generation in plants in the connecting channels. The effects of these hydropower plants on Great Lakes fishes have not been extensively studied. A large pumped-storage hydropower facility on the Lake Michigan shoreline kills large numbers of fishes, and formal measures are now being taken to reduce the loss and provide mitigation (Manny 1984; Northwoods Call 1994). Out-of-basin diversions are occasionally proposed as a panacea for water shortages in the western states, but economic considerations and the governors of the Great Lakes states seem to have forestalled serious consideration of such transfers.

Wetlands

Wetlands are highly valued as recreational sites for hunting, fishing, bird watching, and general aesthetic enjoyment because they support a large number of plants and animals, including species that are not found elsewhere. Wetlands are transitional between terrestrial and aquatic systems (Cowardin et al. 1979). The wetland soil and sediments are saturated with water or covered by shallow water at some time during the growing season of each year and support mostly aquatic or water-loving plants. Included in this definition are bogs, fens, marshes, sloughs, and wet meadows.

Two major types of wetlands, coastal and inland, occur in the region. Great Lakes coastal wetlands are within 1 kilometer of the lakeshore or, if farther inland, are directly influenced by water level changes in the Great Lakes or their connecting channels (Herdendorf et al. 1981). These coastal wetlands are more dynamic, display a greater diversity of landforms, and are less influenced by groundwater inflow than are inland wetlands. Coastal wetlands, unlike inland wetlands, have mainly mineral sediments. They are also subject to short-term (hours-long) flooding and draining by storm tides (seiches), as well as to seasonal and years- or decades-long changes in lake levels (Fig. 4).

Long-term changes in water level cause coastal wetlands to advance lakeward or retreat landward over a period of years. Species lists of

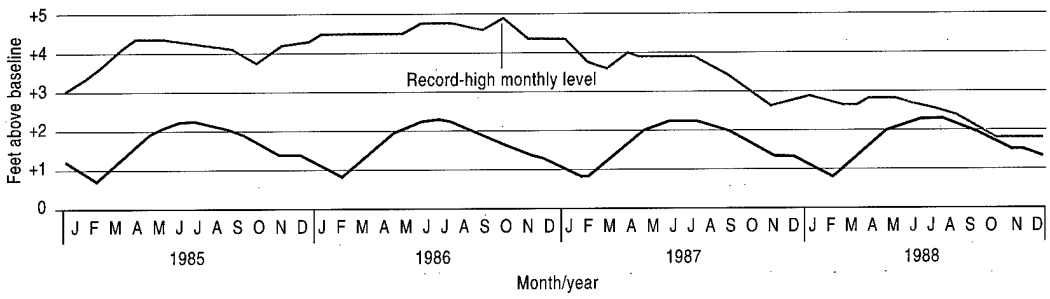


Fig. 4. Seasonal and interannual variation in water levels in Lake Saint Clair, 1985–1988. Lake Saint Clair is a segment of the connecting channel between Lake Huron and Lake Erie. The green line is the recorded monthly level, and the purple line is the 90-year average level (after Edsall and Gannon 1991).

plants and animals of Great Lakes coastal wetlands have been developed by Herdendorf et al. (1981). Brady and Burton (1995) and Wilcox (1995) provide recent descriptions of Great Lakes coastal wetland ecosystems in Lake Huron.

Presettlement wetland area in the United States was estimated at 87 million hectares (Roe and Ayres 1954; Dahl 1990) and, between 1780 and the mid-1980's, about 53% of the total had been drained and converted to other uses (Mitsch and Gosselink 1993). A total of about 14,600 hectares of wetlands was present in Michigan, Minnesota, and Wisconsin in 1780, but by the mid-1980's, about 54% of that had been converted to other uses. Losses in Illinois, Indiana, and Ohio were also high as a result of the draining of the Great Kankakee Marsh on the northern Indiana–Illinois border and the draining of the Great Black Swamp that covered 4,000 square kilometers at the Michigan–Ohio border. Inland wetlands remaining in 1955 were much more abundant in Michigan, Minnesota, and Wisconsin than in the rest of the region (U.S. Fish and Wildlife Service 1971). Much of the remaining inland wetland habitat is in private ownership, and its fate in the face of pressures to develop the land for other uses is uncertain. All the states in the region except Illinois, Indiana, and Ohio have laws to regulate wetland use (Tiner 1984). Existing legislation in the other Great Lakes states presently offers a reasonable degree of protection for these wetlands, but legislative changes currently being considered by the federal government could further reduce the amount of wetlands held by the private sector.

There are no reliable estimates of the total area originally occupied by Great Lakes coastal wetlands, but fewer than 1,200 square kilometers may remain within the United States (Herdendorf et al. 1981). The mean size of these wetlands varies from about 0.3 square kilometers along Lake Ontario to about 1.4 square kilometers along Lake Huron. The largest total number of coastal wetlands and the largest total wetland area occur along the perimeter of Lake Michigan. A unique set of coastal–deltaic wetlands occurs in Lake Saint Clair and in the Saint Clair delta at the mouth of the Saint Clair River on Lake Saint Clair (Edsall et al. 1988). The international border divides the lake and delta. In the United States in 1873, there were 7,200 hectares of wetlands around the lakeshore and on the delta but by 1973, 73% of these had been lost (Jaworski and Raphael 1979). On the Canadian side, about 3,570 hectares of wetlands remained in 1965, but by 1973 about 30% of those had been lost (McCullough 1985). Urbanization and residential or recreational development were responsible for most of the loss on the U.S. side of the border, and conversion to agriculture was the major cause of wetland loss in Canada. Diking of wetlands—a practice that had been common in this portion of the system in areas managed intensively for waterfowl hunting—reduces wetland productivity and withdraws habitat previously used for spawning by Great Lakes fishes. Additional diking of coastal wetlands is unlikely.

Rivers and Streams

The Great Lakes watershed has been divided into river basin groups and flow measurement areas (Great Lakes Basin Commission 1975). The largest catchment basins are the Maumee River in Ohio and Michigan (17,100 square kilometers) and the Nipigon River in Canada (25,258 square kilometers). The numerous small streams that flow directly into the Great Lakes each have catchments of only a few square kilometers. For example, Michigan has 513 of these small coastal streams (flows of 1 cubic meter per second or less) and only 100–150 larger streams (Hudson et al. 1992). In the Precambrian shield bedrock areas in Minnesota, Michigan, northern Wisconsin, and in Canada, the glacial deposits are thin or altogether lacking, and the streams have relatively steep gradients. Glacial drift and glacial landforms dominate the topography in much of the rest of the basin, although there are areas where calcareous bedrock reaches the surface and affects streamflow and the character of the streambed. Streams with relatively steep gradients occur throughout this portion of the region, even in the till plains where an undulating land surface and moraines produce local relief of up to 30 meters (Hudson et al. 1992). The topography and soils, which create many lakes and wetlands in the basin, tend to slow runoff and sustain flow throughout the year. The maximum flow of larger unregulated streams in the basin is usually only about three to seven times greater than their mean flow.

Drainages with clayey soils have higher loads of suspended solids and phosphorus and are more susceptible to flooding than those drainages with sandy soils. Streams with clayey soils occur in the west–southwestern end of the Lake Superior basin, parts of the drainage to southern Lake Michigan, the western basin of Lake Erie, and parts of the Lake Ontario drainage. Sandy soils are dominant in north–central Wisconsin and in northern Michigan in Lake Michigan and Lake Huron drainages; water quality in streams in these areas is high (Sonzgoni et al. 1978; Manny and Owens 1983). Northern streams with good groundwater inflow generally support cool or coldwater fish communities. Other streams usually support warmwater fish communities.

Many streams that are not dammed have runs of fishes that enter them seasonally from the Great Lakes.

The quality of the stream ecosystems is generally highest in undeveloped portions of the region where damming, channelization, sedimentation, and pollution have not occurred and is lowest in areas where there is extensive agricultural, industrial, and urban development. In Illinois, for example, where the land is intensively developed, more than 25% of the total length of sizeable streams in some main river basins has been channelized, and almost every sizeable stream in the state has at least one dam (Illinois Department of Energy and Natural Resources and The Nature of Illinois Foundation 1994). Peoria Lake, the largest, deepest bottomland lake on the Illinois River, lost 68% of its capacity because of sedimentation that occurred between 1903 and 1985. Of the species present in Illinois streams at the turn of the century, about one in five fishes, one in three amphibians and reptiles, more than half the freshwater mussels, and one in five crayfishes have been extirpated or are threatened by extinction. Water quality in Illinois streams is improving, but the quality of stream ecosystems remains low. In 1988 about 66% of the total stream length in the state was in fair to very poor condition and 34% was in good to excellent condition.

Hydropower development creates significant problems in many of the larger stream and river ecosystems in the region. Most of the dams were built early in this century, and few have fish ladders or other devices that allow fishes to pass over or through the dams unharmed. Recent evaluations show that these dams fragment and substantially degrade the stream ecosystem and limit the use of the stream system by resident fishes and by anadromous fishes that migrate up Great Lakes tributaries to spawn. Most of the dams in the region were built in high-gradient stream reaches, which were areas of permanent residence for some fish species and spawning areas for other migratory species. Generally, these high-gradient reaches were also sites of the groundwater inflow that was required to support coolwater and coldwater fish species. Stream fishes in the flooded areas above the dams were replaced by species better suited to a warm lake environment. Stream fishes below the dams were also adversely affected. The dams were usually operated in a daily peaking mode to supply power when it was in greatest demand, usually in the morning, evening, or both. As a result, exceptionally high flows occurred once or twice a day when power was needed, and water was held back at other times. The high flows eroded the streambed, and the intervening low flows drained it. The temperature variation in the stream below the dam was also significantly altered. In Michigan alone, there are 113 operating hydropower plants (Whelan and Houghton 1991). These plants produce only about 1.5% of the existing power demand while impounding about 750 kilometers of riverbed, adversely affecting another 1,200 kilometers of river, and blocking anadromous fishes from 3,300 kilometers of mainstream river habitat.

Many of these dams in the Great Lakes region that are licensed to operate by the Federal Energy Regulatory Commission are now under consideration for relicensing. Relicensing agreements recently reached in Michigan between resource advocates and the power companies will greatly lessen the adverse effects of the dams and should help set an environmentally beneficial precedent for relicensing in other states. Under the agreements, the water release patterns from the dams will closely mimic the inflow pattern to the reservoirs above the dams. In addition, effective upstream and downstream fish passage facilities will be installed in each dam consistent with fishery management plans for the area. These changes will significantly improve habitat quality below the dams and reduce the fragmentation effect that the dams have had on the river ecosystem. The relicensing agreements also provide for dam removal when the dams are declared obsolete.

A number of federally listed endangered freshwater mussels occur in tributaries throughout the Great Lakes region, but the Hungerford's crawling water beetle is the only federally listed endangered insect that is found in Great Lakes basin tributaries. The beetle is only known to occur in the Maple River in the northern Lower Peninsula of Michigan and in one or two other streams in that part of the basin.

Coastal Shore

The coastal shore is a relatively narrow strip of land bordering the Great Lakes shorelines (The Nature Conservancy 1994a). It directly adjoins with and is strongly influenced by the lake environment, including wave action, wind, temperature, water level, humidity, and precipitation. In some areas even the soils of the coastal shore are strongly influenced by the lake environment. Physical features of the zone include bedrock shorelines and gravel, rubble, cobble, and sand beaches. Sand dunes are major features in some areas.

The Great Lakes region contains some of the most extensive freshwater sand dunes on Earth. Some occur near river mouths, others are perched on wave-cut bluffs of glacial till. Dunes and sand beaches reflect sediment transport

Habitat Change in a Perched Dune System Along Lake Superior

Pitcher's Thistle and Lake Level Change

Pitcher's thistle (Fig. 1), listed as a threatened species by the U.S. Fish and Wildlife Service, inhabits the sandy shores of the upper Great Lakes. Its life cycle requires a dynamic habitat that periodically provides both highly disturbed, open patches (affording sites for seed germination on mineral soil in high light under limited competition) and more stable patches for flowering, seed set, and seedling establishment before burial or other site destruction (McEachern 1992). Since water levels of the lakes greatly influence the effects of waves upon the shore, the fine-scale history of lake-level change is relevant to understanding past habitat change, the persistence of Pitcher's thistle, and habitat requirements for restoration and protection of the species.

Fig. 1. Pitcher's thistle.
Courtesy K. McEachern, USGS

Recent studies of lake-edge dunes and beach ridges (Fraser et al. 1990; Lichter 1995; Thompson and Baedke 1995) suggest that because of climatic variation, past levels of Lake Michigan have differed from those of the present by as little as several tenths of a meter to as much as a meter or more. These changes have taken place periodically over decades to centuries during the past 5,000 years. The growth of open habitat patches through dune building in lake-edge dunefields is greatest as low lake levels bare broad sand flats, expanding the source of sand for transport by the wind (Fraser et al. 1990). Perched dunefields, which form high atop lake-facing bluffs, also respond to lake-level change (Marsh and Marsh 1987; Anderton and Loope 1995) but in a mirror-image fashion to those on the lake edge (Olson 1958). In perched dunefields, growth of open habitats (dune building) occurs as rising lake levels destabilize lake-facing bluffs, creating active colluvial slopes and increasing sand supply to the bluff tops.

For both lake-edge and perched dunes, the mix of habitat change may depend upon smaller-scale episodes of lake-level change that are *nested* within larger, longer-term trends (Fraser et al. 1990; Thompson and Baedke 1995; Fig. 2). Lake-level changes, then, have probably mediated expansion and contraction of habitat patches suitable for Pitcher's thistle on several scales (Snyder 1985; Businski 1992; McEachern et al. 1994) since the appearance of the Great Lakes about 10,000 years ago.

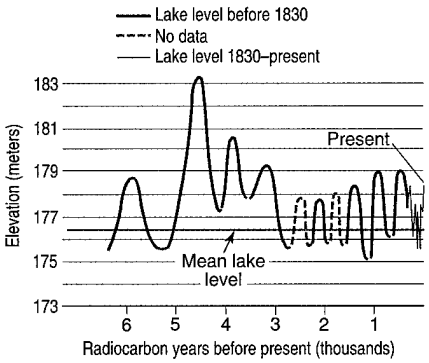


Fig. 2. Hypothetical late Holocene hydrograph proposed for Lake Michigan (Fraser et. al. 1990) in relation to historical lake levels.
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Episodes of habitat change, driven by changes in levels of the Great Lakes, must be considered when assessing human effects upon coastal vegetation and rare species (Schultz 1988; Businski 1992). Paleoecological studies, baseline inventories, and long-term monitoring programs within the Grand Sable Dunes, a perched-dune system along Lake Superior, provide a window on vegetation change at different spatial and temporal scales and also provide an illustrative case study.

Vegetation Change

The modern Grand Sable Dunes are characterized by a shifting mosaic of plant communities and physical dune forms periodically disturbed as sand builds, stabilizes, and erodes away from the dune system (Fig. 3). Exhumed forests and buried soils in this landscape (Fig. 4) attest that vegetation cover has varied significantly over hundreds to thousands of years and give us a crude picture of coarse-scale changes (Anderton and Loope 1995). Analysis of present-day vegetation and plant population dynamics helps reveal how plant communities may change within tens to hundreds of years and allows us to predict habitat suitability for disturbance-adapted species like Pitcher's thistle for the next few decades.

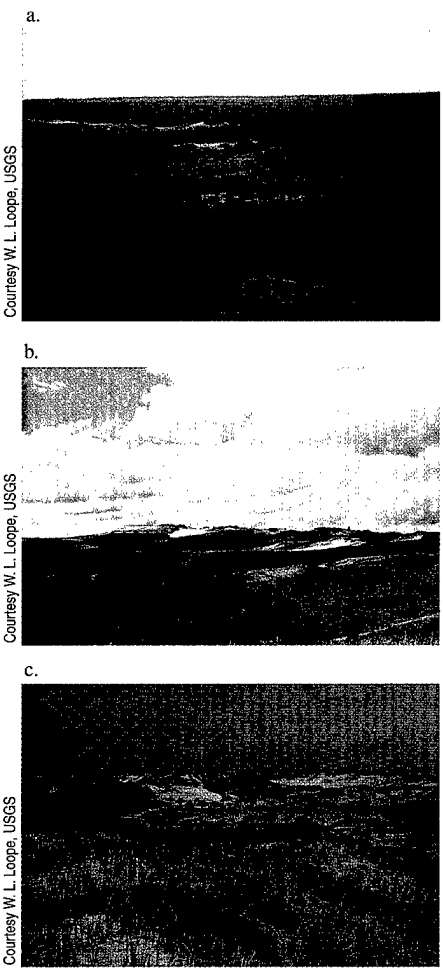

Fig. 3. Grand Sable Dunes vegetation mosaic: a) pine forest, b) grassland, and c) dunes.

Fig. 4. Buried soil in a perched dunefield.

Paleoecological Change

The presence of buried soils within Grand Sable Dunes implies sharply contrasting rates of sand supply to the dunefield. Radiocarbon dating of buried soils suggests that at least 5 and perhaps as many as 11 episodes of soil burial have occurred there over the past 5,500 years (Anderton and Loope 1995). Soil burial events were probably related to a much greater supply of sand than that of the present (Fig. 5a), which occurred as lake-facing bluffs were destabilized by the rising waters of Lake Superior (Fig. 5b). Periods of bluff stability during low water on Lake Superior (Fig. 5c) allowed vegetation to invade sand-starved dunes. Whether each buried soil represents complete forestation of Grand Sable Dunes is questionable, but the presence of charcoal in several soil profiles supports the possibility that vegetation occasionally became continuous enough to carry a fire. During periods of afforestation, Pitcher's thistle would have been restricted to small, isolated, and disturbed areas along the bluff edge or in rare inland blowouts. During periods of high sand supply and dune building, Pitcher's thistle would have been afforded a broader spectrum of open habitat. Rapid dune building may also have limited the availability of *intermediate sites*, which were stable long enough to permit completion of the flowering cycle of Pitcher's thistle but were open enough to permit germination of new seedlings.

Contemporary Vegetation Change

The most striking evidence of contemporary vegetation change within Grand Sable Dunes is the increase of jack pine forest over the last several hundred years. An aerial photo time series shows a fivefold increase in forest cover over the past 50 years. Snyder (1985) and Businski (1992) report similar results at Sleeping Bear Dunes, a perched dune system along Lake Michigan. Stand-age structure within forest patches at Grand Sable Dunes suggests that afforestation began at the landward edge of the dunes at least 125 years ago. The plant species richness in the forest increases with stand age and is strikingly higher than in the fire-influenced pine stands to the south and east of Grand Sable Dunes. Although charcoal from ancient soil profiles (Anderton and Loope 1995) suggests fire-prone vegetation occurred there in the past, burned snags and species usually associated with fire, such as blueberries, wintergreen, and bracken, are absent from modern pine patches.

Within the large-scale trend toward increasing forest cover, open patches are still being created on a smaller scale just landward of the lake bluff and in inland blowouts. Species composition and cover within open patches are determined by proximity to the lake-facing bluff edge and by fine-scale patterns of stability along the bluff face. Dominance of American beachgrass and wormwood along the bluff edge, both of which tolerate burial, reflects a high sand supply and fast patch turnover because of periodic sloughing of the bluff face. Shrubs such as woolly beachheather and bearberry and the bunch-grass, little bluestem, dominate more stable, open patches farther landward of the lake bluff, where there is less blowing sand.

Linking Nested Episodes of Change

Coastal geomorphology is important in understanding and predicting species persistence (Pavlovic et al. 1991). Periods when open habitats become rare or inaccessible to disturbance-adapted species (the *bottlenecks* of Loveless and Hamrick 1988) must have occurred at Grand Sable Dunes during nested landscape changes beginning about 5,500 years ago and continuing into the present.

Repeated episodes of both afforestation and soil burial at Grand Sable Dunes imply varying habitat quality for Pitcher's thistle over late Holocene time. Depending on the magnitude and duration of lake-level changes, open habitats may have been restricted to the bluff edge during low water. During high water, advancing dunes may have limited the extent of intermediate habitat required for the 8- to 10-year life cycle of Pitcher's thistle. The temporal and spatial details of landscape history can be linked

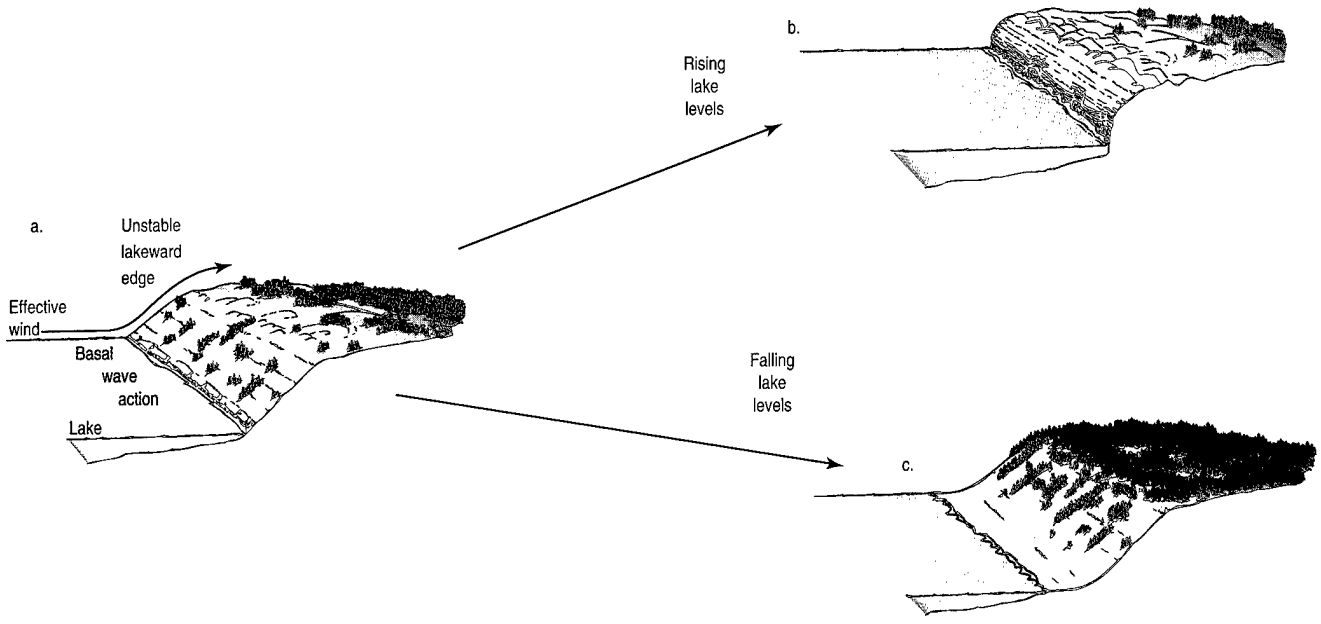

Fig. 5. Drivers of change a) within the modern Grand Sable Dunes, b) under a dune-building future, and c) under a stabilization future.

with species' life histories, which allows for more realistic and spatially explicit population models.

Present successional trends at Grand Sable Dunes seem to be toward increasing forest cover. The landward half of Grand Sable Dunes preserves a record of successional change since the last major destabilization about 500 years before the present; the lakeward half presents a composite picture of changes over the last several hundred years in response to localized changes along the bluff. The same characteristics of perched dunes that make them valuable for studying buried soils and vegetation change over the last 5,000 years also make them valuable for studying recent vegetation trends. The perched dunes are remote from direct wave action and apparently respond only to more sustained changes of lake levels.

Grand Sable Dunes has experienced relative stability for the last 150 years, allowing jack pine to invade portions of the central and eastern dunes. An episode of dune building about 500 years ago buried the red pine and other early successional species that had begun to invade the dunes during a previous stable period. The duration and timing of such episodes have constrained the distribution of dunes-adapted plants during the late Holocene, alternately favoring species adapted to open sites with high sand supply and then favoring those adapted to shaded sites in early stages of succession. These changes in the dunefield habitat mosaic appear controlled by changes in the water levels of Lake Superior.

Regional reconstructions of paleolandscape dynamics have implications for studies of evolutionary ecology of narrowly distributed plants along the shores of the Great Lakes. Current research suggests that the hypothetical multiple successional pathways of Bach (1978) have indeed been a part of the recent history of Grand Sable Dunes. The turnover rate for small patches is presently quite rapid along the lakeward edge of the dunefield and decreases inland. The present turnover rate depends on a relatively low volume of sand along the lake-facing bluff. The sizes, distribution, and turnover rates of patches seem to have changed significantly throughout the late Holocene.

See end of chapter for references

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along the lakeshore. Sand discharged into the lakes from streams and sand moving alongshore near stream mouths form spits and bars that shelter wetlands in drowned river mouths. Some of the best examples of these dunes and drowned river-mouth coastal wetlands occur on the eastern shoreline of Lake Michigan. The larger coastal dunes were formed during periods of higher lake levels that closely followed melting of the ice sheet 10,000–14,000 years ago. Nearly 30% of the globally significant species and communities identified by The Nature Conservancy (1994a) in the basin occur in the coastal shore zone; the coastal dunes alone support more endemic species than any other part of the basin. The unique natural communities of the Great Lakes dunes include the open dunes, the interdunal wetlands, the jack pine barrens, and the sand beaches. The largest dune areas are on Lakes Huron, Michigan, and Superior. Some of the finest dunes occur in the federally owned Sleeping Bear Dunes National Lakeshore and the Indiana Dunes National Lakeshore on Lake Michigan, as well as in the Pictured Rocks National Lakeshore on Lake Superior. Commercial sand and gravel mining is still allowed in some dune areas, and commercial, residential, and recreational developments pose threats in other coastal shore zone areas.

Most of the plants that colonized the dunes came from populations native to the Atlantic coast and to the prairies to the west. Plant species that evolved in the dunes and are unique to them include Pitcher's thistle and Houghton's goldenrod. These two species are federally listed as threatened or endangered. Other unique plant species found in the Great Lakes coastal shore environment include the ram's head lady's slipper and the federally listed dwarf lake iris. The Lake Huron locust, a grasshopper, is also unique to the coastal shore in the basin.

Lake Plains

The lake plains are postglacial Great Lakes lakebeds. They have sandy, silty, or clayey soils, flat topography, and a high water table (The Nature Conservancy 1994a). Sandy ridges marking the locations of previous shorelines are apparent in some areas. At the region's southern end, prairies, savannahs, swamps, wet meadows, sand barrens, and Coastal Plain ponds occupied the lake plains. Most of the prairies, savannahs, and barrens occur near Saginaw Bay on Lake Huron, the Saint Clair delta, and the shores of southern Lake Huron and Lake Michigan and western Lake Erie. In the northern lake plains, fens and wet swales are present in the low areas between old beach ridges. Most of the alkaline shrub–grassland communities (alvars) in the basin occur in the lake plains. During periods of high lake levels, the lake plains probably served as refuge habitat for coastal species and communities that had been displaced by flooding. Groundwater movement and fire probably were important in maintaining savannahs and prairies and the Coastal Plain pond communities. Manipulation of surface- and groundwater movements to aid agricultural development and urban growth has extensively affected the ecosystems of the lake plains,

especially in the southern portion of the basin. Much of the southern lake plain system was developed for agriculture and urban growth, but some large tracts remain near the lakes and on particularly sandy soils. The northern lake plain system is relatively more intact but is vulnerable to development.

The lake plain system supports the largest number of globally significant elements in the Great Lakes basin, and 22% of those restricted to the basin occur only on the lake plains or have their best examples there (The Nature Conservancy 1994a). Globally imperiled species include the eastern prairie fringed orchid and the Karner blue butterfly in the southern lake plain system, and the Michigan monkeyflower and the alvar community in the north. The Michigan monkeyflower is also federally listed as endangered.

Terrestrial Inland

The terrestrial inland system occupies most of the land mass in the region, particularly in that portion lying outside the Great Lakes basin in Minnesota, Wisconsin, and Illinois. The inland terrestrial system is the main catchment area for the region, and its geology, soils, and plant cover determine the basic quality of the surface and groundwaters in the region. The system supports a variety of forest types and most of the region's remaining prairie and savannah lands. Relatively large blocks of public land held by the state and federal governments and managed for recreation or for forest products provide some protection for terrestrial inland systems in northern portions of Michigan, Minnesota, and Wisconsin. In many other areas, however, agriculture, urban development, and construction of highways and recreational homes have fragmented the system, changing the vegetation and making those areas less suitable for use by animals who are intolerant of humans.

Before settlement, most of the region, except the prairie and savannah lands on its western and southern borders, was covered with virgin forest (Fig. 5). By 1920, though, substantial patches of virgin forest remained only in northern Minnesota, Wisconsin, and Michigan (Greeley 1925). Today, the total amount of forestlands in Minnesota, Wisconsin, and

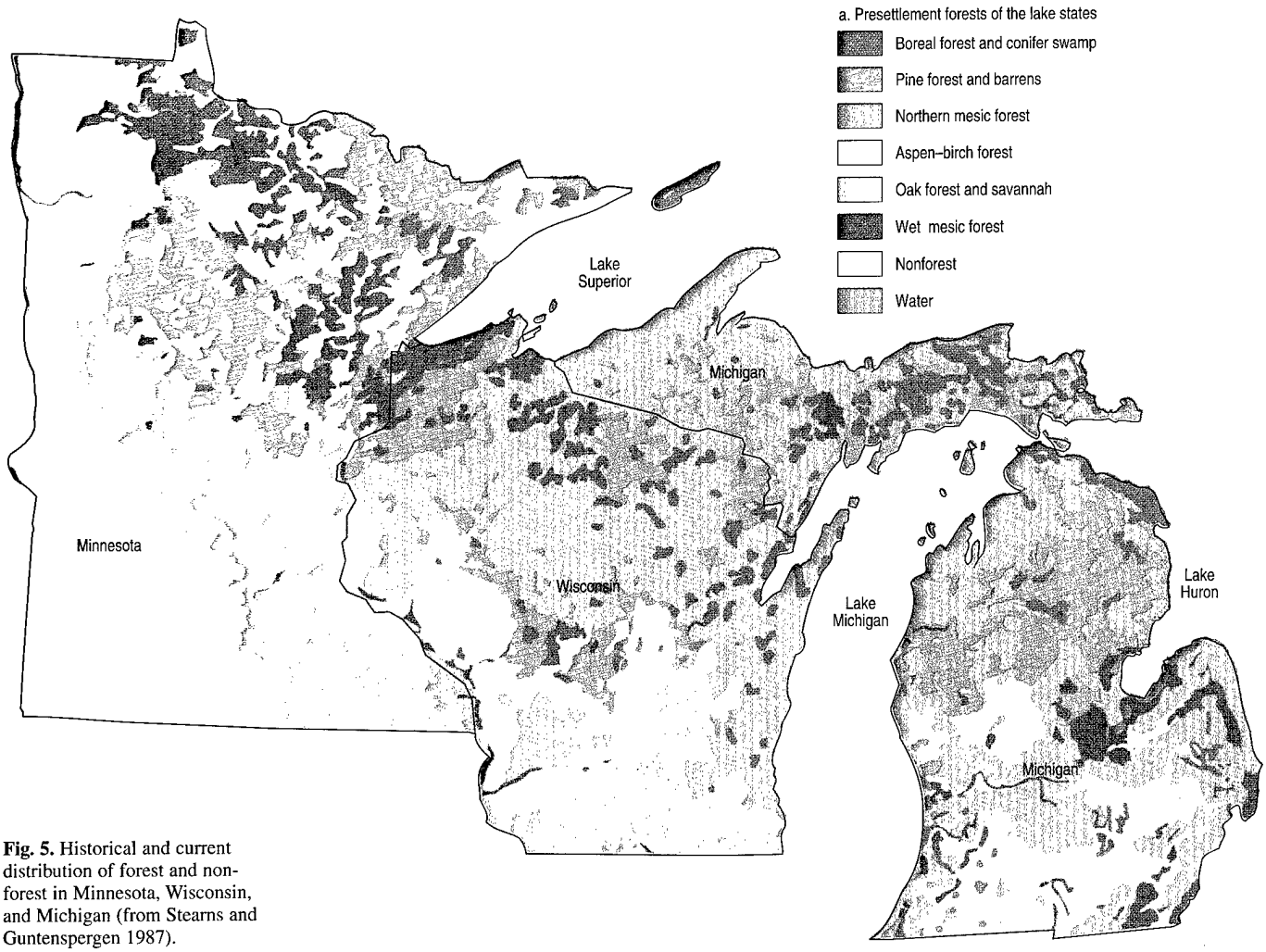


Fig. 5. Historical and current distribution of forest and nonforest in Minnesota, Wisconsin, and Michigan (from Stearns and Guntenspergen 1987).

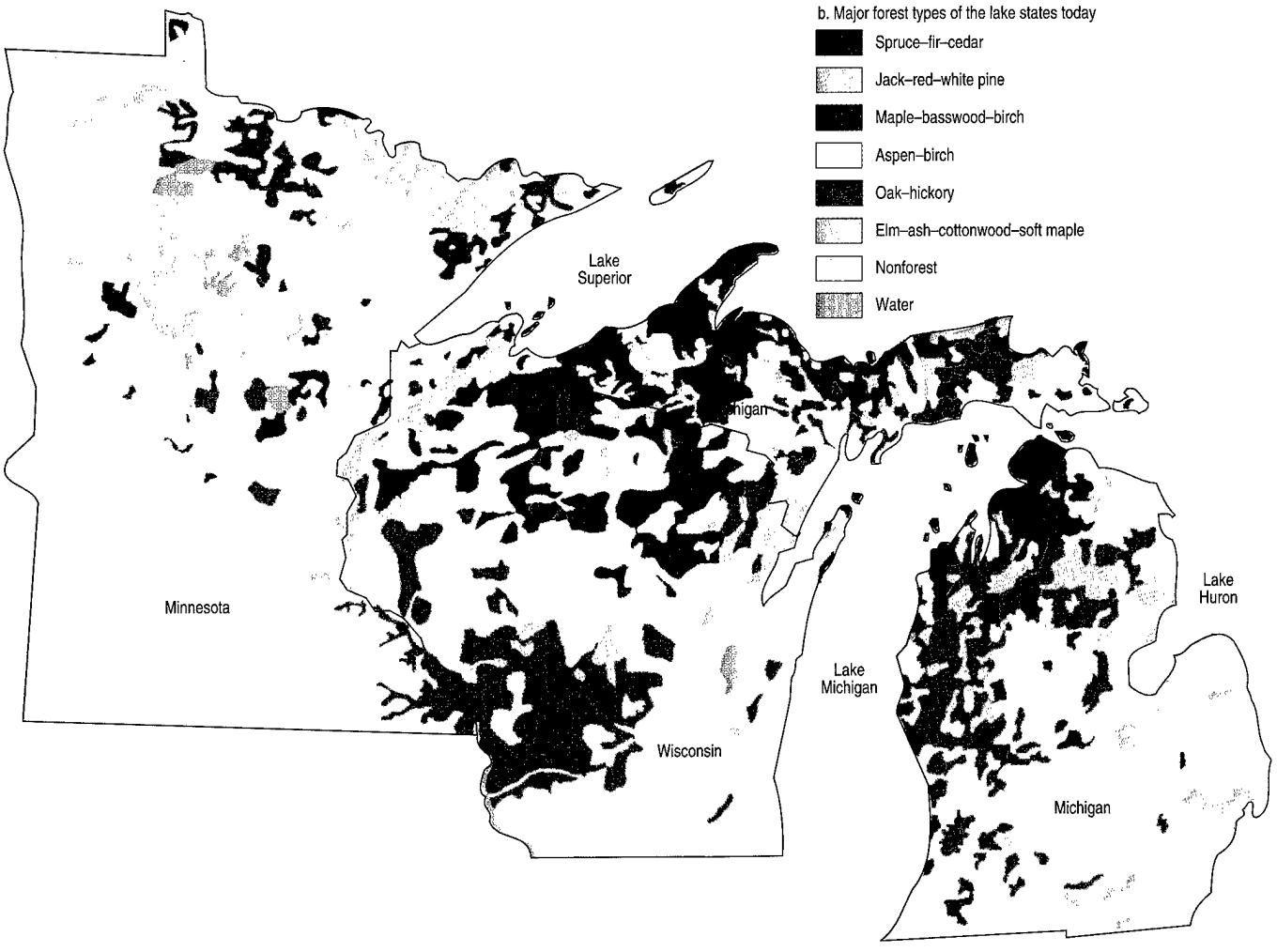
Michigan is substantially less than at the time of settlement, particularly in the southern portions of those states (Fig. 5), and virgin forests occupy only small patches of land in parks and other reserves. The forest in the north has also changed from one dominated by maple–basswood–birch (northern mesic forest), jack–red–white pine (pine forest and barrens), and spruce–fir–cedar (boreal forest and conifer swamp) to one largely dominated by aspen–birch. The large expanses of oak forest and savannah that dominated the southern portions of these three states have also disappeared and are now nonforest, and the area has been converted to other use.

In the Great Lakes basin, only about 8% of the globally significant elements are exclusively or mostly restricted to the terrestrial inland system (The Nature Conservancy 1994a). Still, the terrestrial inland system in the region contains some excellent elements of northern hardwood forest—for example, in the Porcupine Mountains, Huron Mountains, and Sylvania Recreation Area in northern Michigan. Three species of moonwort (a small fern) are globally significant elements in the system. Oak and pine barrens on sandy outwash plains in northern Wisconsin and Michigan are distinct and important community types. Neotropical birds and large mammals are major components of the woodland fauna of the system. In Michigan, the pine barrens support the federally listed Kirtland's warbler. Other federally listed threatened and endangered species that occur in the system include the gray wolf, Indiana bat, bald eagle, and the arctic and American peregrine falcons.

Status and Trends of Plants and Animals

Early Information

The earliest information on the status of the biota and their ecosystems in the Great Lakes region is fragmentary and includes written accounts by the first European explorers and traders. Later records compiled in the 1700's by the Hudson Bay Company and other fur-trading companies showed substantial natural fluctuations in populations of some northern mammals



that frequented the region (Clarke 1954). Information reflecting the status of regional ecosystems and biota during settlement is available from accounts by settlers and early expeditions and resource surveys of the U.S. Government.

The first systematic records of commercial fish production in the Great Lakes were collected in 1867 in Canada and in 1879 in the United States (Baldwin et al. 1979). These records provide an interesting look at the early condition of Great Lakes ecosystems and their fish communities and probably faithfully reflect major declines in abundance of some species that were overfished or subjected to other major environmental stresses brought about by human activities.

Presettlement and later land surveys provided information that has permitted creation of large-scale maps showing the presettlement distribution of regional vegetation and plant community types. Large-scale maps of the vegetation at the time of settlement have been made for most of the region from data provided by either federal land surveys or surveys by the states and others (for example, [Wisconsin] Curtis 1959; [Illinois] Anderson 1970; [Ohio] Hutchins 1979; [Pennsylvania] Brenner 1985; [New York] Andrle and Carroll 1988; [Minnesota] Coffin and Pfannmuller 1988; [Michigan] Albert 1994).

Table 1. Federally listed endangered and threatened plants and wildlife with historical ranges in the Great Lakes region.[a]

Mammals
Indiana bat
Woodland caribou
Gray wolf
Birds
Bald eagle
American peregrine falcon
Arctic peregrine falcon
Piping plover
Least tern
Kirtland's warbler
Freshwater mussels
Clubshell
Winged mapleleaf
Higgins' eye
White cat's-paw
Fat pocketbook
Northern riffleshell
Snails
Chittenango ovate amber snail
Insects
American burying beetle
Hungerford's crawling water beetle
Karner blue butterfly
Mitchell's satyr
Flowering plants
Northern wild monkshood
Mead's milkweed
Decurrent false aster
Pitcher's thistle
Leafy prairie-clover
Minnesota dwarf trout lily
Lakeside daisy
Dwarf lake iris
Small whorled pogonia
Prairie bush-clover
Michigan monkeyflower
Fassett's locoweed
Eastern prairie fringed orchid
Leedy's roseroot
Houghton's goldenrod
Running buffalo clover
Ferns
American hart's-tongue fern

[a]Sources: Coffin and Pfannmuller (1988); Heckert (1991); Cummings and Mayer (1992); Rhodes and Klein (1993); Evers (1994); The Nature Conservancy (1994a); U.S. Fish and Wildlife Service (1994); N. Conrad, New York Natural Heritage Program, personal communication; S. Crispin, The Nature Conservancy, personal communication; T. Freitag, U.S. Army Corps of Engineers, Detroit, Michigan, personal communication.

Contemporary Status and Trends Information

Much of the contemporary status and trends information for the region can be linked to the passage of the Federal Endangered Species Act of 1973 and similar subsequent legislation passed by the states in the region. The federal legislation resulted in the development of lists of species that were, based upon best scientific judgment, either endangered or threatened within the United States. This legislation carried with it provisions for protecting the critical habitat needed to maintain viable populations of the listed species. The federal listings contain species of threatened or endangered plants and animals (U.S. Fish and Wildlife Service 1994) with historical ranges in the Great Lakes states, including 3 mammals, 6 birds, 6 freshwater mussels, 1 snail, 4 insects, 16 flowering plants, and 1 fern (Table 1). Recovery plans (U.S. Fish and Wildlife Service 1992) have been developed for many of these listed species, and substantial progress has been made in restoring some of them to levels of abundance that will permit their removal from the federal lists of threatened or endangered species.

The Great Lakes states developed lists of species that they believed were threatened or endangered in their states. The states also listed communities and ecosystems they believed were threatened or endangered, rare, or otherwise deserving of special attention and protection. These lists (for example, Indiana Department of Natural Resources 1993; [Michigan] Evers 1994; Illinois Endangered Species Protection Board 1994; Minnesota Department of Natural Resources 1994; Pennsylvania Department of Environmental Resources 1994; Wisconsin Department of Natural Resources 1995) are available from the individual states or are in the published literature.

Much of the recent information used by the states to develop and update their listings was collected through Natural Heritage programs (The Nature Conservancy [n.d.]) established in each state. These are independent, cooperating programs that use a technology developed and supported by The Nature Conservancy. The Natural Heritage program staff compiles data from historical records and the literature and conducts field surveys to document locations of rare species and high-quality natural communities. The individual Natural Heritage programs retain precise location data. Global information on species and communities is compiled in and available from The Nature Conservancy data base in Arlington, Virginia. States in the Great Lakes region have some of the largest and most mature Natural Heritage programs and data bases in this network. The first Natural Heritage program in the region was developed in Ohio in 1977 and the last in Illinois in 1987.

The Nature Conservancy Great Lakes Program staff and others in the Great Lakes region recently used the Natural Heritage program data bases prepared by the states to produce a document (The Nature Conservancy 1994a) that provides a basinwide evaluation of biological diversity. The document identifies elements in the U.S. portion of the Great Lakes basin that are of special concern. Each element—including animal and plant species and natural communities—was ranked on a global basis as critically imperiled, imperiled, or rare. The ranking system, which was developed by Natural Heritage scientists and other experts, includes consideration of the world distribution of an element and its occurrence or abundance, health or condition, and vulnerability to disruption or loss. The document comments on the remarkably high biological diversity in the basin and attributes it to the basin's glacial history and to the influence of the Great Lakes on the basin, which together create a diverse and unique environment capable of supporting a diverse biota. Elements judged of greatest concern in the basin were those that occurred only in the basin and whose continued existence there was most in doubt. Elements

whose distributions lie mostly in the basin or whose best examples occur there were also of high concern. Elements with 10%–50% of their known distribution in the basin and those that had 10% or less of their known distribution in the basin were judged of lesser concern. The document identifies 131 globally significant elements, of which 100 are species and 31 are communities. Twenty-two of the 131 were ranked as critically imperiled, 30 as imperiled, and 79 as rare.

Plants and Fungi

Green plants form the foundation of major food chains on Earth by capturing energy from the sun and converting it into organic matter. In the process, they generate the oxygen animals require for respiration. Fungi (molds, lichens, and mushrooms) do not contain chlorophyll but play an equally vital role in the breakdown of organic matter and the recycling of nutrients.

Plants and fungi include the oldest and largest living things on Earth. As such, they contribute to ecological stability in environments where other elements, including most animals, have life spans of less than 1 year. Most woody plants have life spans that are decades long, but some have even longer life spans. For example, individual bristlecone pines as old as 2,435 years have been discovered in rugged habitats in the Rocky Mountains in western North America (Brunstein and Yamaguchi 1992). The quaking aspen, which is the most widely distributed tree in North America (and a common species in the Great Lakes region) has a habit of clonal growth that may qualify it as long-lived (Engle 1991). A grove of aspen may consist of hundreds of trees that are all genetically the same individual, because they are produced from root sprouts of the founding clone tree. Stable clonal groves may reach a hectare in size in the western United States and some may be more than 1,000 years old. Smaller, younger clonal groves are probably more typical of aspen in the Great Lakes region. Fungi also develop underground clonal complexes that are large and long-lived. A clonal mass of the honey mushroom was recently identified in a northern Michigan hardwood forest; it covers more than 15 hectares, weighs more than 10,000 kilograms, and is estimated to be more than 1,500 years old (Smith et al. 1992).

Despite the relative stability of some plants and plant communities, there is clear evidence of major regional changes on a geologic time scale. Changes in vegetation over the past 11,000 years in the eastern United States can be deduced from the pollen grains preserved in the stratified sediments of lakes, bogs, and rivers that have been aged by their carbon-14 content (Webb 1981). Such vegetation changes reflect geological and climatic influences and can be used to trace postglacial changes in climate and to examine changes in animal populations in the Great Lakes region. Contour maps showing the present distribution of spruce, pine, oak, and herbaceous pollen for the Great Lakes region are vastly different from those for the same area 11,000 years ago. The early maps based on pollen evidence show an open spruce woodland with herbaceous ground cover that grew over much of the northern portions of the region. About 10,000 years ago, the forest canopy closed and pine moved westward to replace the spruce. About 9,000 years ago, oak forests gained dominance in southern Michigan, and the prairie moved eastward across Minnesota and into southwestern Wisconsin. By 8,000 years ago, the spruce-dominated woodland had shrunk to a narrow band just in front of the retreating ice front. After the full retreat of the ice sheet from the region 5,000–8,000 years ago, the spruce forests increased both northward and southward, and pine, oak, and prairie all moved westward in the northern Midwest. Conifer–hardwood forests separated the oak-dominated forests from the pine-dominated forests. Finally, the prairie moved westward and reached its present position about 2,000 years ago. These movements reflect both long-term changes in climate established after the final disappearance of the ice sheet from North America and intermittent drought in Minnesota 5,000–7,000 years ago.

The presettlement forest in Minnesota, Wisconsin, and Michigan ranged from boreal, or spruce–fir–cedar, in the north to mesic, or elm–ash–cottonwood–soft maple, in the south. Tallgrass prairie (nonforest) dominated the landscape in western Minnesota and northern Illinois, and oak forest and savannah dominated southern Wisconsin, the southern portion of the Lower Peninsula of Michigan, and northwestern Indiana (Anderson 1990).

Great Lakes vegetation is being studied by The Nature Conservancy and by the Natural Heritage programs supported by Great Lakes states. Trend data are not generally available, but plant listings recently found in the area are being prepared or are available for Illinois, Michigan, Minnesota, and Ohio. The Nature Conservancy and the Natural Heritage network have also collaborated in the production of recent reports describing the biological diversity of the Great Lakes region with emphasis on the region's rare species and plant communities (The Nature Conservancy 1994a,b). Plant communities are emphasized by The Nature Conservancy because species information alone is not sufficient for managing ecosystems to

protect biological diversity. These reports show that the region has many poorly known and interesting species and communities that are unique to the region. Thirty-three rare plant community types in six classes have been listed by The Nature Conservancy (1994b) for the Great Lakes states. These include 6 forest, 12 woodland, 2 shrubland, 2 sparse shrubland, 1 sparsely vegetated, and 10 herbaceous community classes. In addition, 40 rare or imperiled plant species are identified in the basin.

Introduced plant species outnumber all other groups of introduced organisms in the Great Lakes region, but the effect of only a few of these are known (Mills et al. 1993; Edsall et al. 1995). Purple loosestrife has spread throughout the Great Lakes basin and is replacing the cattail and other native plants and is reducing plant and animal diversity in basin wetlands. Eurasian watermilfoil has also had a substantial effect in lakes in the Great Lakes basin. Massive beds of the plant often make boating and swimming impossible and reduce fish and invertebrate populations. Some introduced species of algae have become dominant members of the algal community of the Great Lakes, but their ecological effects are generally unknown. Major nonindigenous terrestrial plants that have become established in the region include garlic mustard in forests, spotted knapweed in prairies, and buckthorn in certain wetlands and upland areas.

Invertebrates

About 90% of the nearly one million species of animals in the world are terrestrial or aquatic invertebrates—animals without backbones. In the Great Lakes region the larger, more easily seen invertebrates include insects and mollusks (snails, mussels, and clams). Insects are the most diverse group of animals (Wheeler 1990), and globally they may have the largest collective biomass of all terrestrial animals (Holden 1989). Some insects are considered beneficial because they pollinate useful plants. Others, like the nonindigenous gypsy moth, which is undergoing a population explosion in parts of the region, are pests. Some insects are terrestrial and others are largely aquatic, emerging from the water only briefly to mate, deposit eggs, and die. There is little status and trend information for most invertebrates in the region (Messer et al. 1991). Taxonomic problems that impede the development of status and trends information for insects are discussed by Hodges (1995).

Lepidoptera

Lepidoptera (butterflies and moths) are among the better-known insects, because most are large, conspicuous, and have aesthetic appeal. The Lepidoptera are the major group of plant-feeding insects, and they are important in plant pollination. Knowledge of the status of the lepidopteran community can reflect the stability and diversity of local plant communities (Powell 1995). There are about 11,000 described species of Lepidoptera in North America, but there is no complete inventory of Lepidoptera species for any state, county, or locality in North America. Compiling an inventory is impeded, in part, by the lack of reliable taxonomic keys. The larger species, including butterflies and larger moths, are well described, but the smaller species are not. In the Great Lakes region, state lists are available for Illinois, Michigan, New York, Ohio, Pennsylvania, and Wisconsin.

Abundance and range data are also scarce for Lepidoptera. The Xerces Society began the Fourth of July Butterfly Count in 1975; the North American Butterfly Association has administered the count since 1993, when participation increased to 209 counts (Swengel 1995). Count data are published annually. Although the data set is still relatively small, it is growing in size and potential utility.

An assessment of the butterfly community of the tallgrass prairie that occupies the western border of the Great Lakes region in Minnesota, Wisconsin, and Illinois and extends into Iowa and Missouri (Swengel and Swengel 1995) revealed about 81,000 individuals of 90 species at 93 sites of 1 to 445 hectares from 1988 to 1993. The species fell into four categories: prairie specialist, grassland, generalist, and invader. The prairie specialists showed a pronounced decline that seemed to persist for 4 years or more after burning of the prairie vegetation. Invaders were most abundant in recently burned areas and least abundant in areas left unburned the longest. Grassland and generalist species were intermediate in their response to fire. Light grazing or mowing every year or two and removal of the cut vegetation seemed to increase butterfly diversity while avoiding the sharp declines noted in some species after a fire. Fragmentation and large-scale destruction of prairie habitat have reduced the habitat available for the prairie-specialist butterflies (Swengel and Swengel 1995), which rarely leave their habitat patches. Fragmentation can lead to small populations, reduced gene flow, local extinctions, and a low probability of recolonization of sites where these butterflies have experienced local extinction.

Despite the major loss of prairie habitat, however, there is cause for optimism. No known prairie butterfly species has yet become extinct, and the potential for management and preservation of habitat required to maintain a high diversity of prairie butterflies is good,

particularly in western Minnesota and adjacent areas to the west of the Great Lakes region. The Karner blue (Fig. 6) and Mitchell's satyr butterflies are the only federally listed threatened or endangered lepidopterans in the Great Lakes region.

Aquatic Insects

Aquatic insects are highly productive, highly specialized animals that represent less than 12% of the total animal diversity in the world (Pennak 1978). About 11,000 species of aquatic insects occur in North America (Merritt and Cummins 1984), many in the Great Lakes region.

The burrowing mayfly is one of the most important and easily identified aquatic insects in the Great Lakes region (Fig. 7). It lives as a nymph burrowed in the stream or lakebed for up to 2 years before emerging as a winged adult. Usually within 2 days after emergence, the mayfly molts, mates, deposits eggs in the water, and dies. The burrowing mayfly nymph eats decaying plant matter and is important in the transfer of energy from the detrital food chain (that is, decaying plants) to fishes, amphibians, reptiles, and birds in the Great Lakes ecosystem.

The best long-term records for changes in the distribution and abundance of the burrowing mayfly in the Great Lakes region are from Lake Erie. Analysis of sediment core samples collected in the central basin of Lake Erie showed that burrowing mayfly larvae tusks (jaw parts) preserved in the sediment provided a useful record of the abundance of the species extending back to about 1740 (Reynoldson and Hamilton 1993). Abundance varied little until about the late 1800's, when the 4,000-square-kilometer Black Swamp at the southwestern end of the lake was drained (Fig. 8). Abundance increased sharply following draining, probably due to temporarily increased nutrient inflow to the lake. In the 1930's, abundance again increased, reflecting a gradual enrichment of the lake as a result of human activities in the drainage area. A sharp decrease in abundance of burrowing mayflies occurred in the central basin after about the early 1950's. This agrees with the decline and near extinction of nymphs that was observed directly in the western basin in 1953 and attributed to anoxic conditions there (Britt 1955a,b). Other pollutants, including metals and oils, have also been shown to reduce the abundance and production of burrowing mayfly nymph populations in the Great Lakes (Edsall et al. 1991; Schloesser et al. 1991). Massive water cleanup efforts beginning in the 1960's sharply reduced the amount of nutrients and toxic pollutants reaching the lake, and there is evidence (Kreiger et al. 1996) that recovery of the burrowing mayfly in western Lake Erie is well under way.

Freshwater Mussels

The United States has the greatest diversity of freshwater mussels in the world (Williams et al. 1992; Williams and Neves 1995). Of the nearly 1,000 species that occur worldwide, about one-third are found in the United States. There are about 50 species of freshwater mussels in the portions of Minnesota, Wisconsin, Illinois, Indiana, Michigan, and Ohio that lie in the Great lakes region (Cummings and Mayer 1992). Freshwater mussels are an important component of the biota in the area. Woodland Indians ate mussels and used their shells as tools and jewelry. Freshwater mussels are also eaten by freshwater drum and wetland mammals, and they are important in the food chains of the region. Historically, freshwater mussels were harvested for their shells, which were cut into buttons. Presently, the shells of harvested mussels are cut into beads that are inserted into oysters to serve as nuclei for cultured pearls.

Freshwater mussels, though, are one of the most endangered groups of animals in North America (Cummings and Mayer 1992). The significant declines in mussel populations that have occurred over the past several decades are attributed to siltation from agriculture, channelization, impoundments, pollution, and competition with nonindigenous species. At the turn of the century, the Saint Clair–Detroit River system and western Lake Erie had 39 species of freshwater mussels—one of the richest known freshwater mussel faunas in North America (Goodrich and van der Schalie 1932). Pollutants entering the Detroit River from the Detroit area in the 1940's and 1950's caused declines in the mussel population downstream from Detroit, but the populations upstream from Detroit in Lake Saint Clair seemed to have been largely spared. In the early 1990's, however, the native mussel populations declined rapidly when the zebra mussel, an invading species from Eurasia, appeared (Schloesser and Nalepa 1995). By 1992 native mussels were virtually or totally extirpated from southern Lake Saint Clair and the offshore waters of Lake Erie. The zebra

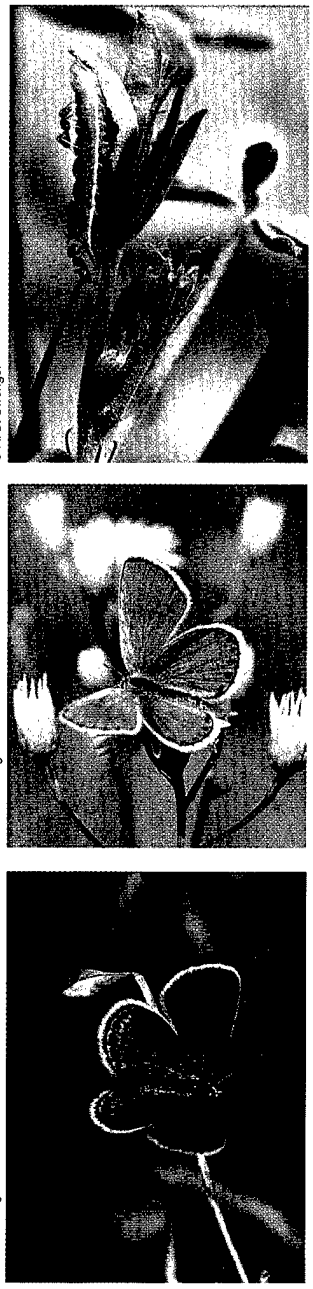


Fig. 6. Karner blue butterfly larva on lupine with tending ants (top), adult male, and adult female (bottom).

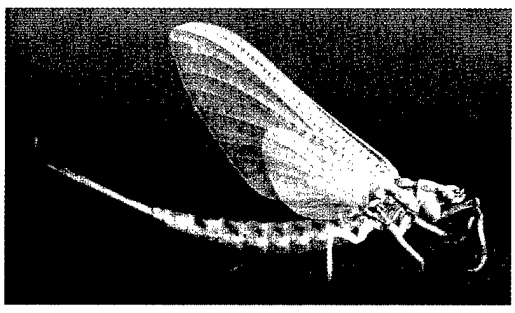


Fig. 7. Adult burrowing mayfly.

Courtesy M. Steingraeber, U. S. Fish and Wildlife Service

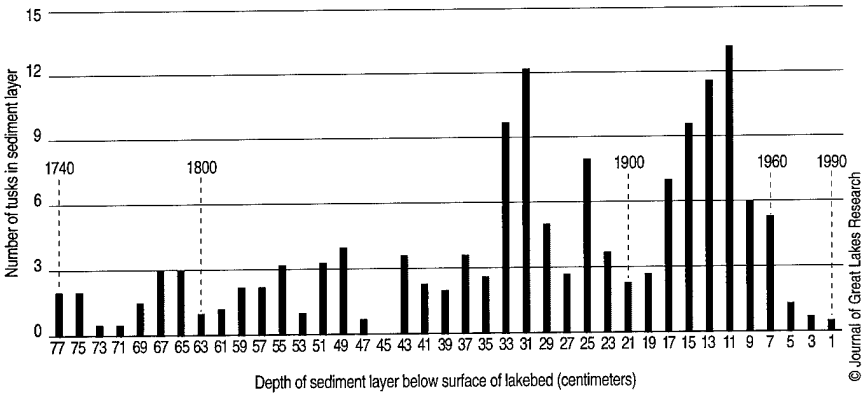
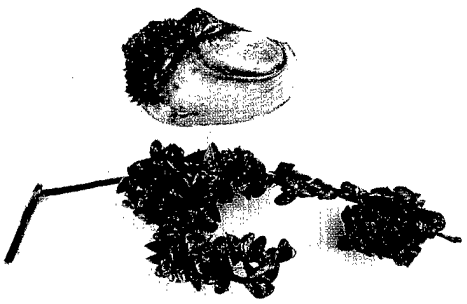


Fig. 8. Abundance of burrowing mayfly nymphs in central Lake Erie from about 1740 to 1990. Abundance was determined from counts of preserved mayfly tusks (jaw parts) in stratified and dated sediment core samples. Draining of the Black Swamp in the late 1880's increased nymphal abundance as shown in sediment layers 33–25 (after Reynoldson and Hamilton 1993).

mussel kills the native mussels by attaching in large numbers to native mussel shells (Fig. 9), causing them to suffocate or starve. Attachments averaging 7,000 zebra mussels per native mussel have been reported (Schloesser and Kovalak 1991; Nalepa and Schloesser 1992).

There are presently six species of federally listed endangered mussels in the region (Table 1). The last known world population of white cat's paw pearlymussels occurs in a tributary of the Maumee River, which enters Lake Erie near Toledo, Ohio.



Courtesy D. Schloesser, USGS

Fig. 9. Native Great Lakes mussel and small, woody debris with heavy infestations of zebra mussels.

Fishes

The fish fauna of the Great Lakes basin is relatively large and diverse, despite the northerly location of the lakes at 40°–50°N latitude and the relatively short time for colonization following the retreat of the glaciers from the region (Bailey and Smith 1981). The native fish fauna of the basin is composed of 153 species in 64 genera and 25 families. The Nipigon system in Canada, which is tributary to the northeastern end of Lake Superior, contains substantially fewer species than the other five systems (Table 2); this probably reflects the shorter growing season and the lower diversity of habitats in the Nipigon system relative to the other systems to the south. The Saint Clair system also has a relatively low number of species, probably because it is small and supports only warmwater species during much of the year.

Some debate has occurred about the origins of the fish fauna that colonized the Great Lakes basin. At different times during the last glacial period, the outlet of the Great Lakes basin connected with the Mississippi River drainage and thus with glacial Lake Agassiz to the northwest, the central United States, and the coast of the Gulf of Mexico. On more than one occasion the outlet also connected with the Northeast and the Atlantic coast via the Saint Lawrence River drainage. Some scientists (for example, Hubbs and Lagler 1964) believed that the fishes that colonized the Great Lakes after the last glaciers retreated came from ice-free areas to the northwest of the basin. More recent analysis suggests that the species present in the basin at the time of European settlement basically entered from the Atlantic and Mississippi

Table 2. Number of fish species in the Great Lakes basin by drainage system component (after Bailey and Smith 1981).

System	Number of species		
	Lake	Tributaries	Both
Nipigon	-	-	40
Superior	53	82	135
Michigan	91	135	226
Huron	90	113	203
Saint Clair	-	-	108
Erie	106	125	231
Ontario	95	125	220

drainages at various times in the last 14,000 years. Thirty-six species may have entered the Great Lakes basin from the Atlantic drainage, 134 from the Mississippi drainage, and 22 from both drainages. These species and their origins are detailed in Bailey and Smith (1981).

The whitefishes are a major element of the native coldwater fishes of the Great Lakes and require special mention here. At the time of European settlement, whitefishes were abundant and ecologically important as food for lake trout and burbot and as food for humans. As many as 40 species and subspecies of ciscoes (whitefishes most closely related to the lake herring) were identified by biologists working in the basin. Most of the whitefish group probably evolved locally; there are no records for any of them, other than the lake herring, from outside the basin. Bailey and Smith (1981) present evidence that the reproductive isolation (absence of interbreeding) that had developed among these species and subspecies over the 10,000 years was unstable and broke down as populations were reduced by commercial fishing and predation by the sea lamprey. Interbreeding among the survivors then caused their offspring to become genetically more

Sea Lamprey in the Great Lakes

The sea lamprey is an invading nonindigenous species that has had an immense impact on fish communities, fisheries, and fishery management in the St. Lawrence River and the Great Lakes of North America. Native to the Atlantic Ocean, sea lampreys probably entered the Great Lakes via the Hudson River and its artificial extension, the Erie Canal, which was opened to Lake Ontario in 1819 (Fig. 1).

Adult sea lampreys, which are shaped like eels, feed by attaching on other fish with their suctorial mouths and extracting blood and other body fluids from the fish. Each sea lamprey may kill as much as 18 kilograms of fish during the 12–20 months of its adult life. The sea lamprey gained access to Lake Erie when the Welland Canal around Niagara Falls was completed in 1829, but they were not noted in Lake Erie until 1921, almost a century later. Thereafter, the invasion quickened; sea lampreys were found in Lake Huron in 1932, in Lake Michigan in 1936, and in Lake Superior in 1946.

Life Cycle

Sexually mature sea lampreys, which are about 46 centimeters long, ascend the tributaries of the Great Lakes in the spring and summer to seek stony, gravelly riffles where they excavate redds, saucerlike depressions that serve as nests. Mating takes place on the redd, where individual females deposit up to 60,000 eggs each. Luckily for the lamprey's prey, the adult dies after spawning. The eggs hatch into larvae, barely visible to the naked eye. These larvae are blind, toothless, and have a fleshy hood overhanging the mouth. For several years the larvae live as filter feeders in burrows they construct in soft sediments of the tributaries. Larvae later transform (metamorphose) into free-swimming juveniles. Transformation involves the disappearance of the hood, the emergence of eyes, and the development of teeth on the tongue and the sucking disk, which surrounds the mouth (Fig. 2).

These *transformers*, silvery in color and about the size of a 13- to 15-centimeter-long pencil, move downstream to the Great Lakes, where they quickly attach to prey fish. The duration of attachment varies, but the site of attachment on the fish's body, the time of year, and the size of the sea lamprey relative to the size of its prey determine whether the attack will be fatal to the prey fish. Captured lake trout sometimes bear wounds and scars indicating that they have survived several attacks by small sea lampreys (Fig. 3). Over their 12–20 months of predatory existence, sea lampreys mature sexually and then repeat the life cycle.

Effects on the Fisheries

Commercial fishermen on Lakes Huron and Michigan went through the grim experience of seeing increasing numbers of sea lamprey wounds on their catch (Fig. 4). Storms also rolled growing numbers of lamprey-killed lake trout into bottom net sets. At the same time the combined annual catch of lake trout, which had averaged 5.9 million kilograms, declined sharply. Despite this alarming decline in lake trout abundance, fishermen tried to maintain the level of their catch because of the food shortage created by World War II and because of their fear that sea lamprey would kill all the lake trout anyway.

The lakewide decline of the fishery in relation to the invasion of sea lamprey was best documented in Lake Superior, where lake trout production held at 1.8 million kilograms from 1930 to 1952. In the following decade, though, production dropped 90%, while the number of sea lampreys caught in a fixed number of assessment weirs rose from 1,000 to 70,000.

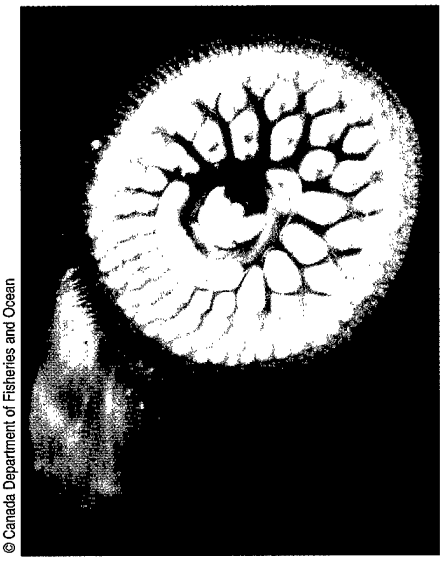


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Fig. 2. The mouth of an adult sea lamprey.

Courtesy USGS

Fig. 3. Sea lampreys attached to a lake trout.

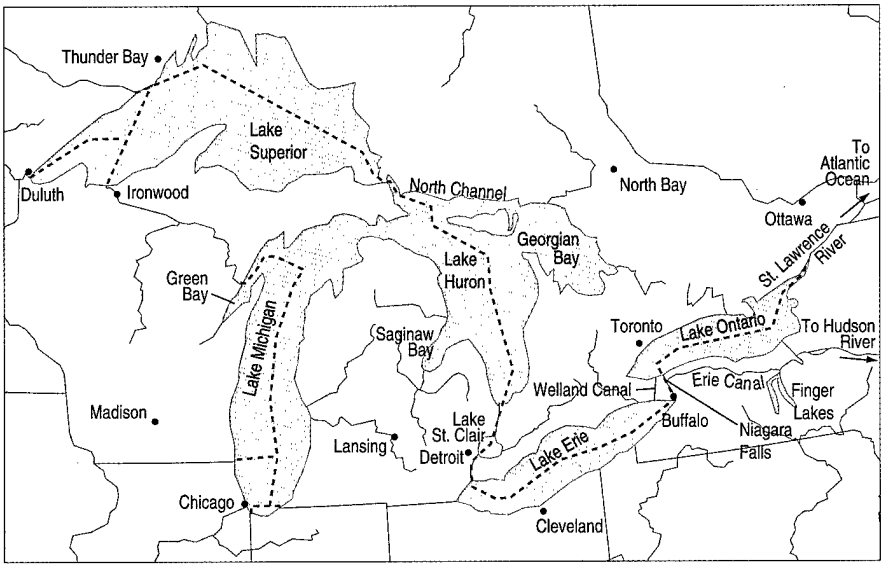

Fig. 1. Jurisdictional boundaries in the Great Lakes. The boundary between Ontario and various states is also the international boundary between Canada and the United States. The natural and artificial waterways between the lower lakes and the Atlantic Ocean are also shown.

Fig. 4. Lake trout with wounds caused by sea lamprey attacks.

Lake trout were the favorite prey of sea lampreys and were also the top predator in the Lake Superior system. As the number of lake trout dropped, the sea lamprey turned to preying on lake whitefish and other members of the whitefish family, the chubs and lake herring. As the top predator in Lakes Huron and Michigan was eliminated, the population of another invader from the salty Atlantic, the predatory alewife, exploded. Alewives became very abundant, and though they were vulnerable to massive spring die-offs, they had adverse effects on many valuable native fish species.

Early Control Efforts

In 1948 a committee representing the governments of the United States and Canada, eight U.S. states, and Ontario—the jurisdictions bordering the Great Lakes (Fig. 1)—was established to begin a sea lamprey control program. The U.S. Fish and Wildlife Service, the state of Michigan, and the province of Ontario led research in defining the life history and distribution of sea lampreys and installing and testing physical barriers designed to prevent sea lampreys from entering streams to spawn. Very early in the program, the committee decided that a chemical selectively more toxic to sea lamprey larvae (lampricide) in streams than to nontarget fishes and other aquatic organisms would be invaluable. The U.S. Fish and Wildlife Service intensively screened some 6,000 chemicals in laboratory tests over 7 years before TFM™ (3-trifluoromethyl-4-nitrophenol) and Bayer™ 73 (2',5-dichloro-4'-nitrosalicylanilde) were chosen for field testing. These effective chemicals are still the major control agents today.

An International Commission

Meanwhile, Canada and the United States realized that to control and manage the sea lamprey and rebuild the Great Lakes fishery, coordination and stable, adequate funding were needed. Thus, the Convention on Great Lakes Fisheries was ratified in 1955, and the Great Lakes Fishery Commission was formed and charged to improve the fisheries, develop and coordinate research, advise governments, and control the sea lamprey. The commission assumed responsibility for ongoing sea lamprey control programs and selected the U.S. Fish and Wildlife Service and the Canadian Department of Fisheries and Environment as its agents to carry out sea lamprey control and research.

Further Control Efforts

By 1959 mechanical weirs and electrified barriers were installed in 135 Great Lakes tributaries. These devices, which contained traps, were generally effective at preventing sea lampreys from reaching spawning areas and also provided information on the number of sea lampreys in the area. During high water and power failures, though, sea lampreys could bypass these devices. Both systems were gradually phased out. The use of electricity was abandoned in the late 1970's, and research into effective electrical blocking systems was delayed by many years. The mechanical barrier program has since been refined and enlarged.

Subsequently, the commission concentrated on chemical control programs, which experienced great success following initiation of chemical treatments in all the lakes (Fig. 5). Information for Lake Michigan, where chemical treatment started in 1960, has not been summarized, but it followed a pattern similar to that of Lake Huron in the early years of treatment (1960–1982; see Lake Huron graph in Fig. 5). Lamprey numbers have increased recently in Lake Michigan, but not nearly as dramatically as in Lake Huron.

Since 1975 the commission, concerned that the control program was overly dependent on chemicals, has emphasized that the chemical control program alone can never bring the sea lamprey under complete control. The success of the chemical applications and the development of a world-class recreational fishery, though, have led the public and the U.S. and Canadian governments to consider the lamprey problem in the Great Lakes solved. Thus, funding for research that was needed to investigate supplemental and alternative control methods, and even funding for maintenance of control programs, was curtailed. The sea lamprey control program directly benefited the fishery and therefore was better funded than the research program.

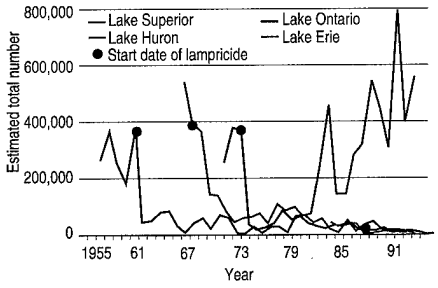

Fig. 5. Numbers of feeding-phase sea lamprey in Lakes Superior, Huron, Erie, and Ontario before and after initiation of lampricide applications in tributaries. Dot indicates start date of lampricide use (G. Christie, Great Lakes Fishery Commission, Ann Arbor, Michigan, unpublished data).

In 1982 the commission began applying integrated pest management concepts to sea lamprey management. Concern about the introduction of chemicals into the environment has led the commission to fund extensive testing of the environmental safety of lampricides. Although no long-term detrimental effects to the ecosystem have been detected, public apprehension about pesticides is a compelling reason to seek alternatives to lampricides. Therefore, the commission's integrated management of sea lamprey includes establishing target levels of sea lamprey abundance (Fig. 6) and reducing lampricide use by 50% by the year 2000 (Great Lakes Fishery Commission 1992). The sea lamprey controls now in use include low-head barrier dams, stream velocity barriers, safer and more effective electrical barriers, mechanical trapping, and the

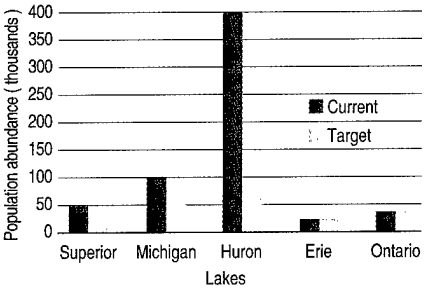

Fig. 6. The 1995 status of sea lamprey populations in the Great Lakes and control program targets for sea lamprey suppression (G. Christie, Great Lakes Fishery Commission, Ann Arbor, Michigan, unpublished data).

release of sterile male sea lampreys, which compete with normal males for mates but produce no offspring. The development of spawning attractants and repellents, which took a large part of the research budget for several years, has not yet yielded a useful control tool.

The St. Marys River, which connects Lake Superior and Lake Huron, contributes an estimated 400,000 sea lampreys a year to Lake Huron, with disastrous effects on the lake trout population there (Figs. 5 and 6). Although a multiphase attack program on sea lampreys spawning in the St. Marys has been developed, it may not be implemented soon.

Rebuilding the Great Lakes Fishery

As sea lampreys became sufficiently controlled, Ontario, state, and U.S. Fish and Wildlife hatcheries produced large numbers of lake trout for stocking. These hatcheries, though, were unable to produce enough fish to fully take advantage of the carrying capacity of the lakes with their huge populations of forage fish. After evaluating the opportunity, the Michigan Department of Natural Resources introduced chinook salmon and coho salmon, which can be grown in hatcheries to stocking size in greater numbers and in shorter times than lake trout. The salmon were first stocked in Lake Michigan, where they survived in excellent numbers, grew quickly on a diet of alewives, were relatively resistant to lamprey attack, and provided an excellent offshore and inshore recreational fishery. Other states around the lakes soon followed Michigan's lead.

Thus, the fishery has been rebuilt through sea lamprey control, water-quality improvement, habitat protection, stocking, establishment of sanctuaries, and enforcement of regulations. At the fishery's peak in the mid-1980's, the annual regional economic effect of the commercial fisheries was estimated at $270 million, and that of the recreational fisheries at $2.0–$4.0 billion (Talhelm 1988). Some 55 million angler-days were spent in pursuit of Great Lakes fish annually, and the fishery-related industries provided employment for between 37,500 and 75,000 people.

The commercial catch of lake whitefish, a valuable species that was also decimated by the sea lamprey, is at historic levels. Lake trout populations have been declared recently to be self-sustaining in Lake Superior, and natural reproduction is finally occurring in the other lakes. Alewife populations are under control, and native species of forage fish are rebuilding. Keeping sea lamprey populations at levels that allow adequate survival of desirable fish communities seems to be the key to success. With adequate funding for current control strategies and further research into innovative alternative control techniques and their application, further declines in sea lamprey populations seem achievable and economically feasible.

See end of chapter for references

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alike. Today the ciscoes are represented only by the lake herring and one to three other closely related deepwater species or subspecies that are extinct, approaching extinction, or simply merging their genetic identities by interbreeding. Similar evolution of subspecies also occurred in lake trout in the Great Lakes proper (Brown et al. 1981; Goodier 1981; Goodyear et al. 1982; Krueger and Ihssen 1995) and in New York's Finger Lakes, which are in the Lake Ontario drainage (Royce 1951).

At least 25 nonindigenous fishes have become established in the Great Lakes since the region was settled, and nearly half of them have had substantial ecological and economic effects (Bailey and Smith 1981; Mills et al. 1993; Edsall et al. 1995). The sea lamprey, a marine species, contributed to the loss of native Atlantic salmon and lake trout in Lake Ontario. Sea lamprey probably entered Lake Ontario from the Hudson River via the Erie Barge Canal, which was opened to barge traffic in 1819 and connects the Hudson River and Lake Ontario drainages via Lake Oneida. Sea lamprey later moved into the upper four Great Lakes, probably through the Welland Canal, which allows ships to go around Niagara Falls. In the upper four lakes, sea lamprey contributed directly to the decline of lake trout and several other large fish species that supported the sport and commercial fisheries of those lakes. Millions of dollars are now spent annually on sea lamprey control in an effort to restore the damaged fish populations.

The alewife is another nonindigenous marine species that has become established in the Great Lakes. It was present in Lake Ontario in 1873 and probably entered the lake and spread throughout the rest of the basin following the same route used by the sea lamprey. It reached Lake Michigan in 1949 (Smith 1972) and by the 1960's had caused major changes in the plankton community (Wells 1970). The alewife also suppressed the native whitefishes, yellow perch, emerald shiner, deepwater sculpin, and spoonhead sculpin, probably through predation on the youngest life stages and competition with the older life stages (Potter and Fleischer 1992). The alewife also may have suppressed the rainbow smelt, a nonindigenous marine forage species that had been deliberately introduced into the Great Lakes in the early 1900's to provide forage for trout and salmon. Researchers generally believe that the alewife would not have reached such high levels of abundance and dominated the fish community in any of the Great Lakes if the large, native predatory fishes had not been destroyed by overfishing and predation by sea lamprey. Eventually, though, the alewife became a major prey species for trout and Pacific salmon and

was considered a beneficial addition to the forage base. Recent information (Fisher et al. 1995a,b), however, shows that an enzyme carried by the alewife destroys vitamin B_1 in Atlantic salmon that eat alewives. Thus, female Atlantic salmon that feed extensively on alewives become B_1-deficient, and the fry that hatch from their eggs die when they are only a few weeks old. Consequently, the invasion of the Lake Ontario drainage by the alewife is strongly implicated in the extinction of the native populations of Atlantic salmon there in the 1800's. The alewife can also cause B_1 deficiency in lake trout and may contribute to the general failure of stocked lake trout to reproduce in Lakes Michigan, Erie, and Ontario, where the alewife is a major food of lake trout (Fisher et al. 1996).

The nonindigenous blueback herring, a marine species closely related to the alewife, is one of the newest additions to the fish fauna of the Great Lakes. This species was recently documented entering the Lake Ontario drainage from the Hudson River via the Erie Barge Canal (L. R. Wedge, New York Department of Environmental Conservation, personal communication)—the same entry route postulated for the sea lamprey and the alewife. This species' effect on the Great Lakes fishes and ecosystems is expected to be similar to that of the alewife, which it closely resembles.

The ruffe, a small perchlike fish from Eurasia (Fig. 10), is another recent addition to the Great Lakes. In the early to mid-1980's it reached the Saint Louis River estuary in Lake Superior via ballast water (Simon and Vondruska 1991; Pratt et al. 1992). Ruffe abundance increased sharply in 1993, and the species spread to other parts of the lake. Yellow perch numbers in the Saint Louis River estuary declined markedly as ruffe abundance increased. Researchers are concerned that similar declines could occur elsewhere in the Great Lakes if the ruffe expands its range and competes with yellow perch for thermal habitat (Edsall et al. 1993) and food (Ogle et al. 1995). The ruffe could potentially occupy nearly 7 million hectares of habitat in the Great Lakes that is presently suitable for use by yellow perch (Edsall et al. 1993). In 1995 two ruffe were captured in Thunder Bay, Lake Huron, near Alpena, Michigan.

Courtesy T. Edsall, USGS

Fig. 10. The ruffe, a small, perchlike Eurasian fish that recently became established in the western end of Lake Superior.

Round and tubenosed gobies are also among the recent ballast-water additions to the Great Lakes. They were first reported from the Saint Clair River in 1990 (Jude et al. 1995). They are expected to compete strongly with native sculpins and other small, bottom-feeding fishes and are considered highly undesirable additions to the region.

The successful stockings of Pacific salmon, rainbow trout, and brown trout in the Great Lakes during the present century had profound and largely beneficial ecological and economic effects on the region. They are large predators that feed extensively on the introduced alewife and rainbow smelt. They also support popular fisheries that contribute significantly to the Great Lakes fishery, which is valued at more than $6.8 billion annually (U.S. Fish and Wildlife Service 1995). There are self-sustaining populations of these fishes in some areas, but in most areas stocking substantially augments the naturally produced fishes.

Status and trend information is available for a number of fishes commonly found in the Great Lakes. The longest set of records is for fish species that were of commercial value and entered the commercial catch. The commercial fishery in the Great Lakes dates back to the 1700's in some areas, but the earliest records are fragmentary or anecdotal and are not useful for demonstrating trends. Continuous records of the commercial fishery in the Great Lakes began in 1867 in Canada and in 1879 in the United States (Baldwin et al. 1979). Because the records do not report the amount of fishing effort expended to catch fishes or the amounts of some fish species that were caught but not brought to land for sale, they must be interpreted carefully. The records for the high-value, intensively fished species like the lake whitefish probably fairly reflect the trends in abundance, whereas records for low-value species like freshwater drum do not. Freshwater drum were often taken incidentally in large numbers in nets set for other high-value species such as yellow perch and walleye. The market price for freshwater drum and the size of the catch of high-value species made by the individual fisherman on any given day probably determined how many freshwater drum were brought ashore for sale and how many were simply dumped back into the lake. Thus, the records for freshwater drum and other low-value species are generally not good indicators of abundance trends. There were, however, periods in particular areas or lakes when the high-value species had been fished to extinction or near extinction, and the only species left to catch were those of low

value. In those situations, the records for the low-value species probably more closely reflect actual trends in abundance.

If these caveats for interpreting the catch data are applied, the history of the early commercial fishery in the Great Lakes can be seen as one of intensive, selective fishing that eventually caused stocks of high-value species to decline and, in some cases, to become extinct.

The lake sturgeon (Fig. 11), a long-lived species that does not reproduce until it is about 25 years old, was one of the first species to approach extinction in the Great Lakes. Annual catches in the U.S. waters of Lake Erie fell from an all-time high of 2.1 million kilograms in 1885 to about 13,000 kilograms in 1917 (Fig. 12). Thereafter, catches never exceeded 10,000 kilograms, and after 1966 the catch fell to zero. Early in the fishery the lake sturgeon was considered a nuisance species because it destroyed nets set for other smaller fish. Later, as markets developed, it became a sought-after species. The construction of dams that denied the lake sturgeon access to its spawning grounds in Great Lakes tributaries also helped accelerate its decline.

The blue pike, another high-value species, was lost to overfishing. Annual catches as high as 9 million kilograms occurred in the mid-1930's in the U.S. waters of Lake Erie, but by the early 1960's the species had been fished to extinction (Fig. 13). The walleye, a closely related species, was also severely overfished in Lake Erie. Catches declined from annual highs of about 2.3–2.8 million kilograms in the late 1940's–late 1950's to about 25,000 kilograms in 1971. The decline was largely attributed by commercial fishing interests to deteriorated environmental conditions. Closure of the fishery because of mercury contamination in the early 1970's, followed by the imposition of more stringent catch regulations, allowed walleye numbers to rapidly increase, and the species again supports a healthy, self-sustaining, and high-value fishery.

High-value coldwater fishes that declined to virtual extinction in all or some of the Great Lakes include the lake trout, lake whitefish, and lake herring. Native populations of lake trout were nearly extinguished in the Great Lakes as a combined result of overfishing and predation by the introduced sea lamprey. The native lake trout populations in Lakes Michigan, Erie, and Ontario were lost, and only a small population survived in a remote area of Lake Huron. In Lake Superior, the nearshore populations of native fishes were sharply reduced by the late 1950's when commercial fishing ended and the sea lamprey was controlled. Lake whitefish populations reached record lows during the 1950's and the 1960's in Lake Huron and in the 1950's in Lake Michigan but have since recovered. In Lake Erie, for example, the U.S. catch fell gradually from a high of 1.6 million kilograms in the late 1800's to zero in the early 1960's, although a recovery may have begun in the late 1980's (Fig. 14). In the U.S. waters of Lake Huron and in Lake Michigan, the catch of lake herring fell to zero in the 1970's. Catches also fell to record lows in Lake Superior in the 1970's. These declines in lake herring populations have been attributed to overfishing and predation of young lake herring by rainbow smelt.

The more recent records of commercial catch in the Great Lakes have not been published but are available from the U.S. Geological Survey, Biological Resources Division. The commercial fishery in the U.S. waters of the Great Lakes is presently quite restricted. Better information on the status and trends of Great Lakes fish populations is now compiled annually for each of the lakes by committees whose memberships represent biologists and managers from the Great Lakes states, the Province of Ontario, Department of Fisheries and Oceans—Canada, the U.S. Geological Survey, and the Native American tribes with treaty fishing rights. These reports reveal the following major trends.

In Lake Superior, the lake trout fishery is presently maintained by stocking and by natural reproduction from wild fishes (Hansen 1994).

Fig. 11. Biologist with a lake sturgeon. The largest lake sturgeon caught in the Great Lakes weighed 140 kilograms.

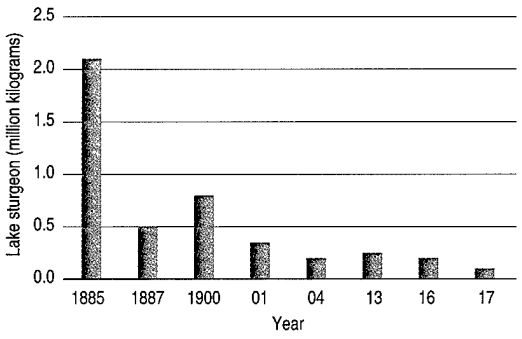

Fig. 12. Commercial catch of lake sturgeon in U.S. waters of Lake Erie, 1885–1917 (Baldwin et al. 1979).

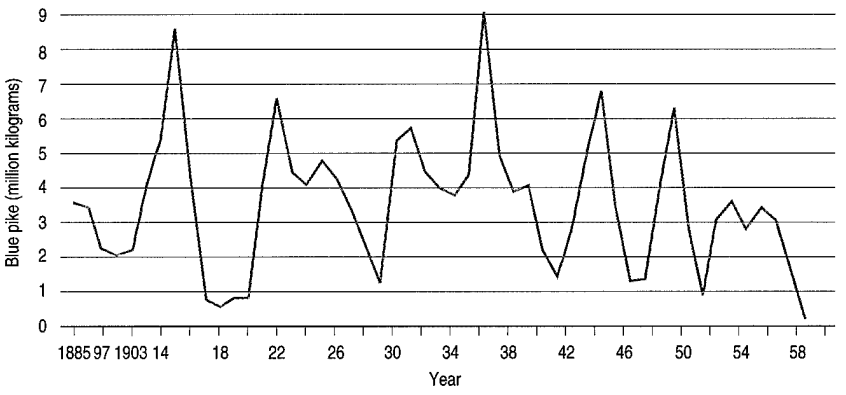

Fig. 13. Commercial catch of blue pike in U.S. waters of Lake Erie, 1885–1960 (Baldwin et al. 1979).

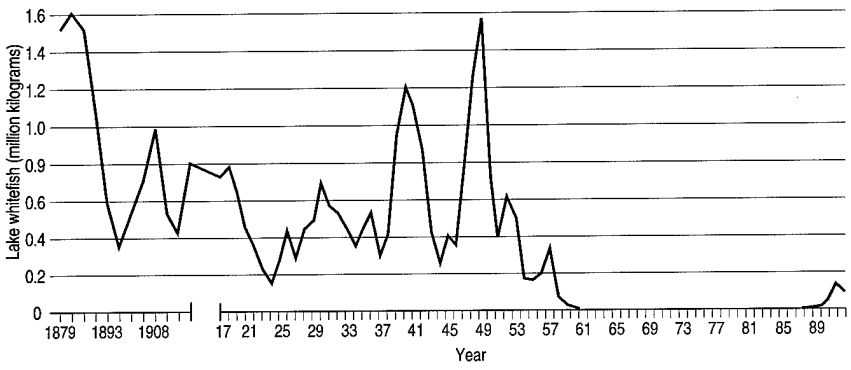

Fig. 14. Commercial catch of lake whitefish in U.S. waters of Lake Erie, 1879–1992 (Baldwin et al. 1979).

Introduced species of trout and salmon support a stable fishery, whereas brook trout and lake sturgeon populations have not recovered from earlier exploitation and are still at low levels. Lake herring numbers are recovering strongly and rainbow smelt are reduced from earlier levels of peak abundance. Deepwater cisco populations have declined, and lake whitefish are abundant and support a productive fishery. The sea lamprey is reduced to about 10% of its former peak abundance, but the ruffe is increasing in abundance.

In Lake Huron, the fish community is recovering but remains unstable after decades of overharvest and the effects of introduced species (Ebener et al. 1995). Modest numbers of stocked lake trout are once again reproducing in the lake, and populations of lake whitefish and deepwater ciscoes are more abundant than at any other time in this century. Walleye and yellow perch are once again abundant. Rainbow smelt and alewife populations are stable but are still reduced over former peak levels in the 1970's. In the 1980's, the sea lamprey increased in abundance in the northern end of the lake, imposing high mortality and reversing recent gains in lake trout restoration in that area.

In Lake Michigan, substantial numbers of stocked, breeding-age lake trout are present in lake trout refuges at several locations throughout the lake (Holey et al. 1995). Spawning and fry production by stocked fish have been recorded at several locations in the lake, and wild yearling and older lake trout have been found in the lake, but substantial numbers of adult wild fish have not been produced. Pacific salmon abundance is sharply reduced over peak levels reached in the 1970's to the mid-1980's. The causes for the decline are complex and not fully understood. Mortality of coho salmon fry soon after hatching has been observed. This mortality can be alleviated by treatment with vitamin B_1, suggesting there is a vitamin B_1 deficiency in the female parent that causes mortality in the fry. Mortality of adult Pacific salmon in the lake is correlated with an incidence of bacterial kidney disease, a pathogen that has been introduced to the Lake Michigan basin. A linkage between virulence of the pathogen and nutritional status of the salmon is being investigated.

The biomass (a measure of abundance expressed as weight) of the three major prey fishes in Lake Michigan has changed significantly since the early 1970's (U.S. Geological Survey, Biological Resources Division, unpublished data). Alewives made up more than 80% of the biomass in catches in the 1970's but declined to about 10% in the mid-1980's–1990's. The biomass of bloaters, a deepwater cisco, increased from less than 10% in the 1970's to more than 80% in the 1980's–1990's, and rainbow smelt decreased from 15%–20% in the 1970's and early 1980's to less than 10% in the mid-1980's and 1990's. Deepwater sculpins were abundant in the late 1970's and the early 1980's but then declined sharply in the 1990's, perhaps in response to competition from the increased biomass of bloaters and to predation by burbot, which have increased substantially in abundance since 1984. Slimy sculpin abundance peaked in the late 1970's but in the 1980's–1990's declined to less than 20% of peak 1970's levels, probably in response to predation by trout, salmon, and burbot.

In Lake Erie, lake trout restoration goals are being met and lake whitefish are showing signs of a recovery (Great Lakes Fishery Commission 1995a). Walleye and yellow perch are intensively managed to provide productive recreational and commercial fisheries in the United States and Canada (Great Lakes Fishery Commission 1995b). The abundance of the major forage fish species in Lake Erie—rainbow smelt, spottail shiners, emerald shiners, gizzard shad, and alewives—seems to be declining.

In Lake Ontario, the fish community has improved considerably from a low point in the 1960's (Kerr and LeTendre 1991; Ontario Ministry of Natural Resources and New York State Department of Environmental Conservation 1994). Reductions in nutrients and other pollutants entering the lake, aggressive sea lamprey control, and stocking of trout and salmon brought about major improvements in the lake's fish community by the 1980's. Water quality had improved, levels of toxic contaminants in fish had decreased, and valuable recreational fisheries were established. Alewife and rainbow smelt abundance declined in the 1980's in response to trout and salmon predation and to reduced nutrient input to the lake, and in the 1990's, stocking of trout and salmon was reduced to bring them into better balance with their food supply. In addition, some native fishes are recovering from low levels observed in the 1960's. For example, lake whitefish,

which typically had been most abundant in the eastern end of the lake, were nearly absent there from the catch in the 1970's. In the 1980's, however, the species began increasing and were 30- to 40-fold more abundant there in the 1990's.

Amphibians and Reptiles

The amphibians and reptiles of the Great Lakes region are an interesting and diverse group that includes 83 species (Table 3). Salamanders, frogs, turtles, and snakes are represented by the greatest number of species (11–28), and toads (4) and lizards (6) by the fewest. There are also another dozen or more subspecies and hybrids, mostly snakes, that are not represented in Table 3. Species richness is highest in Illinois (63 species) and lowest in New York (44). The high richness in Illinois, Indiana, Ohio, and Pennsylvania is remarkable because the areas that are included in the Great Lakes region in those states are relatively small. Minnesota and Michigan, states with large land masses in the region, have relatively low species richness (48 and 51 species, respectively) because the climate is generally less suitable for amphibians and reptiles in those states than in the other states in the region. Many of the amphibians and reptiles that occur in Minnesota are at the northern end of their range. Amphibians are generally less abundant in the drier western portions of Minnesota, and the number of reptiles is low in the colder northern portions of Minnesota and Michigan.

Species that occur throughout the region include the eastern newt, eastern red-backed salamander, mudpuppy, American toad, chorus frog, spring peeper, gray treefrog, bullfrog, green frog, pickerel frog, northern leopard frog, wood frog, common snapping turtle, Blanding's turtle, painted turtle, common map turtle, smooth green snake, racer snake, rat snake, milk snake, common garter snake, Dekay's brown snake, red-bellied snake, and northern water snake. The lizards have the most restricted distributions; their highest richness occurs in the four westernmost states in the region.

Amphibians in many parts of the world have recently declined in number and geographic ranges (Blaustein and Wake 1990; Phillips 1990, 1991; Wake 1991; Livermore 1992). The situation is complex, but many scientists believe that a global problem faces amphibians and that this problem is largely the result of habitat modification by humans. Acid precipitation, shifts in precipitation patterns, intensive agriculture, deforestation, urbanization, highway construction, wetland draining, dam construction, pollution by pesticides and heavy metals, and the introduction of fishes and other predators

Table 3. Numbers of species of amphibians and reptiles in the Great Lakes region.[a]

	Total by state								Total by region
	MN	WI	IL	IN	MI	OH	PA	NY	
Amphibians									
Salamanders	5	7	10	11	11	15	13	12	17
Toads	3	1	2	2	2	2	2	1	4
Frogs	11	11	10	9	10	9	9	8	11
Reptiles									
Lizards	3	4	4	3	1	1	0	1	6
Turtles	9	11	14	10	9	8	9	9	17
Snakes	17	20	23	18	18	20	16	13	28
Total	48	54	63	53	51	55	49	44	83

[a]Sources: Ruthven et al. (1928); Smith (1961); Minton (1972); Pentecost and Vogt (1976); Vogt (1981); Conant and Collins (1991); Shaffer (1991); Oldfield and Moriarity (1994).

can all adversely affect amphibians. Baseline information on the status and health of U.S. populations of amphibians and reptiles is remarkably scarce (McDiarmid 1995), and there are no long-term, quantitative data on amphibians or reptiles in the Great Lakes region. Amphibians in the Midwest do not seem to be experiencing the drastic declines occurring elsewhere (Illinois Department of Energy and Natural Resources 1994), but local declines are apparent for both amphibians and reptiles. Sensitive species—including the spotted salamander, eastern red-backed salamander, four-toed salamander, wood frog, pickerel frog, northern cricket frog, wood turtle, and queen snake—are usually the first to disappear following reductions in water quality, other physical alterations of the environment, and pesticide use (Minton 1972).

Better descriptions of the status of amphibians and reptiles in the region will require more intensive surveys, monitoring, and data-base development. None of the reptile or amphibian species in the Great Lakes region are federally listed as threatened or endangered.

Birds

Birds contribute significantly to the biological diversity of the Great Lakes region. They are visible and valued elements of the regional ecosystems, and collectively they represent substantial recreational resources. Many books and articles have been written about the birds of the Great Lakes region to meet the needs and interests of bird watchers and other nature observers, resource managers, and scientists.

Broad-scale national programs—such as the U.S. Geological Survey's Breeding Bird Survey, annual waterfowl surveys, wintering surveys, and the annual National Audubon Society's Christmas Bird Count—provide status and trend information on as many as 75% of the bird species in the United States (Hall 1995). The information collected for the more abundant species is sufficient to detect large-scale population changes. Specialized surveys provide information on some of the less

abundant species and on those species whose habits make them more difficult to census. The newer status and trends information for individual species is organized in various ways, with much of it being stored in state and national data bases in a geographically referenced manner. Breeding bird atlases or other general texts prepared for each state (for example, [Indiana] Mumford and Keller 1984; [New York] Andrle and Carroll 1988; [Illinois] Bohlen 1989; [Michigan] Brewer et al. 1991; [Ohio] Peterjohn and Rice 1991; [Wisconsin] Robbins 1991; [Pennsylvania] Brauning 1992) also provide useful, detailed information on breeding birds. These books contain species accounts and background information describing the distribution, habitats, and breeding habits. Some of them also describe the status and the trends in abundance of bird species found in the state and provide explanations for observed changes in distribution and abundance.

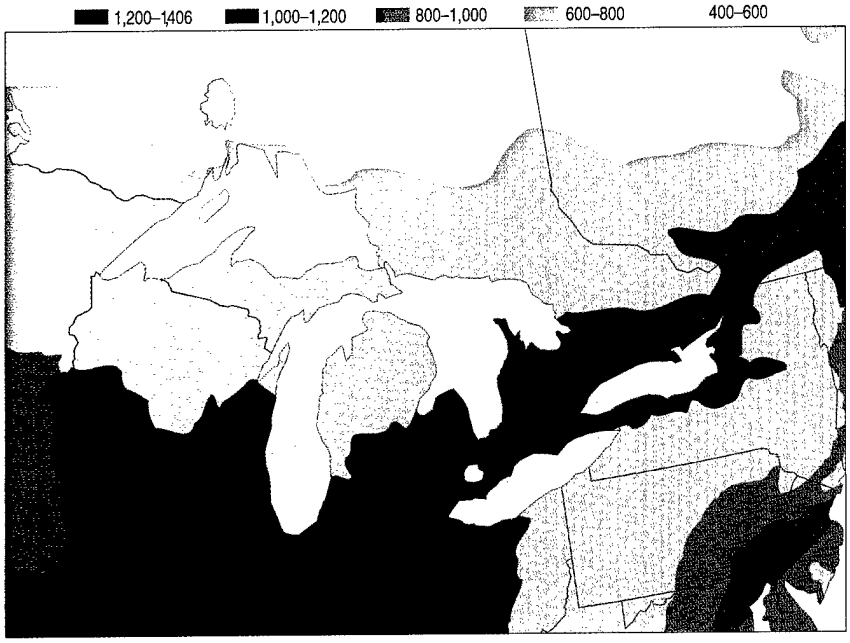

Fig. 15. Relative abundance of breeding birds across North America by physiographic region. Abundance expressed as mean number of individuals per 50-stop Breeding Bird Survey route, 1965–1980 (after Robbins et al. 1986).

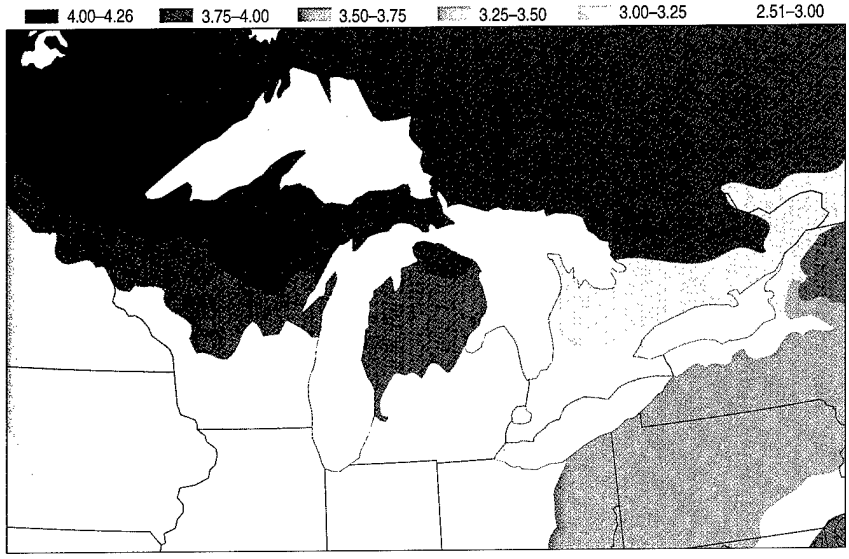

Fig. 16. Species diversity index (H′) for breeding birds across North America by physiographic region. $H' = \sum p_i \ln p_i$, where p_i = the proportion of all birds that belong to the ith species (after Robbins et al. 1986).

Birds are a large and highly diverse group, and it is probably inappropriate to generalize too broadly about the status of the group, although aggregating species data functionally can be useful. On a national scale, such data suggest that many species are presently stable, that some generalist species that can adapt to altered habitats are increasing, and that species less able to adapt to habitat degradation and habitat loss are decreasing (Hall 1995).

The North American Breeding Bird Survey documents species distributions and population trends of about 250 species on national, regional, and local scales. The survey data for 1965–1980 (Robbins et al. 1986) show that the relative abundance of breeding birds (mean number of individuals counted) in 1965–1980 in the southern portion of the Great Lakes region and along the south shore of Lake Ontario was among the highest in the nation (mean of 1,200–1,406 individuals per 50-stop counting route; Fig. 15). Abundance was lower to the west in Illinois and southern Wisconsin (1,000–1,200 individuals), and lowest (600–800) elsewhere in the region. Species diversity in 1966–1979 was lowest (species diversity index H′ = 3.00–3.25) in the southern part of the region where relative abundance was highest and was highest in the region and nationally (4.00–4.26) in the northern portions of the region, where relative abundance was lowest (Fig. 16).

The Breeding Bird Survey data collected since 1979 have not been published in detail. Peterjohn et al. (1995), however, presented a brief summary and evaluation of the data for 1966–1992, showing that 130 species decreased in abundance, 57 of which were confirmed by statistical testing. Some species in all families decreased in abundance, but decline was most common among the Mimidae (mockingbird, catbird, thrashers) and sparrows. Increases in abundance were exhibited by 115 species; 44 of these increases were confirmed by statistical testing. Flycatchers and warblers were prominent among those species that increased nationally. Functional groupings of the species breeding in the United States revealed other trends (Peterjohn et al. 1995). Grassland species showed the most declines nationally and in the Great Lakes region (Fig. 17).

Shrubland and old-field birds also seem to be declining nationally, but the increases and

decreases seem to roughly balance out in the Great Lakes region (Fig. 18). Woodland birds are increasing nationally and in the Great Lakes region as well (Fig. 19). Neotropical migrants show regional declines balanced by increases in other parts of the nation. In the Great Lakes region, Neotropical migrant populations are increasing in some areas and decreasing in others; the net change seems to be positive (Fig. 20). Short-distance migrants are declining nationally and in the southern portions of the Great Lakes region (Fig. 21). Permanent residents are also declining nationally, but seem to be generally increasing in the Great Lakes region (Fig. 22).

Trend data for 106 individual species from the Breeding Bird Survey displayed statistically significant trends in abundance from 1966 to 1992 (Table 4). Fifty-two species increased in abundance over the 26-year period, and 54 decreased. Most rates of annual change were small. The abundance of 57 species changed only 1%–2% per year; 43, 3%–11%; 4, 15%–20%; and 2, 51%–53%. Some of the changes can be related to natural or human-mediated range expansions, changes in habitat availability, competition with introduced species like the starling, and mortality resulting from severe and unusual weather conditions. The largest changes shown in Table 4 occurred

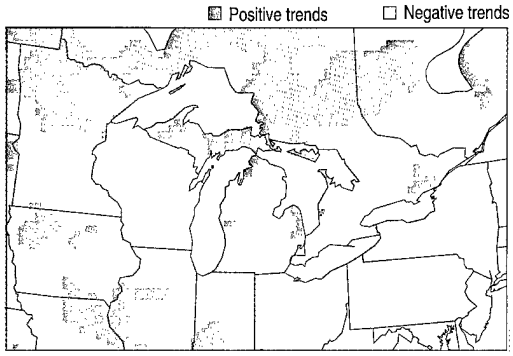

Fig. 17. Geographic patterns in mean trends for grassland bird species, 1966–1992 (from Peterjohn et al. 1995).

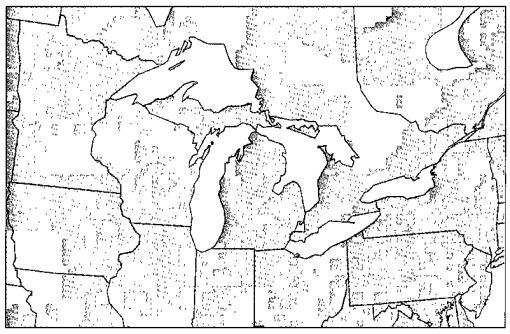

Fig. 20. Geographic patterns in mean trends for Neotropical migrant birds, 1966–1992 (from Peterjohn et al. 1995).

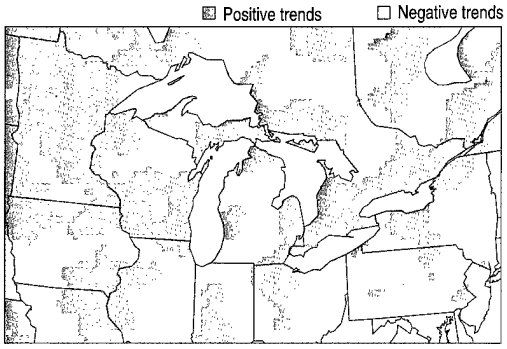

Fig. 18. Geographic patterns in mean trends for shrubland and old-field birds, 1966–1992 (from Peterjohn et al. 1995).

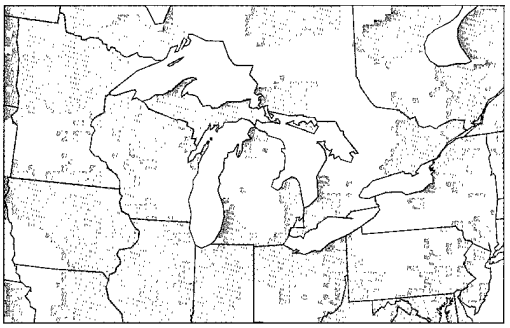

Fig. 21. Geographic patterns in mean trends for short-distance migrant birds, 1966–1992 (from Peterjohn et al. 1995).

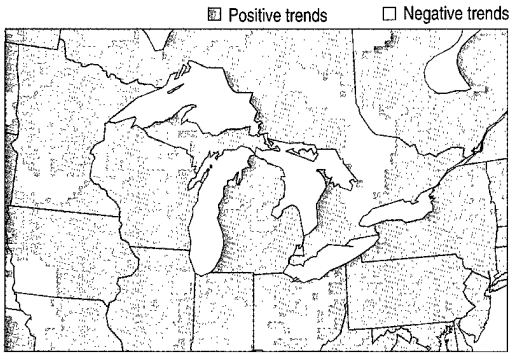

Fig. 19. Geographic patterns in mean trends for woodland birds, 1966–1992 (from Peterjohn et al. 1995).

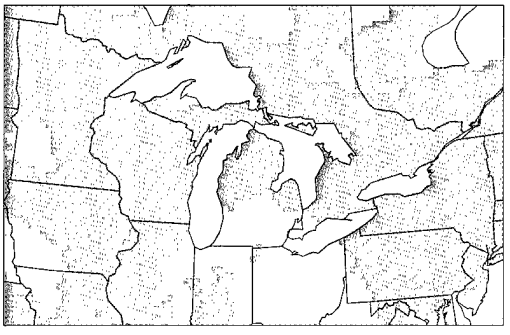

Fig. 22. Geographic patterns in mean trends for permanent resident birds, 1966–1992 (from Peterjohn et al. 1995).

Table 4. Trends in abundance (percent change per year) of birds breeding in the Great Lakes region, 1966–1992.[a]

Group and species[b]	Trend
Loon to heron (10)	
Common loon	3.3
Double-crested cormorant	6.3
Great blue heron	3.2
Swan to duck (14)	
Canada goose	51.1
Wood duck	9.2
Green-winged teal	-2.2
Mallard	3.1
Red-breasted merganser	-5.3
Vulture to hawk (11)	
Turkey vulture	11.9
Osprey	9.1
Bald eagle	7.1
Red-tailed hawk	2.6
American kestrel	1.0
Merlin	18.9
Partridge to quail (7)	
Gray partridge	-7.0
Ring-necked pheasant	-2.1
Sharp-tailed grouse	2.9
Northern bobwhite	-6.4
Rail to plover (11)	
Virginia rail	-7.2
Common moorhen	-20.5
Sandhill crane	15.6
Common snipe	-1.4
Tern and gull (7)	
Ring-billed gull	5.7
Common tern	-8.8
Black tern	-5.9
Dove to cuckoo (4)	
Mourning dove	1.0
Black-billed cuckoo	-1.4
Yellow-billed cuckoo	-2.4
Owl to kingfisher (8)	
Chimney swift	-1.3
Belted kingfisher	-2.9
Woodpecker (8)	
Red-headed woodpecker	-5.3
Red-bellied woodpecker	5.4
Downy woodpecker	2.1
Hairy woodpecker	2.5
Black-backed woodpecker	8.0
Northern flicker	-2.1
Pileated woodpecker	6.0
Flycatcher to swallow (18)	
Olive-sided flycatcher	-2.3
Eastern wood-pewee	-1.0
Alder flycatcher	1.2
Least flycatcher	-2.3
Eastern phoebe	2.0
Eastern kingbird	-0.7
Purple martin	-2.5
Barn swallow	-1.2
Jay and crow (5)	
American crow	1.3
Common raven	3.4
Titmouse to wren (11)	
Black-capped chickadee	2.5
Boreal chickadee	-5.3
Tufted titmouse	4.3
Red-breasted nuthatch	4.4
House wren	0.6
Winter wren	4.1
Sedge wren	2.2
Kinglet to thrush (10)	
Ruby-crowned kinglet	-1.6
Blue-gray gnatcatcher	9.0
Eastern bluebird	3.0
Veery	-1.9
Swainson's thrush	-2.2
Hermit thrush	2.0
Wood thrush	-3.3
American robin	0.6
Catbird to starling (5)	
Brown thrasher	-2.7
Cedar waxwing	1.5
European starling	-1.6
Vireo (6)	
Solitary vireo	4.6
Yellow-throated vireo	2.9
Warbling vireo	-1.0
Red-eyed vireo	1.2
Warbler (32)	
Northern parula	1.2
Yellow warbler	1.3
Magnolia warbler	1.8
Yellow-rumped warbler	1.9
Pine warbler	6.6
Bay-breasted warbler	-4.9
Black and white warbler	1.3
Canada warbler	-2.3
Yellow-breasted chat	-5.0
Tanager to towhee (6)	
Northern cardinal	2.5
Rose-breasted grosbeak	-1.0
Indigo bunting	0.6
Dickcissel	8.3
Eastern towhee	-2.0
Sparrow (15)	
Field sparrow	-2.7
Vesper sparrow	-3.3
Savannah sparrow	-1.8
Grasshopper sparrow	-6.9
Henslow's sparrow	-10.0
Song sparrow	-0.6
White-throated sparrow	-1.8
Junco to oriole (12)	
Slate-colored junco	-3.1
Bobolink	-1.8
Red-winged blackbird	-1.5
Eastern meadowlark	-3.4
Western meadowlark	-7.4
Brewer's blackbird	2.1
Common grackle	-2.1
Brown-headed cowbird	-3.4
Orchard oriole	4.3
Baltimore oriole	-0.8
Finch (9)	
Pine grosbeak	-17.8
Purple finch	-2.8
House finch	53.0
Red crossbill	10.1
Evening grosbeak	-3.8
House sparrow	-1.9

[a]Data provided from the Breeding Bird Survey data bank by J. Sauer, U.S. Geological Survey, Patuxent Wildlife Research Center. The Breeding Bird Survey lists trend information for 209 species for the Great Lakes region; of these, statistically significant trends were detected for the 106 species listed here.

[b]To aid in presentation, groupings may include more than one family (for example, "Loons to herons" includes loons (Gaviidae), grebes (Podicipedidae), cormorants (Phalacrocoracidae), and bitterns and herons (Ardeidae). Number in parentheses is number in group on Breeding Bird Survey list.

among house finch (53% per year) and Canada goose (51% per year) populations and are easily interpreted. The house finch, which is native to the western United States, was introduced to the east coast and is rapidly expanding its range to include most of the eastern and midwestern United States. The resident populations of Canada geese have developed in the Great Lakes region in response to management efforts to improve hunting opportunities. These populations now breed widely in urban and rural areas throughout the region. Causes for the changes in abundance of some other individual species listed in Table 4 are discussed in Robbins et al. (1986) and in bird atlases for the individual states.

Many species overwinter in portions of the United States; the National Audubon Society Christmas Bird Count, which began in 1900, provides data that can be used to describe population trends outside the breeding season. An atlas of North American wintering birds (Root 1988) gives data on distribution and abundance for more than 600 species in count years 1963–1973. More recently, Root and McDaniel (1995) examined national count data collected in 1959–1989 for 50 songbird species whose northern range is limited by low winter temperature. Twenty-seven of these species exhibited a trend in at least one state, and 16 had declining populations in more than half of the states where they occurred. Meadowlarks, sparrows, and other species that eat seeds from grasses and forbs showed a more widespread decline than those that eat berries or seeds from woody vegetation. This supports the finding by Peterjohn et al. (1995) of a nationwide decrease in the grassland species. An analysis by state for the Great Lakes region revealed that more species were increasing than were decreasing.

The Breeding Bird Survey and Christmas Bird Count data are collected in different manners and cannot be compared directly as equivalents. Together, however, they show clearly how species distribution changes between the breeding and wintering seasons. The only such published comparison (Robbins et al. 1986) was made for 1979 (Figs. 23 and 24). The number of breeding species per route in 1979 for the Great Lakes region was 60–67 in the northern portions of the region, 50–60 in the southern portions of the region, and 40–50 in the western portions. The mean number of species during the Christmas Bird Count in 1979 for the Great Lakes region was less than 40 in the northern portion of the region, 40–60 in most of the region, and 60–80 along southern Lake Michigan and most of Lake Erie and Lake Ontario. Many of the species counted along the shorelines of eastern Lake Erie and western

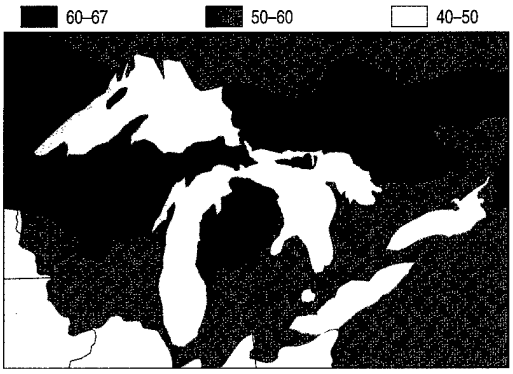

Fig. 23. Mean number of breeding birds across North America per 50-stop Breeding Bird Survey route by physiographic region, 1979 (after Robbins et al. 1986).

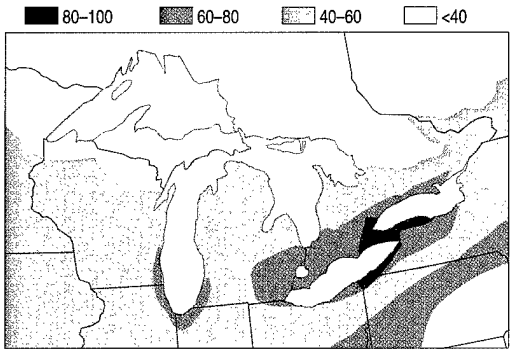

Fig. 24. Mean number of bird species per Christmas Bird Count, 1979, for comparison with distribution during the 1979 breeding season shown in Fig. 23 (after Robbins et al. 1986).

Lake Ontario were wintering waterbirds. The less complex winter distribution suggests that the habitat requirements in winter are simpler than during the breeding season and are probably strongly related to temperature and food availability.

Federally listed threatened and endangered bird species in the Great Lakes region include the bald eagle, American and arctic peregrine falcons, piping plover, Kirtland's warbler, and least tern (U.S. Fish and Wildlife Service 1994). Two of these species, the bald eagle and Kirtland's warbler, are responding favorably to recovery plans designed to restore productive populations and remove them from the list of threatened and endangered species.

The bald eagle is a large, predatory bird that feeds mainly on fishes and waterbirds. The bald eagle was once relatively abundant in the Great Lakes region, but reproductive failure caused by high levels of organic pesticides in its diet caused the species to decline to record low numbers in the 1960's. Contaminant levels have been declining in the region since the 1970's, and the bald eagle is now staging a substantial recovery in some parts of the region (Best et al. 1990). For example, the number of bald eagle breeding territories in Minnesota increased from 115 in 1973 to 400 in 1989 and, in Michigan, breeding pairs increased from 88 in 1977 to 165 in 1989. Despite the observed increases, habitat-related problems remain. Inland populations have expanded and birds produced in those populations have occupied breeding territories along Great Lakes shorelines in the 1980's. The shoreline populations, however, produce substantially fewer young than the inland populations (Table 5). The lower reproductive success of the bald eagle populations near the lakeshore has been attributed to a diet that is higher in contaminants than the diets of inland populations. Human activity, which tends to be higher in lakeshore areas than in inland areas, has been shown to limit the feeding activity of fledgling eagles in shoreline populations and may be a mortality factor. Adult mortality may also be higher among lakeshore populations than among inland populations. The recovery goals for bald eagle populations in the Great Lakes region have been met in Minnesota and Michigan and will probably soon be met in Wisconsin (Table 5). Recovery in the other Great Lakes states is less advanced.

The osprey, another fish-eating bird, is also recovering from reproductive failure and severe population declines caused by organochlorine pesticides in the 1950's–1960's (Ewins et al. 1995). The annual production of fledged ospreys has increased throughout the Great Lakes region since the use of organochlorine pesticides was reduced. Osprey populations nesting within 5 kilometers of the north shore of Lake Huron showed annual increases in abundance of up to 13% per year. On average, almost one young is now produced for each occupied nest—the level believed necessary to maintain a stable population.

The Kirtland's warbler, a Neotropical migrant, is federally listed as endangered. It nests only in young jack pine forest, mainly in the north-central portion of the lower peninsula of Michigan, but limited nesting also occurs in Wisconsin. In Michigan, more than 400 singing males were counted in 1951 and about 500 in 1961 (Fig. 25). The counts stabilized at about 200 from 1971 to 1989 and then increased steadily to slightly more than 600 in 1994.

Table 5. Bald eagle recovery goals and status by Great Lakes state (after Best et al. 1990).[a]

	Number of occupied breeding areas			Number of young per nest	
		Present status			
State	Recovery goal	Inland	Great Lakes	Inland	Great Lakes
Illinois	20	9	0	0.4	
Indiana	5	2	0	0.0	
Michigan	140	163	44	1.0	0.7
Minnesota	300	390	0	1.1	
New York	50	10	0	1.1	
Ohio	20	12	11	0.8	0.6
Pennsylvania	10	9	0	0.7	
Wisconsin	360	336		1.4	

[a] Zeros are measured values; blanks indicate no information available.

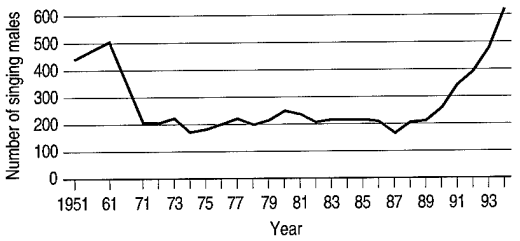

Fig. 25. Counts of singing male Kirtland's warblers in Michigan, 1951–1994 (Weinrich 1995).

Because Kirtland's warblers nest on the ground in stands of immature jack pine, their increase in abundance may be a response to habitat improvements that included an accidental burning of mature jack pine forests and reestablishment of large stands of immature jack pine.

Mammals

As a result of environmental changes and extinctions at the end of the Ice Age, the mammalian fauna of North America about 11,000–10,000 years ago generally resembled the present fauna (Hibbard et al. 1965; Lundelius et al. 1983). A description of the recent native mammals of the Great Lakes region (Burt 1967) listed 74 species living wild in the region. Of these 74 species, 28 ranged widely throughout the region; their areas of geographic origin could not be determined. Seventeen of the other species were southern forms that reach the northern limits of their ranges in the region, 16 were northern forms at the southern limits of their ranges, 8 were at their eastern limits, and 5 at their western limits. This confluence of range limits in the Great Lakes region indicates the region is a transition area, especially on a north-to-south axis. Northern boreal species do not seem to penetrate farther south than the limits of the coniferous forest that occupies the northern portion of the region, and southern species do not seem to move farther north than the northern edge of the deciduous forest in the southern portion of the region. The Great Lakes also seem to be barriers to distribution for some of the other species whose range limits occur in the region.

A more recent description of the native mammalian fauna of the north-central United States (Jones and Birney 1988) lists 99 species and covers Minnesota, Wisconsin, Illinois, Indiana, Ohio, and Michigan. This newer work extends coverage to the prairie and grassland communities bordering the western end of the Great Lakes region, but it excludes the portions of Pennsylvania and New York that compose the eastern end of the region. Jones and Birney (1988) found substantial faunal similarities among the states. The same seven taxonomic orders were represented in all six states, and the number of species in each order was generally similar in each state. The only marsupial in the region, the Virginia opossum, occurred in all six states. The number of insectivores (shrews and moles) was similar among the states (7–9). The number of bat species varied within the region and was fewest in Minnesota (7 species) and highest in Ohio (13 species). Rabbits or hares or both (2–3 species) occurred in each state. The number of rodents also varied within the region and was highest in Minnesota (31 species), largely because of the inclusion of grassland and northern faunas; in the other five states the numbers were similar (20–24 species). There were 18–20 species of carnivores, including one or more of the following in each of the six states: coyote; gray wolf; fox; black bear; raccoon; marten and fisher; ermine, weasel, and mink; wolverine; badger; skunk; river otter; and mountain lion, lynx, and bobcat. Slightly more antlered and horned animal species—including elk, deer, moose, pronghorn, and bison—occurred in Minnesota (7 species) than in Wisconsin and Michigan (5 species each) or in Illinois and Indiana (3 species each). There were more mammal species in Minnesota (78) because it has both grassland and northern species; the other five states have 65–70 species. Rodents and carnivores made up 58%–67% of the total mammal species in the six states.

Changes in the region's mammalian fauna that began with European settlement will almost assuredly continue as the human population grows and the habitat is further fragmented by development and more intensive land use. Species that have been extirpated from most or all of their former range in the region (for example, the bison, wolverine, pine marten, fisher, mountain lion, caribou, moose, elk, and gray wolf) will find it difficult to spread from any wild source populations that remain in the region or to become reestablished by emigration from wild source populations in bordering regions. Successful reintroduction is possible for some species, however, as evidenced by the relatively recent reestablishment of self-sustaining populations of pine marten, moose, and elk in portions of the region where the habitat can still support them and where human interaction can be controlled. The reintroduced population of elk in the northern portion of the Lower Peninsula of Michigan now supports a limited annual hunt. Gray wolves migrate intermittently from Canada into the Upper Peninsula of Michigan; natural reproduction now occurs there as well as in neighboring areas of Wisconsin (Ann Arbor News 1995). Fifty-nine moose were captured in Ontario and released in the Upper Peninsula of Michigan in 1985 and 1987. They bred successfully, and the herd is now estimated at 400–500 animals (Gwizdz 1995).

The mammalian fauna will also continue to change as the human population in the region continues to increase and species that are tolerant of human presence replace those that are not. The coyote, for example, probably had been extirpated in the region, but it now occurs widely and has even been seen in urban areas. The Virginia opossum, eastern cottontail, and the fox squirrel are other examples of species whose range extensions in the region are related to favorable environmental changes brought about by humans. Although the future of the region's mammalian fauna is difficult to predict, it is clear that many species—and particularly the larger species that are intolerant of human presence—will continue to be at a major disadvantage unless special efforts are made to protect them. Most of the small mammals that occurred in the north-central region 400 years ago still occur there today, and their future as a group presently seems secure (Jones and Birney 1988). In contrast, the region's larger carnivores and the antlered and horned species have undergone extinctions, extirpations, and large range changes as a result of human activities. The future of these species is not certain unless special measures are taken to assure their presence in the area's faunal communities.

The Indiana bat is federally listed as endangered in all states in the Great Lakes region except Minnesota. The species seems to be recovering in Indiana. The major threat to the Indiana bat is human disturbance of populations hibernating in caves. The gray wolf is listed as endangered in Michigan and Wisconsin and as threatened in Minnesota. The populations in northern Michigan and Wisconsin are growing slowly but need protection from humans.

Information Gaps and Research Needs

Areas that should be given particular attention in developing an initiative designed to protect biological diversity and support healthy ecosystems in the Great Lakes region are listed next. The list provides consideration of species of traditional management interest including game species and other species with economic or aesthetic values as well as species and communities that have become regionally or globally rare or are threatened with extinction.

- Field inventories and field and laboratory research should be conducted as demonstration projects to show how the ecosystem approach can be successfully applied to protect biological diversity and resources of management interest in the Great Lakes region.
- Formal, empirically based approaches for measuring ecosystem health need to be developed and tested for use in the region.
- Contaminant levels should be monitored as a component of ecosystem health.
- Research is needed to determine the effects of contaminants on specific ecosystem components.
- Introduced species should be monitored and studied as a component of and threat to ecosystem health.
- The function and performance of native species and communities in healthy Great Lakes ecosystems should be studied to provide baseline information that can be used to assess the health of stressed or threatened ecosystems and particular ecosystem components and to guide protection, management, and restoration activities.
- Research should be conducted to determine and better demonstrate the value of undisturbed communities and ecosystems as voucher or baseline elements for use in assessing ecosystem health.
- The role and value of long-lived, old-aged, large-sized individuals as components of healthy aquatic populations and ecosystems should be recognized and documented.
- More status and trend information is needed for many plant and animal groups in the region. Invertebrate, fish, amphibian, and reptile species and communities are underrepresented in most regional data bases.
- There is uneven geographical representation among regional data bases. Some states are more advanced than others in developing resource inventories and assessments.
- State data bases need to be more fully developed so that data can be easily and effectively aggregated to aid ecosystem management at multistate, regional, or national levels.
- Assessment of information in existing data bases may not be keeping pace with data-base construction. Additional field research may be needed to permit interpretation of observed changes in distribution and abundance of species of interest.
- Aquatic community classification systems should be developed as a framework for understanding and managing regional aquatic resources in the Great Lakes, connecting channels, and tributary ecosystems.
- Aquatic and terrestrial ecosystems should be described in terms that permit them to be linked for analysis.
- Considerable research is needed to understand the effects of a variety of specific land- and water-resource use practices and projects on species and communities so that adverse effects can be minimized or avoided and biological diversity and ecosystem health can be maintained.
- The effect of measures or practices employed to control undesirable introduced species (such as the sea lamprey) should be assessed in the context of ecosystem health, as should the role of hatcheries and artificial propagation in the management of game species.

- The effect of commercial or recreational enhancement and harvest on the health of plant and animal populations and communities should be assessed and related to the health of the ecosystems to which these elements belong.
- Field research and surveys at the watershed and landscape scales are needed to better identify ecosystems and ecosystem elements that are particularly susceptible to perturbation by human activities common to the region.
- Methods should be developed for restoring aquatic habitats damaged by pollution and physical alteration.
- Governments and private sector organizations with resource management authority should be encouraged to cooperate in developing land-use inventories and guidelines or regulations that reflect the ecosystem approach to resource management.

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Acknowledgments

The following persons provided materials, information, or advice that contributed to the preparation of this manuscript: D. Albert, R. Baker, N. Conrad, S. Crispin, B. J. Farley, G. Guntenspergen, T. Janevic, M. Penskar, B. Peterjohn, M. Rabe, R. Ramey, D. Rankin, J. Sauer, K. Schneider, P. Seelbach, Gerald Smith, Graham Smith, J. Soule, A. Swengel, T. Weise, L. Wilsmann, and A. Zimmerman.

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Southeast

The ecosystems of the Southeast range from the spruce–fir forests of the highest mountains east of the Mississippi River to the tropical hardwood hammocks of southernmost Florida. A tremendous diversity of ecosystems lies between these extremes: the sawgrass marshes, mangrove forests, and pine rockland of south Florida; the carnivorous plant wetlands, baldcypress swamps, live oak maritime forests, longleaf pine savannas, and dunes of the Coastal Plain; the oak–hickory forests, bottomland forests, prairies, glades, and barrens of the Piedmont and continental interior; the springs and extensive cave systems of limestone areas; and the old-growth deciduous and hemlock forests, cliffs, rocky stream gorges, and grassy and heath balds of the southern Appalachian Mountains.

Although broad-scale climatic patterns explain much of this diversity, the Southeast's most distinctive characteristic is diversity at small scales. Variation in topography determines soil moisture and temperature regime, influences soil fertility, and produces change in ecosystem composition and structure over relatively short distances. The Southeast is also underlain by a wide variety of geological substrates and soils; thus, where ecosystem boundaries are abrupt, a mosaic of community types results. Usually, however, changes in community types are gradual, and classification of community types itself becomes arbitrary. Many animal species move among and depend on the diverse aquatic and terrestrial habitats of southeastern landscapes.

In addition to environmental variation, there are other explanations for the Southeast's biological diversity. Historically, the Southeast was not covered by continental glaciers, nor was much of the present land surface submerged by past rises in sea level. As a result, plants and animals have evolved in the Southeast over long periods. This long evolution, combined with the isolation that characterizes some habitats, has produced striking levels of endemism (species restricted to certain habitats) in many groups of plants and animals. Narrowly restricted endemism is most prominent in groups with limited dispersal ability and those found in isolated habitats. For example, narrow endemism is frequent in plants, amphibians, fishes, mollusks, and aquatic insects in the Southeast but is weak in birds and mammals.

Because of diverse environments and long evolutionary isolation, a number of groups reach continental high points of species richness in the Southeast, making the region one of the richest areas in the temperate zone, surpassed only by eastern Asia (Hackney et al. 1992; Martin et al. 1993a,b). Groups that have their highest North American diversities in the Southeast include amphibians, fishes, mollusks, aquatic insects, and crayfishes throughout the region; salamanders, land snails, fungi, and plants in the southern Appalachians; and carnivorous plants on the Coastal Plain.

This chapter describes the status and trends of the rich biological diversity of the Southeast. The very diversity and local complexity of the region's ecosystems complicate our task. Long-term data are scarce and often are available for only a few study areas or taxonomic groups. The trends that are available are usually derived from expert opinion rather than extensive data sets and often concern loss of habitat area rather than change in populations or ecological processes (Noss et al. 1995). Our emphasis is on ecosystems because they are the best context for the consideration of biological diversity, but we also summarize status and trends for vertebrates and several other well-studied groups.

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Environments of the Southeast

Landforms and Geology

The Southeast is divided into 4 physical divisions and 11 regions of distinctive landscapes (Isphording and Fitzpatrick 1992; Martin and Boyce 1993; Fig. 1). Bedrock consists of a variety of metamorphic, igneous, and sedimentary rocks that range greatly in chemistry and resistance to erosion and weathering. Acidic rocks are widespread in the Piedmont and mountains, but limestone and other basic rocks dominate in areas of the continental interior and much of peninsular Florida, and are scattered in other provinces.

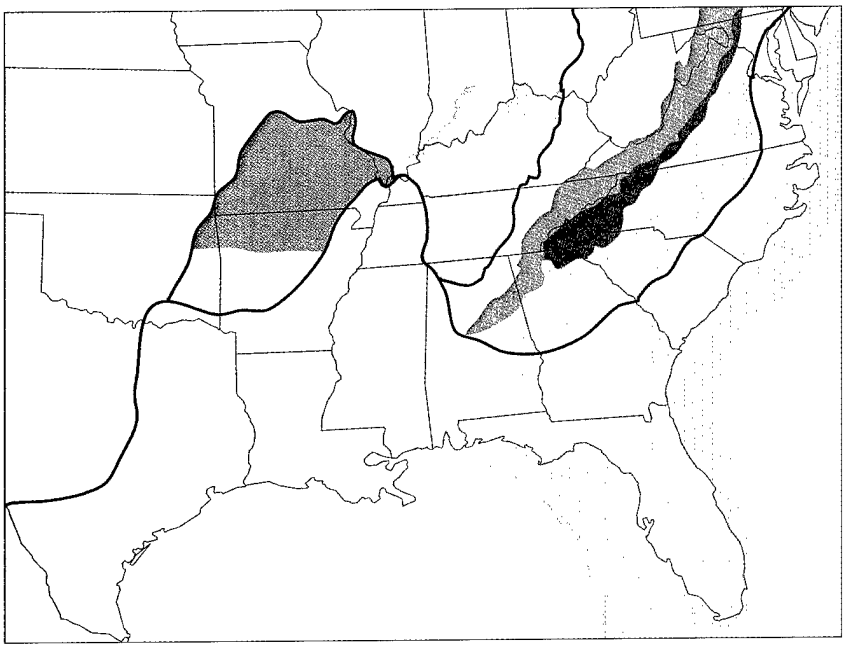


Fig. 1. Physiographic regions of the southeastern United States (redrawn from Martin and Boyce 1993).

The Coastal Plain includes the Atlantic Coastal Plain, the Gulf Coastal Plain, the Mississippi River valley (including the Mississippi Embayment that extends northward to Missouri and Kentucky), and peninsular Florida. Topographic relief is low, with maximum elevations reaching only 50–150 meters. An extensive system of barrier islands occurs along the Atlantic and Gulf coastal plains. Unconsolidated substrates in the Coastal Plain include peats, coarse sands, silts, acid clays, calcareous clays, loess, and shell hash.

Sand deposits in the Coastal Plain are derived from three sources (Christensen 1979). Marine sands occur on recently exposed terraces in a relatively narrow strip along the coast itself. Inland from the coast are aeolian sands, and yet farther inland and adjacent to the Fall Line (the border of the Piedmont and Coastal Plain) from North Carolina to Georgia are the Sandhills, a distinctive landscape of rolling hills (Christensen 1979). Elevations in the Sandhills are up to 100 meters higher than in adjacent areas, and the area's permeable sands make soils extremely dry despite high rainfall. Sandhill vegetation includes xeric oak and pine, pine savanna, and open herbaceous barrens. The driest places, in which vegetative cover is incomplete, are sometimes called *deserts*, an ironic title for a region with high rainfall.

The Appalachian Highlands include four parallel units: the Piedmont, Blue Ridge, Ridge and Valley, and Appalachian Plateaus. The Piedmont, with an elevation of 150–600 meters, is dominated by erosion-resistant metamorphic rock. The Blue Ridge encompasses the high peak region of the southern Appalachians, with the highest point in eastern North America on Mount Mitchell, North Carolina, at 2,037 meters. Erosion-resistant igneous and metamorphic rocks dominate the high elevations. The Ridge and Valley province, with elevations of 600–900 meters, consists of northeast–southwest trending valleys on limestone bedrock and intervening ridges of more resistant sandstones. The Appalachian Plateaus, with elevations of 600–900 meters, have areas with mountain peaks that rise above the plateau surface (though not reaching the height of the Blue Ridge) and other areas in which rivers have cut steep-sided valleys below the more gentle topography of the plateau surface.

The Interior Low Plateaus of central Tennessee, central and western Kentucky, and northern Alabama are part of the Interior Plains physical division. Limestone is a major influence on landforms, and karst features, such as extensive cave systems and sinkholes, are frequent. Relief is moderate, and elevation is about 300 meters.

The Ozark Plateaus and Ouachita Mountains of the Interior Highlands physical division dominate southern Missouri and northern Arkansas. Limestone, shale, and sandstone dominate these areas, and karst landforms are frequent.

Soils

All major soil orders are present in the region and are associated with particular landforms and geographic areas. Soils vary greatly in texture, fertility, and moisture-holding capacity (Hackney and Adams 1992; Martin and Boyce 1993). Ultisols dominate the upland soils of the Southeast, underlying about three-quarters of the area (Martin and Boyce 1993). Upland ultisols (udults) are developed on deeply weathered parent material and are acidic and leached. Long agricultural use has reduced organic matter content in many areas. Aquults (a waterlogged soil) occur in wetter areas on unconsolidated sediments, especially along the Atlantic Coastal Plain.

Climate

Southeastern climates are humid and warm-temperate to subtropical. Major variation in climate occurs with change in latitude and elevation. Longitude has a more subtle influence on climate than latitude, as a result of maritime influence to the south and east and continental influences to the north and west.

Latitudinal gradients in temperature are steeper in winter than in summer, producing a strong geographic pattern in freeze-free periods and cold temperatures. The gradient in average minimum January temperature spans 22°C, whereas the gradient in average maximum July temperature spans only 4°C (Ruffner 1985; Martin and Boyce 1993; Table 1). The freeze-free period decreases northward, from 365 days in the Florida Keys, which experienced freezing temperatures in fewer than half of the years on record, to 180 days in Arkansas and 150 days in northern Virginia. The freeze-free period also decreases with elevation, to 110 days at the highest elevations in the southern Appalachians. Canadian air masses bring the coldest winter temperatures, penetrating the Southeast from the continental interior and generally producing decreasing minimum temperatures westward at a given latitude. Annual snowfall shows the same steep gradients as cold winter temperatures, increasing from zero in south Florida to over 100 centimeters northward and to over 200 centimeters in the high mountains.

Annual precipitation averages 110–140 centimeters over much of the area, with a slight decrease northward to about 100 centimeters. Excluding the high mountains, the highest annual precipitation occurs along the Gulf of Mexico coast and in south Florida (140–160 centimeters). Annual precipitation increases to 200 centimeters where elevations surpass about 1,700 meters. The highest values are not, however, at the extreme elevations but are affected by the position of the mountain front relative to precipitation sources. The first high mountains encountered by moist air masses from the Gulf of Mexico coast and the Atlantic are those at the southern edge of the Blue Ridge near the joint boundaries of the region of North Carolina, South Carolina, and Georgia. This region has the Southeast's highest precipitation (as much as 250 centimeters) and the highest rainfall in the United States east of the Pacific Northwest.

Precipitation occurs throughout the year but is generally lowest in fall and highest in summer, when convective thunderstorms develop. Thunderstorms in Florida occur an average of 80–130 days annually, in the Gulf Coastal Plain 80–100 days annually; the number of thunderstorms decreases northward, occurring an average of 40–60 days a year in Kentucky, Virginia, and interior regions.

By combining climate and physiography, McNab and Avers (1994) classified the Southeast into 2 domains (humid temperate and tropical), 3 divisions (humid temperate, hot continental; humid temperate, subtropical; and humid tropical, savanna), 9 provinces, and 28 sections, the latter representing distinctive landscape types (Table 2).

Table 1. Climates of the Southeast (from Ruffner 1985).

Location	Mean temperature (°C)				Mean annual precipitation		Relative humidty (%)
	January		July		Rain	Snow	
	Low	High	Low	High	(cm)	(cm)	
Elkins, West Virginia	-7	5	14	27	109	170	50
Baltimore, Maryland	-4	6	19	31	102	56	66
Louisville, Kentucky	-4	6	19	31	109	43	70
Little Rock, Arkansas	-2	10	21	34	125	13	71
Asheville, North Carolina	-3	9	17	29	114	46	75
Richmond, Virginia	-2	8	20	31	109	36	68
Memphis, Tennessee	0	9	22	33	125	15	69
Atlanta, Georgia	1	11	21	31	122	4	70
New Orleans, Louisiana	7	17	23	32	145	0.5	76
Miami, Florida	15	24	24	32	152	0	73

Table 2. Landscape diversity in the Southeast: ecological subregions of the southeastern United States as mapped by the U.S. Forest Service (McNab and Avers 1994), based on Bailey's ecoregions.

Domain	Division	Province	Number of	
			Sections	Vegetation types[a]
Humid temperate	Hot continental	Eastern broadleaf forest–oceanic	4	5
		Eastern broadleaf forest–continental	3	6
		Central Appalachian broadleaf forest–coniferous forest–meadow	3	6
		Ozark broadleaf forest–meadow	1	2
	Subtropical	Southeastern mixed forest	7	7
		Ouachita mixed forest–meadow	1	1
		Outer Coastal Plain mixed forest	7	7
		Lower Mississippi riverine forest	1	2
Humid tropical	Savannah	Everglades	1	5

[a]Küchler (1964). See Table 3 for Küchler vegetation types.

Natural Disturbances

The Southeast's frequent thunderstorms provide an ignition source for natural fires. In the past, Native Americans and European settlers also burned natural vegetation regularly. Regardless of ignition source, fire frequency and intensity have been dominant forces throughout the Southeast on all but the wettest and coldest (high mountain) sites. The mid- to late 1900's represent a period of reduced fire frequency, size, and intensity, a shift that is a major source of change in the region's ecosystems, leading to increases in mesic species (that is, species adapted to moister conditions), increased understory stem density, increased woody cover in formerly open habitats, and decreases in fire-dependent species and ecosystems.

Tropical storms are also a major recurrent disturbance, with much of the area experiencing about two damaging storms per decade. Between 1871 and 1981, 138 tropical storms affected south Florida (Davis and Ogden 1994a). Although storm incidence declines

from coastlines to the interior, tornadoes are more frequent in interior areas, where nearly 10 violent tornadoes per year have occurred over the last 100 years (Grazulis 1984; Martin and Boyce 1993).

The heavy rainfall that accompanies these and less violent storms is an important natural disturbance, especially in the Appalachian Mountains, where debris avalanches create open habitats in the forested matrix and flash floods scour stream banks and affect stream biota. Throughout the Southeast, the natural flooding and erosional dynamics of rivers were and are an important natural process for biological diversity; impoundments, changes in the quality and quantity of water, draining of bottomlands, and channelization of rivers are major causes of loss in the biological diversity dependent on dynamic stream and river systems.

Evolutionary History

Although consideration of environmental variation is one key to understanding the Southeast's biological diversity, a deeper look at the pattern reveals a second major explanation, one based on evolutionary history and geography. Because some habitats in the Southeast have long been isolated from one another, evolution could produce a geographic turnover of species with restricted distributions. This phenomenon is most striking in the biota of rivers and streams and in groups with low dispersal abilities. For example, aquatic taxa evolved in relative isolation in river basins, with interchange made possible at rare intervals by stream capture or by rare dispersal events. This phenomenon has given a geographic pattern to the distribution of freshwater fishes and mollusks (Sheldon 1988; Walsh et al. 1995). A terrestrial example of the evolution of endemism in isolated areas is provided by Lake Wales ridge, an area of Florida that has been continuously above sea level for 3 million years (Martin 1993).

Even though the Southeast was not glaciated, changing climates did result in the migration of plant and animal populations over considerable distances, with some terrestrial species becoming restricted to isolated refugia (Delcourt et al. 1993). This historical fragmentation of range for some taxa allowed further opportunity for separate evolution. In addition, some species never rebounded from glacial refuges.

These mechanisms enriched the Southeast in its number of local endemics. For example, some of the continent's rarest woody plants are found in a series of river valleys in south Georgia and northern Florida: Florida torreya (now in a 35-year decline, with no sexual reproduction having occurred in the last 15 years [Schwartz and Hermann 1993, 1995]), Florida yew, and Franklinia, last seen in the wild in the early 1800's but widely grown in gardens. In the southern Appalachians, an imprint of evolutionary history can also be seen in plants (for example, Rugel's ragwort is limited to but abundant in the Great Smoky Mountains) and animals (for example, salamanders) that are limited to particular parts of the mountains. The presence of local endemics further complicates our overview of biodiversity trends in the Southeast because it means that the species composition of a particular kind of ecosystem may vary from one place to another—and this variation often involves the very species (local endemics) that are most at risk.

Human Populations and Land Use

Native Americans have occupied the Southeast for more than 10,000 years, but their influence on ecosystems and species varied considerably through time (Delcourt et al. 1993). Shifting agriculture on bottomlands and alluvial terraces became dominant during the Woodland Period (3,000 to 1,200 years B.P.). The wide use of maize as a staple crop plant marked the period of maximum cultivation in the Mississippian Period (1,200 to 500 years B.P.). In this period, productive floodplains and lower river terraces were extensively cleared and large settlements were created whose influence included the harvest of wood for fuel and building materials in peripheral areas (Delcourt et al. 1993). Native American populations declined sharply after 1500 because of the spread of European diseases and displacement by European settlers.

European settlement, including its concomitant and ubiquitous introduction of livestock and new crop plants, resulted in more extensive conversion of upland forests to agriculture. The time of maximum clearing varied across the Southeast, but for many areas the peak occurred in the mid-nineteenth to the early twentieth century. Old-growth forests that survived this period were almost always on less productive or hard-to-cultivate land. Although logging took place throughout the region from the earliest settlement times to the present, mechanized logging was particularly destructive in the southern Appalachians between about 1880 and 1920. Soil erosion is a problem on farmed and logged sites and may have permanently reduced productivity over large areas. In addition, soil erosion produced a heavy sediment load in aquatic systems; this load has only recently begun to decrease (Mulholland and Lenat 1992).

Because human influences have changed over the last century, upland forests are

undergoing successional change over much of the Southeast. Skeen et al. (1993) argue that pine-forest cover in the region peaked in about 1965. Since then, forest cover has declined because of the reductions in fire frequency that began about 1900 and because of the senescence of old-field pine that had colonized farms that were abandoned in the mid- and late nineteenth century.

After a peak in cleared land in the mid-nineteenth to early twentieth century, a major period of farm abandonment occurred, starting about the time of the Civil War and continuing until about 1940. These old fields were invaded by pines; some patches of shorter-lived pine species, such as short-leaf pine and Virginia pine, which live 80–120 years, are now senescing (Skeen et al. 1993).

For pine stands that originated through fire or farm abandonment, a native insect, the southern pine beetle, is often the immediate agent of death. Outbreaks of this insect are more common in older and stressed trees. Human activities may have resulted in larger blocks of pine forest of relatively uniform age, producing landscapes more susceptible to large outbreaks of this beetle. Although these outbreaks can be alarming and can render trees hazardous to human life and property, the southern pine beetle is a native species that may play a role in natural fire regimes by helping produce heavy fuel loads (White 1987).

Understanding fragmentation effects and managing for tracts of unbroken forest in the midst of growing human populations have become critical issues. For example, the persistence of common forest interior bird species such as the wood thrush requires a minimum of 40 to 100 hectares (Robbins et al. 1989); some species, though, such as the ivory-billed woodpecker (extirpated in the Southeast but perhaps surviving in Cuba), require 2,000 to 40,000 hectares to achieve status as a source population (that is, a long-persisting population that has excess production for colonizing new areas [W. C. Hunter, U.S. Fish and Wildlife Service, Atlanta, Georgia, unpublished report]). Fragmentation of forests will be a dominant issue in conservation of biological diversity across the Southeast during the coming decades.

Destructive logging and soil erosion in the Southeast were major stimuli to the conservation movement in the early twentieth century; this movement led to the creation of national forests, national parks, state parks, research stations, and other protected areas. In contrast to the western United States, the Southeast had little public land—less than 10%—and these areas had to be created by purchase of private lands. Today, public land is mostly in the mountains, with less public land in the Piedmont and Coastal Plain (Boyce and Martin 1993; Fig. 2).

The Southeast has one of the country's most rapidly growing human populations. Population growth was 20% from 1970 to 1980, 13.4% from 1980 to 1990, and an estimated 10%–19% for the 1990's (U.S. Bureau of the Census 1994). The continued growth of the human population and changes in the way humans interact with the natural landscape present a challenge to conservationists concerned with the survival of diversity in this biologically rich region.

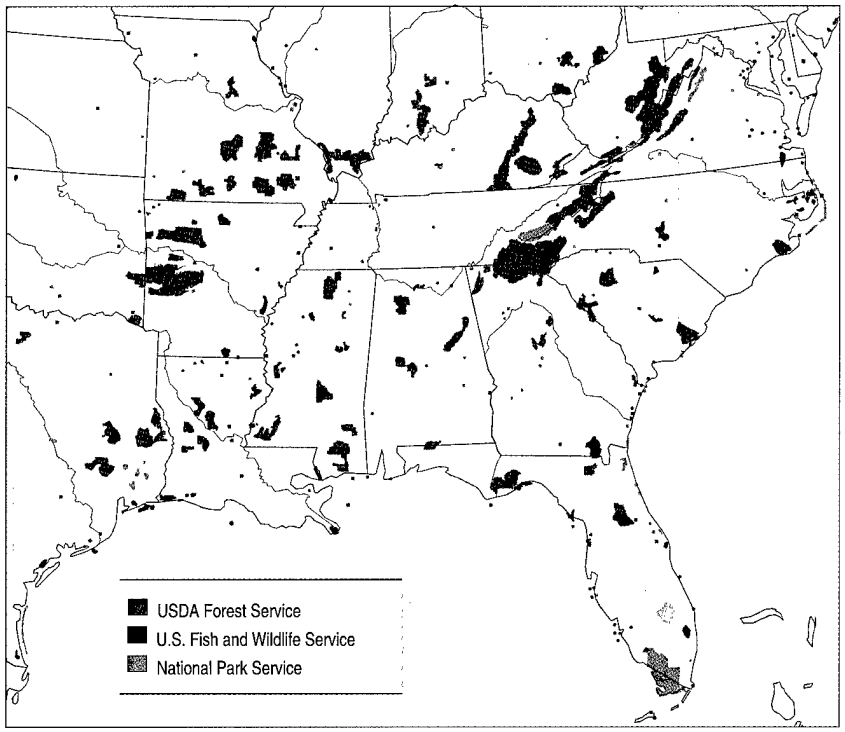


Fig. 2. Distribution of federal land in the southeastern United States, including national parks, forests, and wildlife refuges of significant area. The Southeast has little public land in comparison to the western United States.

Land-Use Trends

Data from 1987 show that although 55% of the land was forested then, the trend was downward, with a decline of 5% since 1960 (U.S. Forest Service 1988; Martin and Boyce 1993). The rest of the land was used for crop and pasture (31%) and miscellaneous purposes (roads, towns, cities, airports; 14%). Urban areas are growing at the fastest rate, but the rate of growth varies by region. For example, in North Carolina, urbanization occurred three times faster in the Piedmont than in either the mountains or Coastal Plain (see review in Boyce and Martin 1993). While the high total of forested land indicates potential for the survival of biological diversity, these forests are largely privately owned (less than 10% of the forested land is in federal ownership [U.S. Forest Service 1988]) and are not managed for biological diversity per se. Further, because these lands have almost all been disturbed by logging

and agriculture, they have already lost communities and species.

Forestland has been predicted to decline by 15% over the next 50 years (with additional forestland converted from natural to plantation forests), agricultural land to decline slightly (with a continued shift from small to large farming operations), and urban areas to increase in area (see discussion in Boyce and Martin 1993), suggesting that further habitat loss and fragmentation will occur near human population centers. We know too little about the survival of biological diversity in human-dominated landscapes, but we do know that the biodiversity of these areas will generally decrease with habitat fragmentation (Harris 1984). Some human-dominated landscapes, however, have the potential to support the diversity of some groups. For example, some crop systems support bird diversity (Allen 1995; Hunter, draft report) by cultivating marginal lands, including some wetlands.

Ecosystem Diversity

The natural landscape of the Southeast is dominated by broad-leaved deciduous trees and pines (Bryant et al. 1993; Skeen et. al. 1993; Stephenson et al. 1993). On uplands, a compositional continuum occurs from mesic sites dominated by maples, American beech, and other species to drier upper slopes and ridges dominated by oaks, hickories, and pines. Except for pines and eastern redcedar (widely distributed in the Southeast, particularly on calcium-rich soils), other gymnosperms are more restricted in distribution. Hemlock, spruce, and fir are found only in the southern Appalachian Mountains, with Atlantic white-cedar and baldcypress limited to the Coastal Plain. Broad-leaved evergreen trees, including southern magnolia and live oak, are prominent in some Coastal Plain habitats. Tropical hardwoods are limited to south Florida and are unique in the continental United States.

Most southeastern forests are closed-crowned, but savanna occurs on dry and fire-affected sites. Historically, longleaf pine savanna was widely dominant on the Coastal Plain; oak savanna was important on the margin of prairies in the continental interior. Open habitats, including fens, bogs, glades, barrens, and prairies; freshwater and saline marshes; sand dunes; and salt flats and rock outcrops form islandlike habitats within the matrix of closed forest. The occurrence of such open communities is variously explained by frequent fires, thin soils, unusual soil chemistry, or flooding.

How many kinds of ecosystems occur in the Southeast? What are the distributions and extents of these ecosystems? Unfortunately, we cannot answer these questions with much precision, although The Nature Conservancy (Grossman et al. 1994; The Nature Conservancy and Environmental Systems Research Institute 1994), in cooperation with State Heritage programs and the U.S. Geological Survey, has embarked on a long-term project to fill this gap in our knowledge. Although the lack of data on the definition and distribution of ecosystem types is a problem throughout the United States, the local complexity of southeastern ecosystems makes the problem particularly severe.

We have chosen to outline ecosystem diversity in the Southeast at two scales. First, for relatively coarse scales, we will summarize Küchler's (1964; McNab and Avers 1994) map of potential natural vegetation, a work also used as a starting point in Hackney et al. (1992) and Martin et al. (1993a,b). For relatively fine scales, we will use The Nature Conservancy's national classification scheme (The Nature Conservancy and Environmental Systems Research Institute 1994).

Regional Ecosystem Diversity: Coarse Scale

Küchler (1964) mapped 24 potential natural vegetation types in the Southeast (map scale, 1:3,168,000), of which 12 were forest types (Table 3). Six types were widely distributed, 3 were restricted to the Appalachian Mountains, and 13 were restricted to the Coastal Plain, with 7 of those restricted to Florida (Table 3). The final 2 types are cedar glades (restricted to the continental interior and generally found on dry sites over calcium-rich bedrock) and rock outcrops (scattered throughout).

The coarse scale of the Küchler types is evident in a recent treatment of the Southeast (Martin et al. 1993b). For example, in Florida, Küchler mapped 2 communities in the Everglades, whereas Gunderson and Loftus (1993) described 13; Küchler mapped 1 mangrove community, whereas Gilmore and Snedaker (1993) described 5; and Küchler mapped 2 pine communities, whereas Stout and Marion (1993) described 5.

Regional Ecosystem Diversity: Fine Scale

The Nature Conservancy's national classification (The Nature Conservancy and Environmental Systems Research Institute 1994) includes 7 hierarchical levels, the first 5 of which are determined by noncompositional factors: system (terrestrial, aquatic, or subterranean), physiognomy (growth form, height, phenology, and cover of the strata), and

Küchler type	Distribution in the Southeast
Widely distributed, upland forests	
Southern mixed	Virginia, North Carolina, South Carolina, Georgia, Alabama, Mississippi, Louisiana, Texas, Florida
Oak–hickory–pine	Virginia, North Carolina, South Carolina, Georgia, Alabama, Mississippi, Louisiana, Arkansas, Texas
Oak–hickory	Arkansas, Kentucky, Tennessee, Alabama, Mississippi
Appalachian oak	West Virginia, Maryland, Virginia, Tennessee, North Carolina, South Carolina, Georgia, Kentucky
Mixed mesophytic	West Virginia, Kentucky, Tennessee, Alabama
Widely distributed, wetland forest	
Southern floodplain forest	Throughout the Southeast
Restricted, mountain forests	
Northeastern spruce–fir	High mountains only: West Virginia, Virginia
Southeastern spruce–fir	High mountains only: Virginia, Tennessee, North Carolina
Northern hardwoods	Mountains only: West Virginia, Virginia, Tennessee, North Carolina, Georgia
Restricted, Coastal Plain vegetation	
Live oak–sea oats	Coastal Plain: North Carolina to Alabama
Pocosin	Coastal Plain: Virginia to South Carolina
Northern cordgrass prairie	Coastal Plain: Virginia, North Carolina
Restricted, Florida	
Mangrove forest	Coastal Plain: south Florida
Marl Everglades	Coastal Plain: south Florida
Everglades	Coastal Plain: south Florida
Subtropical pine forest	Coastal Plain: south Florida
Cypress savannah	Coastal Plain: south Florida
Sand pine scrub	Coastal Plain: Florida
Palmetto prairie	Coastal Plain: Florida
Other restricted types	
Cedar glades	Various sections: Tennessee, Alabama, Missouri, Arkansas
Blackbelt	Coastal Plain: Alabama, Mississippi
Bluestem–sachuista prairie	Coastal Plain: Texas, Louisiana
Southern cordgrass prairie	Coastal Plain: Texas, Louisiana
Rock outcrops	Scattered throughout the Southeast

Table 3. The distribution of the 24 Küchler (1964) types of potential natural vegetation mapped in the Southeast.

environmental factors (including heat, moisture, seasonality, and dynamics. The lowest two levels, alliance and community elements, are based on plant composition. The Nature Conservancy's draft scheme for its terrestrial system constitutes a rough index of ecosystem variation in the Southeast (Table 4). The scheme includes 480 alliances and 629 community elements (The Nature Conservancy and Environmental Systems Research Institute 1994). Over one-half (274) of the alliances are in the forest or woodland physiognomic class (versus 13 forest vegetation types in Küchler 1964; Table 3).

These large numbers of alliances and elements partly reflect the difficulty of classifying the Southeast's plant communities. Southeastern landscapes have mosaiclike arrangements of contrasting ecosystems and continuous variation between obvious extremes. Past disturbances, particularly fire, also have influenced ecosystem composition and boundaries. Even though the draft classification is an index to structural and compositional diversity, more work remains to be done.

Rare, Endangered, and Threatened Ecosystems

Grossman et al. (1994) used The Nature Conservancy classification to produce the first list of rare plant communities in the United States. Global ranks ("G" ranks) were assigned to each type of plant community based on the

Table 4. The Nature Conservancy's classification of structural and compositional variation in vegetation: the terrestrial system in the Southeast (Grossman et al. 1994; The Nature Conservancy and Environmental Systems Research Institute 1994).

Physiognomic class	Physiognomic subclass	Number of			
		Formation groups	Formations	Alliances	Community elements
Forest					
	Evergreen	4	12	72	99
	Deciduous	1	6	77	120
	Mixed	2	6	44	54
Woodland					
	Evergreen	2	8	46	77
	Deciduous	1	3	21	25
	Mixed	1	2	4	20
Sparse woodland					
	Evergreen	4	7	16	19
	Deciduous	2	8	16	16
	Mixed	1	4	5	5
Shrubland					
	Evergreen	3	7	31	36
	Deciduous	1	5	19	19
	Mixed	1	3	5	5
Sparse shrub					
	Evergreen	2	4	10	12
	Deciduous	1	2	3	3
Dwarf shrubland					
	Evergreen	1	2	4	4
	Deciduous	1	1	1	1
Sparse dwarf shrubland					
	Evergreen	1	3	3	3
Herbaceous					
	Tall grassland	2	10	32	40
	Medium-tall grassland	1	5	17	22
	Short grassland	1	5	7	7
	Tall forb	1	3	6	6
	Low forb	2	5	8	8
	Hydromorphic	2	3	12	16
Miscellaneous					
	Cliffs	1	2	5	5
	Saltwater	2	3	6	7

number of occurrences, areal extent, trends in areal extent, condition, threats, and fragility. Excluding Texas and Oklahoma (which are in The Nature Conservancy's Southeast Region, but which include many midwestern and western ecosystem types), there are 58 plant communities found throughout the Southeast that have global ranks of G1 or G2, of which 44 are endemic to this region. (G1 = most endangered; found in 1–5 occurrences globally. G2 = found in 6–20 occurrences globally; if found in 21–100 occurrrences, then found on fewer than 4,047 hectares total.) Twenty-one types occur in the Coastal Plain (excluding south Florida), 5 in south Florida, 17 in the southern Appalachian Mountains, and 11 in the continental interior (Table 5). Major threats to these communities are invasions by nonindigenous species, development, hydrological alteration, fire suppression, recreation, grazing, agricultural conversion, and fragmentation (Table 5).

Table 5. Summary of distributions and threats for The Nature Conservancy's 57 rare plant communities of the Southeast (after Grossman et al. 1994).

Geographic area	Habitat	Number of communities	Threats (number of community types)
Southern Appalachian Mountains	Spruce–fir	2	Nonindigenous species (5), recreation (4), air pollution (3), past logging (2), hydrological alteration (2), succession (1)
	Beech	2	
	Bog, fen	7	
	Grassy bald	1	
	Cliff, gorge	4	
	Other	1	
South Florida	Tropical hardwood	2	Development (4), nonindigenous species (4), hydrological alteration (2), fire suppression (2), burning (2), fragmentation (1), agriculture (1), recreation (1)
	Slash pine	3	
Coastal Plain	Barrier island	9	Development (9), grazing (7), fragmentation (6), hydrological alteration (5), fire suppression (5), nonindigenous species (5), agriculture (3), logging (3), mining (2), burning (2), recreation (2)
	Longleaf pine	3	
	Other forests	3	
	Glade, prairie	6	
Continental interior	Forest	7	Fire suppression (3), agriculture (3), recreation (2), grazing (2), logging (1), nonindigenous species (1), succession (1), mining (1), hydrological alteration (1)
	Glade, prairie	3	
	Other	1	
Other	Outcrop	1	Recreation (1), grazing (1), agriculture (1), hydrological alteration (1), fire suppression (1)
	Forest	1	
	Canebrake	1	

Noss et al. (1995) based their work on information sources similar to those used by Grossman et al. (1994), namely a survey of the State Heritage programs, but they also surveyed other researchers and reviewed published works. Unlike Grossman et al. (1994), Noss et al. (1995) did not attempt a hierarchical classification or a standard definition of types; thus, their ecosystem types are more generalized. The importance of the assessment by Noss et al. (1995) lies in its summary of trends in habitat loss and fragmentation. Our own review and discussion will follow the Noss et al. (1995) list closely.

If we allow for the broader definition of types in Noss et al. (1995), all of the 57 rare plant communities of Grossman et al. (1994) appear in the top categories of percentage loss (Table 5 versus Table 6). There are three ecosystems listed by Noss et al. (1995) but not by Grossman et al. (1994): old-growth deciduous forest (in the top category of endangerment), Atlantic white-cedar (listed because of habitat loss in two states rather than rangewide habitat loss), and cedar glades (listed because of habitat loss in one state). The lack of listing of old-growth forest by Grossman et al. (1994) pointed out that The Nature Conservancy's draft classification hierarchy does not include an important aspect of biological diversity conservation: an undisturbed remnant of a given community type may not differ in structure (closed forest) or dominance (the major variable for definition of alliances is canopy composition) from a second-growth forest and yet may possess intact soils and associated biological diversity (for example, understory herbs, soil biota, amphibians) that are absent from disturbed sites (Meier et al. 1995).

Noss et al. (1995) reported 50 endangered and threatened ecosystems in the Southeast: 14 critically endangered ecosystems (greater than 98% loss), 25 endangered ecosystems (85%–98% loss), and 11 threatened ecosystems (70%–84% loss). An additional 24 communities were reported as having at least 50% loss of area (Table 6). Major themes of loss on the Noss et al. (1995) list are as follows: old-growth forest because of logging, agriculture, and development (Tables 6 and 7); wetlands and bottomland forests because of hydrological alteration and conversion to agriculture (Tables 6 and 7); spruce–fir forests because of logging, an exotic insect invasion, and air pollution; longleaf pine and other pine ecosystems because of fire suppression and conversion to plantation forestry; prairies and glades because of grazing, development, fire suppression, and conversion to agriculture; Atlantic white-cedar because of logging and hydrological alteration; and maritime forests and other coastal communities because of development. Whether on private or public land, pristine areas and rare habitats in the Southeast have suffered heavy losses (Hackney et al. 1992; Martin et al. 1993a,b; Grossman et al. 1994; Noss et al. 1995). Further, human effects have permeated the region, rather than encroaching into the region along one or even several fronts.

Regionwide Themes of Change

As the previous overview indicates, changes in southeastern ecosystems include three major regionwide trends: loss of old-growth forest and pristine habitats in general, reduction in the importance of fire, and alterations to natural hydrology. We will further define these themes of change before discussing individual ecosystem types.

Ecosystem type	Geographic area
>98% loss: critically endangered	
Old-growth deciduous forests	Southeast
Southern Appalachian spruce–fir	Tennessee, North Carolina, Virginia
Longleaf pine	Coastal Plain
Rockland slash pine	Florida
Loblolly–short-leaf pine	West Gulf Coastal Plain
Canebrakes	Southeast
Bluegrass–savannah–woodland	Kentucky
Blackbelt prairie, Jackson prairie	Alabama, Mississippi
Dry prairie	Florida
Wet and mesic coastal prairies	Louisiana
Atlantic white-cedar	Virginia, North Carolina
Native prairies	Kentucky
Bottomland forest	West Virginia
High-quality oak–hickory	Cumberland Plateau, Tennessee
85%–98% loss: endangered	
Mesic limestone forest	Maryland
Red spruce	Central Appalachians
Spruce–fir forest	West Virginia
Upland hardwoods	Coastal Plain, Tennessee
Old-growth oak–hickory	Tennessee
Cedar glades	Tennessee
Longleaf pine	Texas, Louisiana
Longleaf pine forest, 1936–1987	Florida
Mississippi terrace prairie, calcareous prairie, Fleming glades	Louisiana
Live oak, live oak–hackberry	Louisiana
Prairie terrace–loess oak forest	Louisiana
Mature forest, all types	Louisiana
Short-leaf pine–oak–hickory	Louisiana
Mixed hardwood–loblolly pine	Louisiana
Xeric sandhill	Louisiana
Stream terrace–sandy woodland–savannah	Louisiana
Slash pine, 1900–1989	Florida
Gulf coast pitcher-plant bogs	Coastal Plain
Pocosins	Virginia
Mountain bogs	North Carolina
Appalachian bogs	Blue Ridge, Tennessee
Upland wetlands	Highland Rim, Tennessee
Aquatic mussel beds	Tennessee
Natural barrier island beaches	Maryland
Ultramafic glades	Virginia
70%–84% loss: threatened	
Bottomland and riparian forest	Southeast
Xeric scrub, scrubby flatwoods, sandhills	Lake Wales ridge, Florida
Tropical hardwood hammock	Florida Keys
Saline prairie	Louisiana
Upland longleaf pine	Louisiana
Live oak–pine–magnolia	Louisiana
Spruce pine–hardwood flatwoods	Louisiana
Xeric sandhill woodlands	Louisiana
Flatwood ponds	Louisiana
Slash pine–pondcypress–hardwood	Louisiana
Wet hardwood–loblolly pine	Louisiana
60%–70% loss	
Pocosins	Southeast Coastal Plain
Pocosins, 1952–1979	North Carolina
Sand pine	Florida
Baldcypress–tupelo	Mississippi, Tennessee
Mixed mesophytic forest	Cumberland Plateau, Tennessee
Bottomland forest	Tennessee
Oak–hickory forest area	Cumberland Plateau, Tennessee
Flatwoods–swale habitats	Florida
50%–60% loss	
Bottomland hardwood and baldcypress, 1900–1978	Southeast
Herbaceous marsh	Florida
Southern mesophytic forest	Louisiana
Calcareous forest	Louisiana
Hardwood slope forest	Louisiana
Freshwater marsh, interior saline marsh, interior salt flat	Louisiana
Scrub–shrub swamp	Louisiana
Baldcypress–tupelo swamp	Louisiana
Bayhead swamp	Louisiana
Small stream forest	Louisiana
Bottomland hardwoods	Louisiana
Cove hardwood forest	Blue Ridge, Tennessee
Barrier island dunes	Maryland
Coastal Plain seasonal ponds	Maryland
Cedar glade area	Tennessee
Cedar woodlands	Louisiana

Table 6. Estimates of ecosystem loss from Appendix A of Noss et al. (1995), compiled from published papers, State Natural Heritage programs, The Nature Conservancy, and expert opinions. Ecosystems are listed in declining order of percentage loss. As discussed in detail in Noss et al. (1995), some estimates are based on more quantitative analysis than others, and not all states had data to report.

Loss of Upland Old-Growth Forests

The Southeast's forests have overlapped broadly with intense human activities from Native American times to the present. Even though forests now make up 55% of the land in the Southeast, nearly all forests are second-growth, and many sites experienced soil erosion and loss of fertility during logging and agricultural use. Some logged lands have been converted to plantation forestry, a practice that results in low-diversity pine stands. Even surviving old-growth forests have experienced human-caused changes, including the loss of large grazing animals (for example, woodland bison and eastern elk), the loss of predators (for example, red wolves, gray wolves, and mountain lions), periods of understory livestock grazing (including by feral pigs), recent increases in white-tailed deer populations, invasions by nonindigenous species, and reductions in fire frequency. Some nonindigenous species have caused many adverse effects, (including wild boar in the mountains and feral pigs in the Coastal Plain, horses on some barrier islands, chestnut blight in the oak–chestnut forests of

Geographic area	Description	Loss (percent)
Alabama	Wetlands 1780–1980	50–60
Arkansas	Wetlands	70–84
Florida	Wetlands	25–50
	Original forest 1940–1980	27
Georgia	Wetlands	20–25
Piedmont	Original forest	70–84
Kentucky	Wetlands 1780–1980	70–84
	Old-growth forest	>98
Louisiana	Wetlands 1780–1980	25–50
Tensas Basin	Forested wetlands, since 1937	85
Mississippi	Wetlands 1780–1980	50–60
Maryland	Wetlands 1780–1980	70–84
North Carolina	Wetlands 1780–1980	25–50
South Carolina	Wetlands 1780–1980	25–50
Southeast Coastal Plain	Presettlement wetlands, 1986	25–50
Tennessee	Wetlands 1780–1980	50–60
Blue Ridge	Old-growth forest	85–98
Cumberland Plateau	Old-growth forest	85–98
Highland Rim	Upland wetlands	85
Texas	Wetlands 1780–1980	50–60
Big Thicket	Old-growth forest since 1960	85–98
Virginia	Wetlands 1780–1980	25–50
West Virginia	Wetlands 1780–1980	20–25

Table 7. Percentage losses of forest and wetland by geographic area. Wetland losses from Noss et al. (1995) and Dahl (1990). Losses of old-growth forest and forest area from Noss et al. (1995). Data for specific wetland types are listed in Table 6.

Texas Natural History: A Century of Change

The conservation of Texas's diverse and unique biota depends on reliable data about the flora and fauna of the region before it was negatively affected by humans. The recent discovery of the original files of a historical biological survey (conducted by the federal government from 1889 to 1906) gives a virtual natural history picture of every region of the state as it existed a century ago. This information provides crucial baseline data to compare with the results of current biological surveys and to assess landscape and biotic change information useful to land managers and others seeking to improve land and ecosystem management.

Texas was very different at the turn of this century; in 1900, the human population was fewer than 3 million, compared with about 17 million people today, and at the turn of the century more than 80% of the population was rural, compared with fewer than 20% today. Agriculture and ranching were the primary occupations then, whereas today the state is much more urbanized and industrialized.

Besides the biological diversity of Texas land, its other most significant characteristic is that about 97% of the land area is in private ownership, which is a major factor in biological resource management. Unlike other states, Texas entered the Union as an independent nation and retained its private lands, which were sold to pay indebtedness, build the government, and endow public schools.

The Biological Survey of Texas

Toward the end of the 1800's, the United States government established a new government program to inventory wildlife and assess its practical value. C. Hart Merriam was selected in 1885 to head this new division of the U.S. Department of Agriculture, called the U.S. Biological Survey (Sterling 1989). Merriam picked a series of states, including Texas, for intensive biological survey and inventory. Over about a 20-year period (1889–1906), a team of 12 scientists and field agents led by Vernon Bailey extensively surveyed the state. Bailey's most famous collaborator was ornithologist Harry C. Oberholser, who prepared the bird report. Bailey prepared the mammalian component and assembled the more incidental accounts of reptiles.

In Texas, the federal field agents worked an equivalent of more than 5 years of continuous fieldwork. They prepared written reports describing the state's physiography and plants and listing the birds and mammals they observed or captured at 178 different sites in all 10 ecological regions of the state. Many of these sites have changed dramatically.

The field agents devoted much work to mapping life zones and documenting agricultural crops and pests. They equated life zones with crop zones to help predict new crops that might be grown in the state; this was the practical part of the survey. Merriam, who believed that temperature was the predominant factor governing the distribution of plants and animals, divided Texas into three life zones: the lower austral zone, with a humid austroriparian region, its gulf coastal strip, and the more arid lower Sonoran divisions; the upper austral zone of the Staked Plains and the foothills of the western mountains; and the transition zone, which was restricted to the Chisos, Davis, and Guadalupe mountains above 1,850 meters in the Trans–Pecos region. The field agents developed a detailed map of these life zones and took more than 1,000 black-and-white photographs of Texas landscapes, habitats, plants, and animals. In addition, the agents developed numerous maps of plant and animal species and their distributions.

Bailey and the field agents relied heavily on local naturalists and landowners while conducting the survey. Bailey particularly relied on an Englishman named Howard Lacey, who owned a ranch near Kerrville in the Hill Country of central Texas. Bailey visited Lacey's Ranch (Fig. 1) on several occasions, and he named a new subspecies of mouse after Lacey from specimens he collected there.

Local residents contributed much to the wildlife information base in the historical survey. For example, Ab Carter, a farmer from the Big Thicket region in the southeastern part of the state, provided Bailey with information about the demise of bear populations in this area. According to Carter (Fig. 2), he and a neighbor personally helped kill 182 bears over a 2-year period within a 16-kilometer radius of their property in the Big Thicket.

The culmination of the survey was the 1905 publication, *Biological Survey of Texas* (Fig. 3), which was authored by Bailey and included information about life zones, reptiles, and mammals (Bailey 1905). Oberholser made his study of the bird life of Texas a life-long project; his report did not appear until 1974 (Oberholser 1974).

The Archival Project

The 1905 and 1974 publications are only a small part of the information generated by the survey. Other archival materials included scientific specimens of birds, mammals, and reptiles, museum catalogs of the scientific specimens, field-trip diaries describing the travels of the field agents, detailed biological reports of significant events, physiographic reports of each place visited in Texas, special correspondence with landowners and field agents, and the photographs previously described. These archival materials represent a detailed depiction of Texas natural history at the turn of the century.

Bailey's 1905 book has been out of print for more than 75 years. The associated

Photo 3015, National Photographic Archive, Washington, D.C.

Fig. 1. Lacey's Ranch near Kerrville, Kerr County, Texas, 1906.

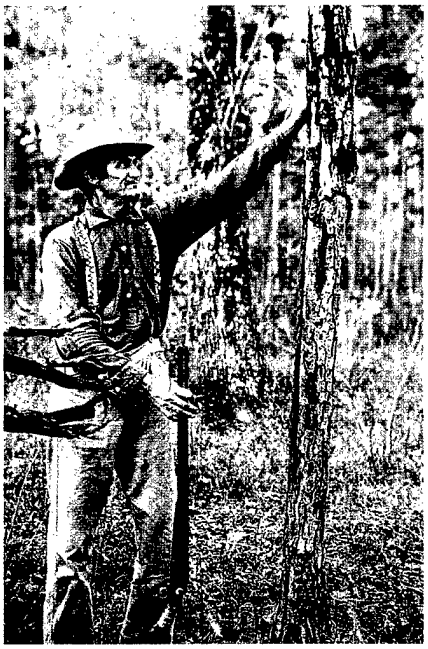


Photo 7236, National Photographic Archive, Washington, D.C.

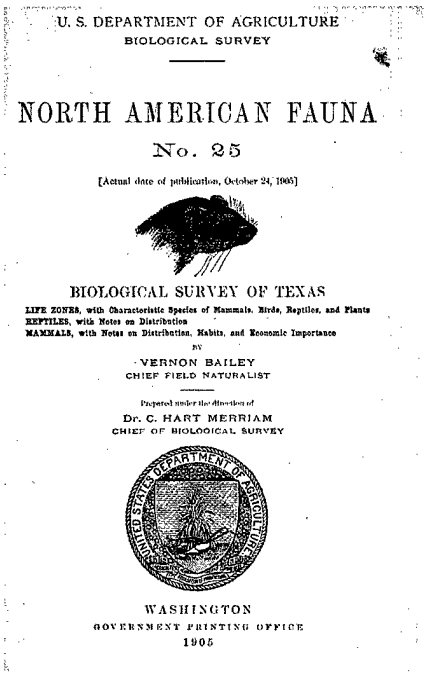
Fig. 2. Ab Carter, a bear hunter, stands next to a bear-gnawed tree near Tarkington Prairie, Hardin County, Texas, 1904.

archival materials are deposited at the Smithsonian Institution, but most modern biologists are unaware of the full scope of information that exists. In 1992 a project was initiated to document the archival natural history information from the Texas biological survey. The project has two objectives: to publish an annotated version of the original *Biological Survey of Texas* and to create a series of computer data bases by using the original documentation.

Five data bases of historical data are being created:

- Data base 1—a directory to the location of all files archived in the Smithsonian Institution;
- Data base 2—a description of each photograph available from the biological survey of Texas;
- Data base 3—the original survey reports (mammal, bird, plant, and physiography);
- Data base 4—field journals of the field agents; and
- Data base 5—specimen catalogs of the field agents.

The information obtained from current biological surveys of the state will be greatly enhanced by the availability of this historical data to document changes in species distribution, abundance, and diversity, as well as changes in land use. These historical documents also provide insight into public attitudes and the role of government agencies in conservation issues at the turn of the century.



U. S. DEPARTMENT OF AGRICULTURE
BIOLOGICAL SURVEY

NORTH AMERICAN FAUNA

No. 25

[Actual date of publication, October 24, 1905]

BIOLOGICAL SURVEY OF TEXAS

LIFE ZONES, with Characteristic Species of Mammals, Birds, Reptiles, and Plants
REPTILES, with Notes on Distribution
MAMMALS, with Notes on Distribution, Habits, and Economic Importance

BY

VERNON BAILEY
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WASHINGTON
GOVERNMENT PRINTING OFFICE
1905

Fig. 3. The title page of North American Fauna, *Biological Survey of Texas*, published in 1905 and authored by Vernon Bailey.

Changes in Texas Ecosystems

Mammals illustrate some of the patterns of faunal change in Texas during this century. Mammals and birds were the major types of vertebrates featured in the historical biological survey, and the publication of a recent book (Davis and Schmidly 1994) summarizing the current status of mammals provides a context for understanding change in this highly visible component of the fauna. The mammal survey by the federal biologists was comprehensive; Bailey documented 119 of the 141 native terrestrial species of mammals (about 85%) that occur in Texas today. The only group he failed to document accurately was bats (17 of 32 species), which is not surprising given that mist nets and modern bat-detection techniques were unavailable. Nine new taxa of mammals were described from material collected during the survey.

Although a detailed analysis of the archival material is not yet complete, some general statements can be made about past conditions and the extent of change in this century. For mammals, the most significant changes include the extinction of populations, subspecies, and species; introductions of nonindigenous species; and major changes in species or subspecies distributions.

Species extinctions have been common. By 1905 the only species of mammals extirpated from Texas were bison, grizzly bear, and elk, although several other species, such as beaver, black bear, spotted cats (ocelot and jaguar), pronghorn, and bighorn sheep, were markedly reduced in distribution or in numbers. Today, the gray wolf, red wolf, black-footed ferret, jaguar, margay, and the bighorn sheep have also been extirpated from the state.

Since the turn of the century, however, a few species have expanded their ranges—the nine-banded armadillo and the northern pygmy mouse are notable examples among mammals (Figs. 4 and 5)—whereas others, such as the pronghorn (Fig. 6), have undergone drastic range reductions. Entire populations of some subspecies, such as the hog-nosed skunk in the Big Thicket, have become extinct (Davis and Schmidly 1994).

Nonindigenous species, which were never encountered by Bailey, now openly range over much of the state. A prime example is the nutria, which was introduced into the state in the 1930's and now occurs

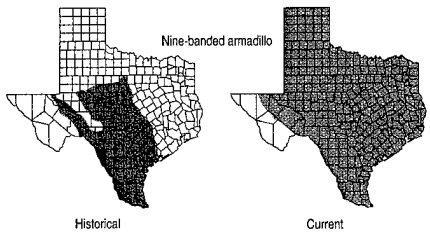

Fig. 4. Historical and current range of the nine-banded armadillo in Texas (adapted from Davis and Schmidly 1994).

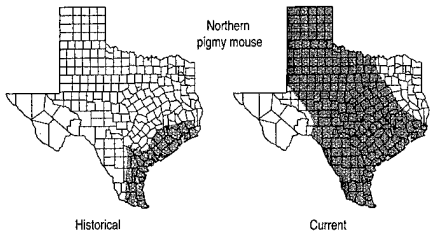

Fig. 5. Historical and current range of the northern pygmy mouse in Texas (adapted from Davis and Schmidly 1994).

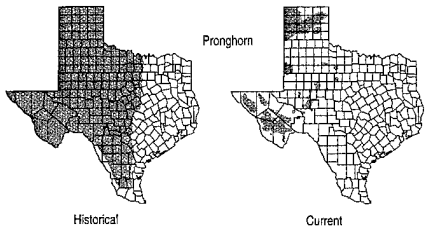

Fig. 6. Historical and current range of the pronghorn in Texas (adapted from Davis and Schmidly 1994).

over most of the eastern half of Texas and is still expanding its range. Ungulates introduced from Africa and Asia now occupy rangelands in proliferating numbers. During the 1990's, a colony of feral Japanese macaques even became established in south Texas.

Anthropogenic pressures on wild species today are totally different from those earlier in the century. In the early 1900's, overexploitation resulting from unregulated market hunting was a serious threat to wildlife. Poisoning, trapping, and unrestricted killing decimated many species (Fig. 7). Today, hunting of game species is an important management tool regulated by state law, and the revenue from hunting has become an effective market incentive for landowners to manage for wildlife habitat. Likewise, there are laws to prevent unregulated taking of endangered or threatened nongame species.

Today, the problems are mostly those related to wildlife habitats that have been destroyed, altered, and fragmented. Loss of critical habitat is the most serious threat to the modern fauna. Early Texas was a magnificent place, with a tremendous diversity of habitats, but human population growth and settlement through the past two centuries have significantly affected the state. Among the most altered places are prairies and grassland habitats, wetlands, riparian and riverine ecosystems, and the rangelands of the Edwards Plateau, Rolling Plains, the South Texas Plains, and the Texas Panhandle (Sansom 1996). When Texas entered the Union, it was the largest prairie state, but today fewer than 2,025 hectares of the original 5 million hectares of blackland prairies remain. Texas has lost more than 60% of its wetlands and about the same percentage of its bottomland hardwood forests (Baker 1995).

Photo 26611, National Photographic Archive, Washington, D.C.

Fig. 7. Trapper catch for 20 February 1904 (coyotes, bobcats, ocelots, raccoons) from Sauz Ranch, Cameron County, Texas.

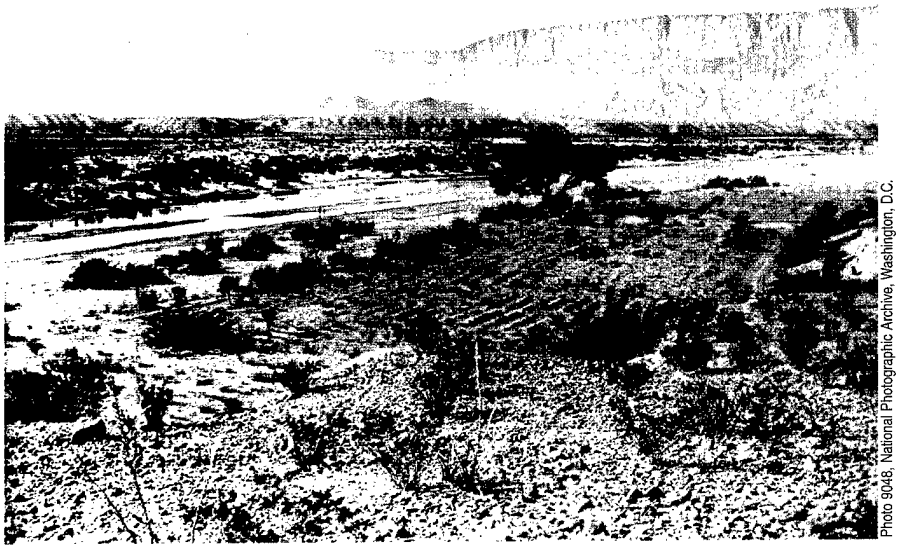

Photo 9048, National Photographic Archive, Washington, D.C.

Fig. 8. Lower entrance to Santa Elena Canyon of Rio Grande, Brewster County, Texas, 1901.

Comparison of old photographs taken by the survey field agents with modern landscapes from the same areas help document local habitat change. Bailey and his survey party were the first to survey wildlife in the Big Bend region of Texas, in what is today part of Big Bend National Park. One of their photographs (Fig. 8), taken at a working cattle ranch and farm near the mouth of Santa Elena Canyon, depicts open habitat and cottonwood trees along the river. Today this region is covered with a dense stand of river cane and introduced saltcedar, with few native cottonwoods. It becomes evident when assessing the old photographs that the amount of natural, unpolluted surface water has declined greatly this century. Almost every photograph those agents took of a stream or river showed abundant natural surface water (Figs. 9 and 10), which is not true of most of those places today, although the total amount of surface water in the state is probably greater today because of the construction of tens of thousands of tanks and large reservoirs.

A little-appreciated but important factor affecting natural ecosystems in Texas today has been the rapid change in the land-tenure systems (Sansom 1996). Unfortunately, an unprecedented breakup of family lands is now occurring in many places, brought about by changing economic conditions, inheritance taxes, and a state financial structure that is extremely dependent on property taxes. For example, throughout much of central Texas, where only tiny remnants of the native landscape survive today, the average tract size in many counties has dropped in this generation alone from thousands of hectares to fewer than one hundred. These areas, which once provided large blocks of land for wildlife habitat and outdoor recreation, now consist of tiny plots of introduced vegetation that cannot sustain the native wildlife. Meanwhile, the fear of litigation and regulation has closed off lands whose owners once welcomed and cooperated with scientists and conservationists.

Conservation Challenges

Successful wildlife conservation in Texas requires finding a way to involve landowners in a positive way by providing them incentives to manage for wildlife habitat and to cooperate with scientists and state and federal land managers in conservation programs and practices (Bartlett 1995). No effective conservation can exist without the support, participation, and cooperation of private landowners, many of whom fear that scientific knowledge will be used to usurp their landowner rights. Again, a valuable lesson can be learned from the old biological survey. The federal agents who worked in Texas relied on landowners for much of their information, and they saw the survey as benefiting landowners.

To conserve its wildlife diversity, Texas faces a daunting challenge. If conservation is to be successful, it is imperative that disparate groups (landowners, private conservation organizations, commodity groups, and state and federal agencies) begin to communicate, build trust, and find consensus solutions that satisfy the goals of society. To avoid past mistakes we must understand what has happened to our fauna and flora. Conservationists working in Texas are fortunate in having a baseline inventory that provides a detailed and scientifically accurate description of the entire state. This archival information base can be exceptionally useful as we develop and implement future management strategies for our wildlife resources.

Photo 6144, National Photographic Archive, Washington, D.C.

Fig. 9. First Creek, Lipscomb County, Texas, 1903.

Acknowledgments

This project is sponsored by The Texas Nature Conservancy with funding from the Robert and Helen Kleberg Foundation. Funds also were provided to the author by the Wray Foundation. W. Cox, assistant archivist at the Smithsonian Institution Archives, graciously assisted with locating archival materials. L. Bradley, research scientist, organized and computerized the archival materials.

See end of chapter for references

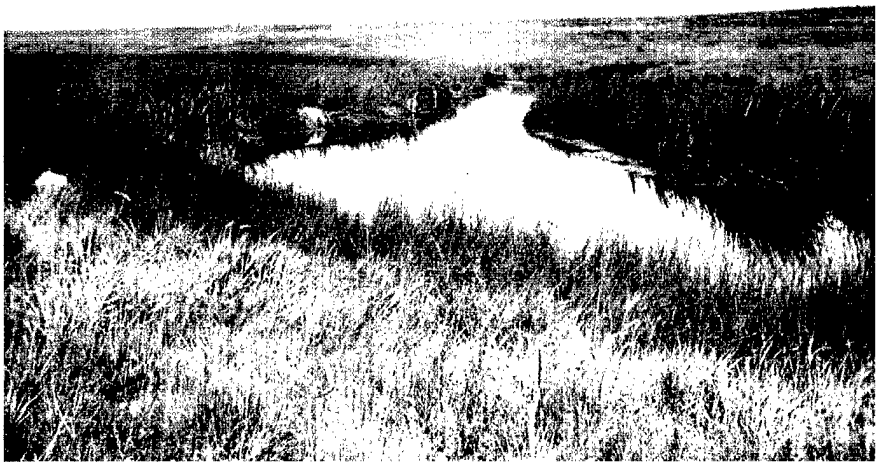

Photo 3187, National Photographic Archive, Washington, D.C.

Fig. 10. Tierra Blanca Creek, near Hereford, Deaf Smith County, Texas, 1901.

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Environmental Change in South Texas

South Texas is bounded on one side by Mexico and the Rio Grande River and on the other side by the Gulf of Mexico and its barrier islands and bays (Fig. 1). Between these boundaries lies the Texas Lower Rio Grande valley, one of the nation's most important agricultural regions, producing fruit, vegetables, sugarcane, grain, cotton, and beef. Sensitive or imperiled environmental resources of south Texas include native Tamaulipan brushlands, the seagrasses and tidal flats of Laguna Madre, and the Rio Grande itself.

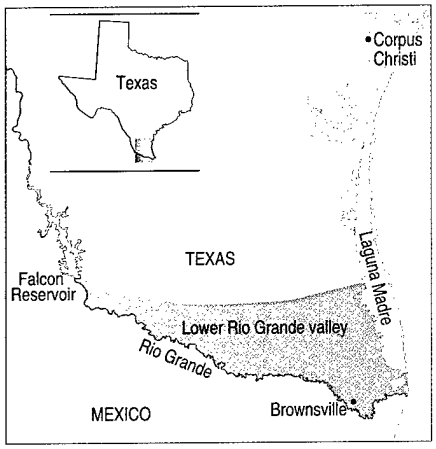

Fig. 1. South Texas.

The most important human-caused components of environmental change over the last 30 years have been water diversion and flood control, brushland clearing, human population increases, contaminants, and continued dredging of the Intracoastal Waterway in Laguna Madre. Extensive agriculture has fragmented and reduced the areas of native ecosystems. The North American Free Trade Agreement will play an as-yet unknown part in the future of environmental change in south Texas. In addition to human effects, parts of the Rio Grande watershed have been in a severe drought since 1993, exacerbating water quantity and quality problems. Also, an unprecedented chrysophyte algal bloom, known as the brown tide, has persisted in the Laguna Madre for more than 5 years.

Tamaulipan Brushland

Tamaulipan brushland is a unique ecosystem that dominates the Lower Rio Grande valley. Although Tamaulipan brushland is composed of several distinct biotic communities, all are characterized by dense, woody, and usually thorny vegetation and high biological diversity (Jahrsdoerfer and Leslie 1988). Vegetation is taller and lusher in the riparian areas (Fig. 2) than in the dry uplands (Fig. 3). Uplands are sometimes veined with thin riparian areas known as *ramaderos*, which not only provide important nesting and feeding habitat but also serve as corridors for animal movement. Tamaulipan brushland is home to more than 600 vertebrate species and more than 1,100 species of plants (Jahrsdoerfer and Leslie 1988). Many animals and plants of this area are found nowhere else in the United States, including two endangered cats, the jaguarundi and the ocelot.

Clearing of Tamaulipan brushland for agriculture started in the early 1900's. By 1988 more than 95% of all brushland habitat had been cleared for agricultural or urban use, including more than 90% of the riparian habitat (Fig. 4). Little of what remains in private holdings is expected to last until the end of this century. Remaining brushland often occurs in small, fragmented pieces, which are not in themselves capable of supporting the naturally high biological diversity of this ecosystem (Howe et al. 1986). To preserve and integrate what remains of this unique habitat, the U.S. Fish and Wildlife Service is purchasing land and easements in the Lower Rio Grande valley to form the Rio Grande Valley Wildlife Corridor, which now includes 25,000 hectares of federally managed land; the U.S. Fish and Wildlife Service plans eventually to double that amount (L. Ditto, U.S. Fish and Wildlife Service, McAllen, Texas, personal communication).

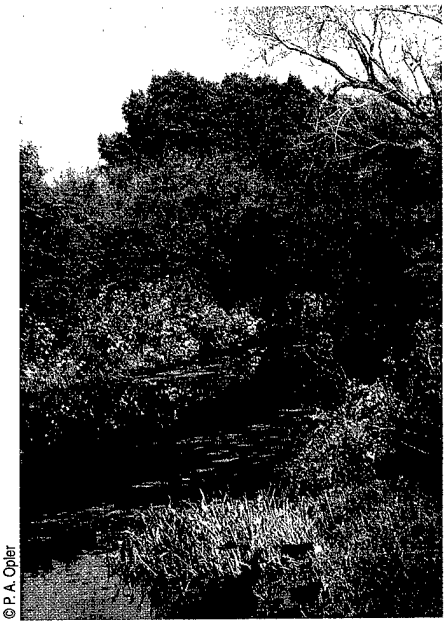
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Fig. 2. Riparian area in Tamaulipan brushland, Santa Margarita Ranch.

Laguna Madre

Laguna Madre extends the whole length of the south Texas coast from Corpus Christi Bay to the Mexican border. It is 200 kilometers long, with a maximum width of

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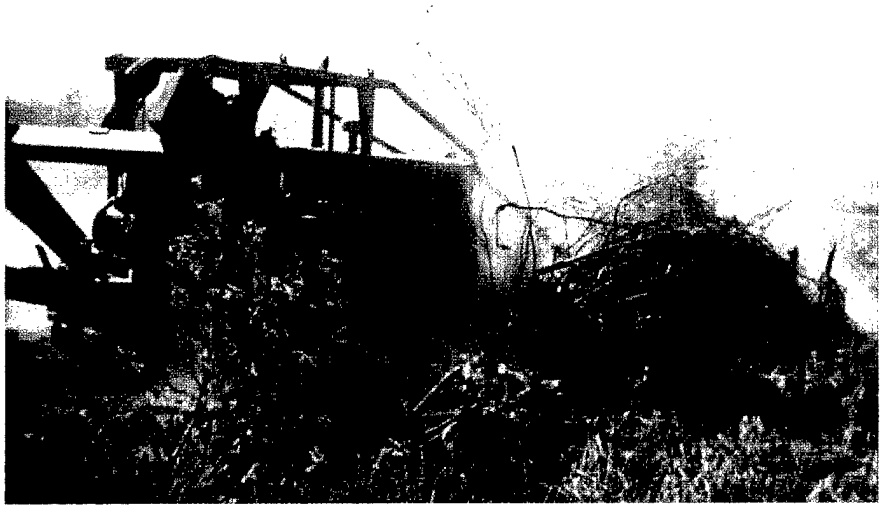
Fig. 3. Upland vegetation in Tamaulipan brushland, with palmettos.



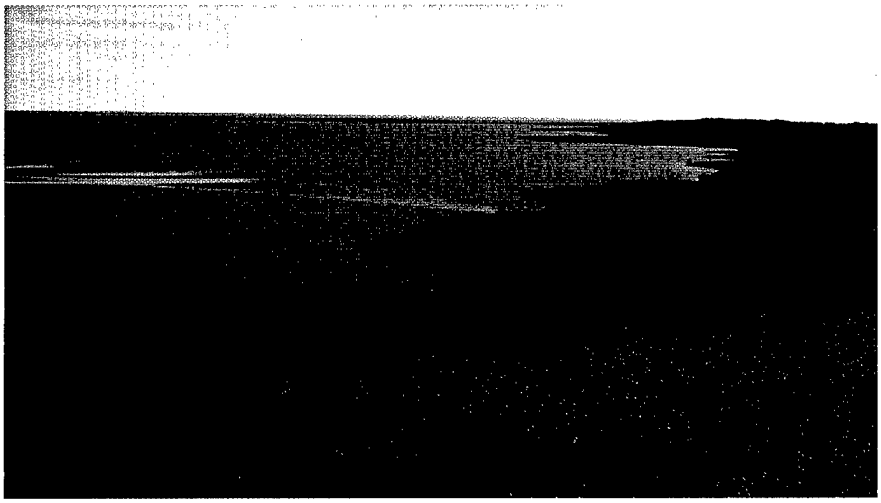
Courtesy A. Coykendall, U.S. Fish and Wildlife Service

Fig. 4. The clearing of Tamaulipan brushland.

11 kilometers, and is one of the few hypersaline lagoon systems in the world. Laguna Madre supports 75% of Texas's seagrass meadows (Fig. 5). The status of seagrasses in Laguna Madre is a great concern to resource managers because seagrass meadows are valuable nursery areas for wildlife. One species of seagrass, shoal grass, is the sole food of redheads on their most important wintering area. Between the mid-1960's and 1988, in the lower Laguna Madre, seagrass cover was lost over 150 square kilometers because of reduced water clarity caused by maintenance dredging (Onuf 1994). Seagrass was displaced over another 190 square kilometers as a result of long-term salinity moderation. The principal causes of salinity moderation were the excavation of a permanent water connection between the upper and lower Laguna Madre in 1949 (the Gulf Intracoastal Waterway) and the increased base flows from Arroyo Colorado and other agricultural drains (Quammen and Onuf 1993). Although seagrass cover increased in the upper Laguna Madre over the same period, the lagoon as a whole suffered a 30% decline of seagrass between the mid-1960's and 1988.

Since June 1990, brown tide, a monospecific algal bloom of unprecedented duration, has occurred in Laguna Madre. The brown tide is most concentrated in the upper Laguna Madre, except in winter when the focus shifts to the northern part of the lower Laguna Madre under the influence of the strong north winds accompanying cold fronts. Although high salinity and a nutrient pulse from a fish and invertebrate kill caused by a hard freeze promoted the development of the bloom, its unprecedented persistence is not understood (Stockwell et al. 1993). Contributing factors include low levels of zooplankton grazing on the brown tide alga, limited flushing of the lagoon, and the input of added nutrients, all of which require further investigation to determine whether management is feasible. Shading of seagrasses by the brown tide resulted in reduced seagrass biomass in deeper parts of upper Laguna Madre in 1991 compared with 1988 and even more severe reductions in 1992. By 1993, 3 square kilometers of seagrass meadow were bare, and by January 1995, the holes in the meadow had expanded to 9 square kilometers. Based on minimum light requirements of seagrass, 20–30 square kilometers will be bare by the time the distribution of zooplankton reaches a steady state with the brown tide-influenced light regime (Onuf 1996).

Plans are now in place for construction of the Gulf Intracoastal Waterway in Mexico. Expanded use of the canal system will increase the need for methods of dredge material disposal that will protect seagrass resources by minimizing effects on water



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Courtesy D. Chapman, USGS

Fig. 5. Laguna Madre and its fringing salt marshes.

clarity. Also, disposal of dredge materials may interrupt the necessary hydrological connection between the lagoon and the fringing expanses of wind tidal flats. Although these tidal flats are infrequently flooded, they support dense blue-green algal mats, are essential habitat for species of concern such as piping plovers, snowy plovers, and reddish egrets, and are important staging areas for peregrine falcons. Appropriate placement of dredge materials will be critical to the conservation of biological resources along the waterway as it is constructed through Mexico's Laguna Madre.

Irrigation, Water Diversions, and the Rio Grande

The Rio Grande is almost 3,200 kilometers long, the second-longest river in the United States. Despite this length, it is dwarfed in discharge volume by many of the nation's other rivers. Although the Rio Grande's snow-fed beginning is in the Rocky Mountains of southern Colorado, the river winds most of its length through hot and arid regions. Because of water withdrawals and drought, some stretches occasionally are completely dry. In these arid lands, the Rio Grande's water is critical to native flora and fauna and to human development. Between 243,000 and 283,500 hectares of land are irrigated each year by Rio Grande water in the Lower Rio Grande valley alone. This amount has remained fairly constant over the last 40 years because little additional appropriate uncultivated land remains (Fig. 6).

The Lower Rio Grande valley is not truly a valley but a broad delta with a single existing distributary, the Arroyo Colorado, which is now disconnected from the river. In the Lower Rio Grande valley, irrigation water that does not evaporate does not return to the river, as would be the case for most irrigated areas. Instead it passes through drainage systems into the Arroyo Colorado and the North Floodway, which function as huge drainage structures for the Lower Rio Grande valley. Municipal and industrial discharges are also added to the Arroyo Colorado, which eventually empties into the Laguna Madre approximately 72 kilometers north of the Rio Grande's mouth. Although the Arroyo Colorado is used for recreation, it is highly contaminated, and pollution-induced oxygen depletions are common (Jahrsdoerfer and Leslie 1988).

The hydrology of the Rio Grande is tightly controlled for much of its length by dams and channelization. Withdrawals for irrigation and municipal use occur along the length of the Rio Grande and its tributaries. Because of upstream diversions, most of the water that the Rio Grande delivers to the lower valley is attributable to the Rio Conchos, a tributary that drains the state of Chihuahua in Mexico (Vi Risser 1995). As is true in most desert regions, annual precipitation in Chihuahua is highly variable and results in corresponding variability in the Rio Conchos discharge (Fig. 7). The Chihuahua province was in a severe drought between 1993 and 1996. Discharge from the Rio Conchos in 1995 was extremely low, and the Rio Grande in the Big Bend National Park and the 314-kilometer section of the Rio Grande designated as a National Wild and Scenic River were barely flowing during parts of 1995 (J. Cisneros, National Park Service, Big Bend National Park, personal communication).

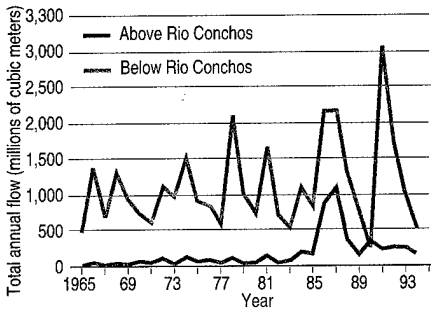

Fig. 7. Total annual flow of the Rio Grande at sites above and below the confluence of the Rio Conchos, in millions of cubic meters. Data from the International Boundary and Water Commission.

As a hedge against future droughts, the Mexican government plans to increase water-holding capacity in the Rio Conchos watershed. In the long term, this will likely reduce the water that reaches the Rio Grande. Ironically, the Colorado and New Mexico mountains have experienced heavy snowfall in recent years, and New Mexico reservoirs are full. Because of legal water rights, little of this water is available to Texas and Mexico downstream of El Paso (Vi Risser 1995). Other rivers, such as the Pecos and Devil rivers on the United States side and the San Juan and Salado rivers on the Mexican side, join the Rio Grande below the National Wild and Scenic River section. Much of the water from these rivers is also diverted for agricultural and municipal use. Water diversions have reduced yearly average flow in the lower part of the Rio Grande by 30% to 50% (Edwards and Contreras-Balderas 1991). Despite and because of such reductions, Webb County has recently proposed that a new dam be built just above the city of Laredo.

Humans have altered the natural cycle of flooding in the Lower Rio Grande valley, which has decreased the quality and number of wetlands, especially the oxbow lakes known as *resacas*, an important wildlife habitat. Altered flood cycles in the Lower Rio Grande valley contribute to replacement of mesic riparian woodland trees with more xeric species such as mesquite (Jahrsdoerfer and Leslie 1988). Loss of the flood cycle has also been implicated in recent increases in nonindigenous species; native species are adapted to the periodic disruptions, which probably kept the nonindigenous species in check (Edwards and Contreras-Balderas 1991). The effects of channelization in the

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Fig. 6. Low water flows in the Rio Grande below Falcon Dam.

Rio Grande have not been studied, but in general the negative effects of channelization on aquatic and riparian biodiversity are well known.

Agricultural Contaminants

Agricultural chemicals (insecticides, herbicides, and fertilizers) are used yearround in the Lower Rio Grande valley. In 1986 more than 100 different chemicals were used on crops throughout the region (U.S. Fish and Wildlife Service 1986). Six intensively used pesticides are atrazine, aldicarb, dicrotophos, methomyl, carbofuran, and dicamba (Bryant et al. 1993; see chapter on Environmental Contaminants). Agricultural chemicals reach surface waters through aerial application and subsequent drift and overspray, field runoff, and irrigation return flows. Resacas and other aquatic environments accumulate contaminants in their sediments. The Arroyo Colorado and other agricultural drains route potentially dangerous amounts of agricultural, municipal, and industrial contaminants to the Laguna Madre, a sensitive, shallow estuary that has little water exchange with the Gulf of Mexico (White et al. 1983; Custer and Mitchell 1987, 1991).

The proximity of agricultural lands to Lower Rio Grande valley refuges and the importance of the valley as a migratory bird flyway increase the potential for adverse effects on fish and wildlife. The aplomado falcon, an endangered species recently reintroduced at Laguna Atascosa National Wildlife Refuge, feeds on dragonflies, other insects, and small birds that may be accumulating contaminants from cultivated fields. A study of mosquitofishes from the Lower Rio Grande valley demonstrated that fishes can develop inheritable resistance to the lethal effects of pesticides (Andreasen 1985). Organisms that accumulate high concentrations of contaminants are a potential threat to species higher on the food chain.

Irrigation of salt-bearing soils in the region often results in return flows with a high dissolved salt content. Salinity in some agricultural drains regularly exceeds four parts per thousand (International Boundary and Water Commission 1992). The Pecos River is a major contributor to salinity of the Rio Grande because of natural salt deposits within the New Mexico portion of its watershed. Increased salinity in the Rio Grande negatively affects native fishes and encourages invasion by nonindigenous species such as the salt-tolerant blue tilapia, now the dominant fish species in the Brownsville area. Some reduced abundance of freshwater species also may be due in part to the expansion of salt-tolerant estuarine species upstream (Edwards and Contreras-Balderas 1991). Increased salinity threatens human use of the water as well, because water may become too salty for agricultural use and human consumption.

Industrial and Municipal Effects

Until 30 years ago, contamination in the Lower Rio Grande valley was primarily associated with agriculture. Since then, urbanization and economic development programs have significantly altered the border area. Today the valley is affected not only by chemicals and fertilizers from crop production but also by a wide range of municipal and industrial pollutants.

Maquiladoras are production plants in Mexico that process or assemble components from United States businesses into finished products, then send the products back to the United States. There are now 224 maquiladoras in the Mexican Lower Rio Grande valley, and until recently, the waste they generate has not been seriously regulated. Data pertaining to this waste are scarce, but it has been estimated that as little as 30% of maquiladora wastes are repatriated as required by United States–Mexico agreements, and that 98% of maquiladoras lack treatment systems for their wastewaters. Texas has recently developed a new tracking system for waste generated in Mexico, which may ameliorate part of this problem, but according to the World Bank, many maquiladoras are suspected of storing or illegally disposing of their waste byproducts. The maquiladora industry was initially predicted to grow under the North American Free Trade Agreement by a moderate 7% to 10% per year, but these forecasts have been revised to 29% per year; the first 6 months of 1995 saw a 67% rise in maquila permits over 1994.

Mariculture, the cultivation of marine organisms, is a new and expanding agroindustry in the region and is an additional source of contaminants and nutrients to the Arroyo Colorado and the Laguna Madre. The threat of introduction of nonindigenous species and their diseases by mariculture operations is currently a high-visibility environmental concern.

Air quality in the Lower Rio Grande valley is affected by several sources, including localized problems due to vehicular traffic between the United States and Mexico, sugarcane burning, brick manufacturing, and maquiladora industries. A 1,400-megawatt, coal-fired electric generating plant across the border from Eagle Pass about 200 kilometers south of Big Bend National Park is of great concern. This plant, which recently became fully operational, is projected to contribute 250,000 tons of sulfur dioxide per year to the atmosphere.

Human population has sharply increased in the Lower Rio Grande valley over the last 30 years (Fig. 8), and because of poverty and the low tax base of the region, the infrastructure has not kept pace. Part of the population increase in the region is in impoverished, rural, unincorporated subdivisions known as *colonias*, which are characterized by substandard living conditions, most without sewage treatment systems. In 1995 there were approximately 1,400 colonias and 340,000 colonia residents in south Texas (Texas Water Development Board 1995). The number of people now living in colonias is about two-thirds of the entire 1970 population of the Texas Lower Rio Grande valley. Lack of sewage treatment in colonias contributes to contamination of groundwater and surface waters and is a human health problem. Release of untreated wastewater from Mexican municipalities into the Rio Grande is an even greater problem.

The Mexican population of about 8 million persons in the Rio Grande basin is 4 times the population on the United States portion of the Rio Grande watershed (Colorado, New Mexico, and Texas combined). Most of these people reside in cities with little or no sewage treatment (Texas Natural Resource Conservation Commission 1994). However, an environmental side agreement to the North American Free Trade Agreement created the Border Environment Cooperation Commission and the North American

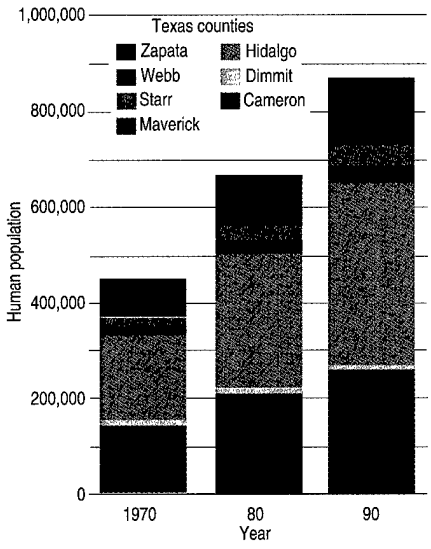

Fig. 8. Human population of Lower Rio Grande valley counties bordering the Rio Grande in Texas. Data from the U.S. Bureau of Reclamation (1995).

Development Bank, agencies charged with organizing and financing the environmental infrastructure of the region. Costs for wastewater treatment plants for Mexican border towns alone are expected to reach 2 billion dollars (Texas Natural Resources Conservation Commission 1994).

See end of chapter for references

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the Appalachians, and more recently, gypsy moth infestations and dogwood anthracnose disease, both of which are increasing in the Southeast).

The old-growth stands represent only a part of the original productivity gradient. The most productive sites (moist, nutrient-rich sites on deep soils) were selected for and have generally remained in agricultural use. For example, the Great Valley (part of the Ridge and Valley province) between the southern Appalachians and the Cumberland Plateau in east Tennessee is dominated by farmland over large areas. Forests are restricted to dry sandstone ridges, most wetlands have been drained, and no old-growth forests remain.

Less than 0.1% of the original upland forests is estimated to have survived (Parker 1989; Martin et al. 1993b; Noss et al. 1995; White and White 1995). Stahle and Chaney (1994) reported a somewhat higher value (0.78%) for oak–hickory on poor, noncommercial sites in Arkansas. Davis (1995) described a total of only 237,061 hectares of known primary forest in the Southeast. In general, the surviving old-growth forests represent a biased sample of the original forests; they tend to be on steeper, drier, rockier, or wetter sites that were harder to farm or less valuable for harvest (reviewed by White and White 1995). These remnant stands have not received sufficient study for conclusions to be drawn about the differences in biological diversity that exist between old-growth and second-growth forests. Except for the mountains, remnants of old-growth forest are very small, mostly less than 100 hectares.

Even though most mountain forests were logged, Great Smoky Mountains National Park and several national forests protect exceptional remnants of old-growth forest, including some of the largest such tracts in the eastern United States. On mesic sites, trees reach 2.5 meters in diameter, 40 meters in height, and 300–500 years in age (Yost et al. 1994). In some unlogged forests, however, the nonindigenous chestnut blight fungus decimated one of the largest tree species, American chestnut, between 1920 and 1950 (Fig. 3). This species was widely distributed on environmental gradients, dominating submesic to subxeric sites, and was a consistent bearer of hard mast, an important resource for wildlife populations. Chestnuts grew in species-rich forests, and the species' competitors increased as it declined. No loss of vertebrate or plant species has yet occurred (chestnut sprouts continue to decline with age, indicating a gradual loss of the gene pool and species [Griffin 1992; Parker et al. 1993]), but at least one moth species has become extinct as the result of the chestnut decline (Opler 1978). In addition, several insects living in association with chestnuts were lost. Mesic old-growth forests dominated by other hardwoods and hemlock have been minimally affected by chestnut blight, but two other nonindigenous insect species now expanding toward the Southeast—hemlock woolly adelgid (found as far south as Virginia) and gypsy moth (detected in many

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Fig. 3. Downed logs of American chestnut are conspicuous against a snowy background in the southern Appalachians. Eliminated as a dominant tree by the exotic chestnut blight from eastern Asia, the American chestnut was a forest dominant over wide areas of the eastern United States. Chestnuts were an important food for forest wildlife.

places in the Southeast but not yet causing outbreaks south of Virginia and the northeastern mountains of North Carolina)—have the potential of forever altering the last old-growth stands in the mountains just as another nonindigenous insect, the balsam woolly adelgid, has already drastically altered the high-elevation, old-growth spruce–fir forests saved from logging.

Duffy and Meier (1992) stimulated an important controversy in reporting that logged stands had lower diversities of spring wildflowers than old-growth stands (Elliott and Loftis 1993; Johnson et al. 1993). Meier et al. (1995) confirmed earlier results and argued that other taxa, such as salamanders, also show negative long-term effects of clear-cut logging. Although the trend has certainly been toward lower diversity for most groups, more work is needed on the effects of past land-use practices on biological diversity in the southern Appalachians and on techniques to restore previously farmed or logged lands to their former conditions.

Inventories are now under way on federal lands to map and evaluate the remnant old-growth stands (for example, Yost et al. 1994). These inventories will be critical for drafting a regional plan for the conservation of these unique remnants of the presettlement Southeast.

Fire Suppression

Fire was and is important to many southeastern ecosystems, including many Coastal Plain and south Florida ecosystems, pine-dominated forests of the Coastal Plain and Appalachian Highlands, oak and oak–hickory forests, oak savannas, glades, barrens, and prairies. Because most natural communities in the Southeast are dependent on fire, more than 50% of the rarest plants in the region also possess this dependence. Fire may also explain the occurrence of canebrakes, dense stands of the Southeast's only native bamboo, which were frequently described by earlier travelers but which have vanished from the landscape except for small remnant patches (Noss et al. 1995; Fig. 4). Although natural fires were quite important, Native Americans and European settlers also set fires frequently. When fire suppression became effective in the 1940's, dramatic changes in ecosystem composition and structure began.

Pine dominance was produced by intense fires, with subsequent lower intensity fires reducing competing hardwoods in the pine understories. Given the age of pine stands, intense, stand-initiating fires must have occurred at least once every 100–200 years; less intense fires occurred much more frequently—every 2–12 years. In the absence of fire, oak, hickory, and pine replace longleaf pine on the Coastal Plain (Stout and Marion 1993), and oak-dominated forests replace pitch pine and Table Mountain pine on the dry ridges of the Appalachians. The net trend of these landscapes is away from pine-dominated ecosystems, leading to declines in species associated with those systems.

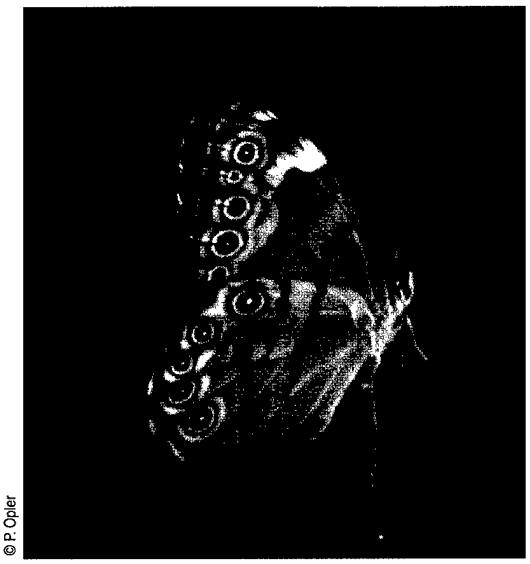

Fig. 4. Creole pearly eye, a butterfly whose caterpillars feed on switch cane. This insect is limited to swamp forests and dense cove forests in the Southeast.

Outbreaks of the native southern pine beetle can not only hasten the succession from pine to hardwoods but can also result in high fuel loads. On dry topographic sites and in drought years, high-intensity fires can occur because of these fuel loads. Such hot summer fires are critical to pine regeneration.

Although oaks and hickories increase on the driest sites with reductions in fire, these trees are declining on moister sites where fire was important in limiting mesic hardwoods (Christensen 1977). Thus, throughout the Southeast, there is a general trend toward an expansion of mesic species and a contraction of dry-adapted and fire-dependent species. Understory stem densities have also increased. A failure of oak to regenerate on sites where the species now dominates is a widely observed phenomenon in the eastern United States. McGee (1986) and other researchers hypothesized that this change is caused not only by fire suppression but also by other factors such as air pollution (Kessler 1989). Low fire frequencies have also allowed woody plants to invade the glades, barrens, and prairies once associated with oak and hickory forests. Early descriptions of the southeastern landscape suggest frequent forest openings, larger areas of grassland and savanna, and upland forests with open understories (Skeen et al. 1993).

Changes in Hydrology and Water Quality

Alteration to the hydrological regime is a common disturbance in a variety of southeastern ecosystems: bottomland and floodplain forests, mountain bogs, rocky stream gorges,

longleaf pine savanna, Carolina bays, pocosins, Atlantic white-cedar swamps, barrier-island communities, mangrove forests, rivers, streams, caves, lakes, and the Everglades mosaic of communities. Hydrological change has altered flood depth, duration, frequency, and seasonal timing in many of these systems, leading to a raising and lowering of the water table in specific cases.

Hydrological change is caused by sedimentation, construction of dams and other barriers, and channelization (Adams and Hackney 1992). Portions of almost all major southeastern rivers have been impounded during the last 75 years. For example, a 1974 stream survey in Maryland showed that all 14 drainages in 17 tidewater counties had dams (258) or other blockages (89; Lee et al. 1984). Other barriers include farm or mill pond dams, weirs, and raised culverts. Dams result in changes to water temperature and unpredictable releases of water. Channelization, which includes straightening the streambed, smoothing bottom contours, and removing logs, obstructions, and plants, alters the rate and timing of water flow (the local water table is lowered, resulting in increased flooding downstream), aquatic productivity, microhabitats within the channel, and food webs. Sedimentation, blockages, and channelization often occur within one river system, leading to decreases in native fishes and other aquatic species, a loss of species intolerant of such changes, and increases in tolerant species and nonindigenous species (Crumby et al. 1990).

The dynamics of flooding and meandering rivers are a major natural process in southeastern ecosystems. Many plant and animal species are dependent on the natural dynamics of water flow. The overall tendency is for human influence to make a dynamic environmental factor less variable. Succession favors the species best adapted to the more uniform conditions, and diversity decreases. In natural systems, however, extreme hydrological events are an important agent in the maintenance of species diversity.

Other factors responsible for depletion of aquatic faunas are pollution (including chemical and thermal pollution) and introduction of nonindigenous fishes and aquatic plants. Invasive nonindigenous plants that are capable of altering function (for example, hydrology, amount of photosynthesis, and food webs) in aquatic systems in the Southeast include Eurasian watermilfoil, hydrilla, parrot feather watermilfoil, curlyleaf pondweed, water hyacinth, and water chestnut (Hotchkiss 1967; Lachner et al. 1970).

In recent years, the Clean Water Act has done much to reduce point sources of pollution by requiring water treatment. Nonpoint-source pollution and sedimentation are harder to control, though. Sedimentation is a serious problem for most aquatic organisms, particularly primary producers as well as benthic (bottom-dwelling) macroinvertebrates and fishes that require gravel or rock substrates. Medium-sized rivers are particularly vulnerable to alteration of substrate composition and texture (Etnier and Starnes 1991).

Status and Trends of Southeastern Ecosystems

In this section, we review trends for ecosystems that are known or suspected to be experiencing loss of diversity. Our list was developed from Boyce and Martin (1993), Grossman et al. (1994), and Noss et al. (1995; Table 8). Because vertebrates often range across ecosystem types and reveal the linkage between terrestrial and aquatic systems, they often experience similar trends or threats across ecosystem types; for these reasons, we have included summary sections for fishes (in the aquatic section) and for reptiles and amphibians, birds, and mammals (at the end of the sections on ecosystems). In the course of this overview, we also present summary sections for other groups.

Table 8. Ecosystems discussed in this chapter, with cross-references to Boyce and Martin (1993), Grossman et al. (1994), and Noss et al. (1995). Boyce and Martin (1993) placed ecosystems of concern in three categories: resilient (upland areas that were still forested, though much affected by human impacts), threatened, and remnant or island-like (isolated habitats that were formerly more widespread than at the present, whether in historical or geological time).

Ecosystem	Boyce and Martin (1993)	Grossman et al. (1994)	Noss et al. (1995)
Widely distributed			
Upland forest	Resilient	x	x
Bottomland forest	Threatened		x
Glade, barren, and prairie	Remnant	x	x
Mountains			
Spruce–fir forest	Remnant	x	x
High-elevation deciduous forest	Remnant	x	
Heath bald	Remnant		
Pine forests			
Mountain bog	Threatened	x	x
Grassy bald		x	
High-elevation cliff	Remnant	x	
Rocky stream gorge	Remnant	x	
Coastal Plain			
Longleaf pine forest	Remnant	x	x
Carolina bay	Threatened		x
Pocosin	Threatened		x
Atlantic white-cedar forest	Threatened		x
Maritime communities	Remnant	x	x
South Florida			
Tropical hardwood		x	
Slash pine		x	x
Florida sand pine scrub	Remnant		
Mangrove	Threatened		
Everglades	Threatened		

Southern Appalachian Mountains

Spruce–Fir Forests

The southern Appalachian spruce–fir forest is disjunct from and compositionally different from the spruce–fir forests of the central and northern Appalachians (White and Cogbill 1992). For example, 12 species of vascular plants, including the narrowly restricted endemic Fraser fir, a dominant tree, occur only in southern Appalachian spruce–fir forests. Although more than one-half of the original extent of spruce–fir forest was protected as old-growth forest in the 1920's and 1930's, two human-caused changes have forever altered these ecosystems: invasion by nonindigenous insects and air pollution.

Until large-scale logging began in the late 1800's, these mountain forests were undisturbed because they were too steep and remote for settlement by either Native Americans or Europeans (Pyle and Schafale 1988). The original extent of the southern Appalachian spruce–fir forest has been estimated as 12,100–14,200 hectares (White and Cogbill 1992), but by 1930 logging had reduced this total by about one-half (Saunders 1979). Slash fires and severe soil erosion often followed logging, and some damaged sites remain in herbaceous or shrub-dominated vegetation, even after at least 70 years of succession.

Conservationists, though, were successful in bringing 93% of the remaining spruce–fir forest into public ownership, including the East's largest block of old-growth, spruce–fir forest, which was protected when the Great Smoky Mountains National Park was established in 1934. At that time, 50% of the original old-growth spruce–fir forest seemed to have been securely protected, by far the largest fraction of any southeastern ecosystem. These forests, though, were to be forever altered by human influences that are less obvious than logging.

Red spruce, the most valuable tree of these forests, failed to regenerate on logged lands. In the 1930's, foresters began trials of a variety of conifers in an early attempt at restoration. Unfortunately, these trials were probably the means by which a Eurasian insect, the balsam woolly adelgid, entered the southern Appalachians (Fig. 5). This pest proved devastating for the narrowly restricted endemic Fraser fir, a dominant of this system, and heavy mortality of this species began in the late 1950's. The pest has now spread throughout the southern Appalachians.

There is no practical way to eliminate the adelgid. Individual stands of Fraser fir (including fir plantations—Fraser fir is the South's most valuable and popular Christmas tree) and other trees can be sprayed, but this is costly and not always effective because of the difficulty of reaching all feeding sites on the trees. In the short term, seed samples of the genetic diversity of Fraser fir must be stored for possible future restoration.

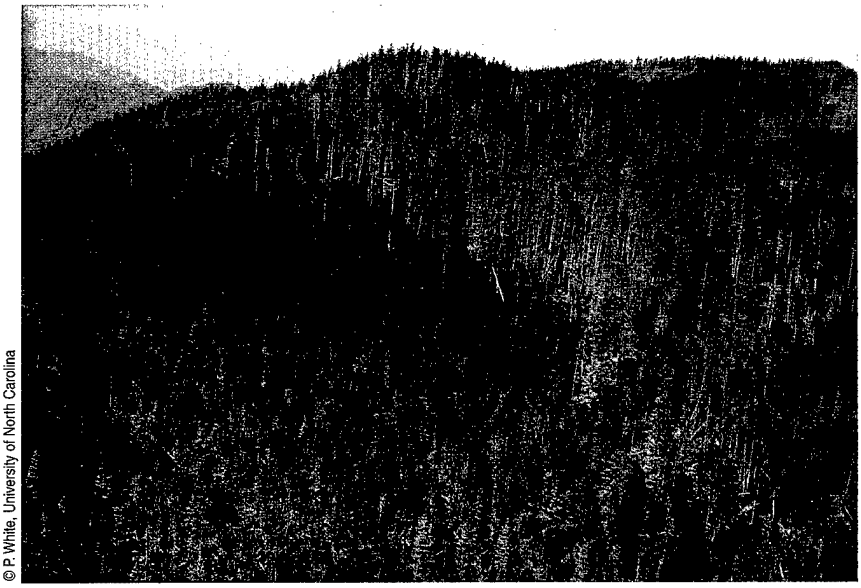
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Fig. 5. The summit of Mt. LeConte, Great Smoky Mountains National Park, Tennessee, shows patches of green young trees that have not yet reached the stage in which they are vulnerable to balsam woolly adelgid, a nonindigenous insect from Eurasia. This insect has caused heavy mortality of the mature trees of a southern Appalachian endemic tree, Fraser fir. Acid rain possibly played a minor role in this mortality, but pollution has caused more dramatic effects in high-elevation streams and may be responsible for growth declines in red spruce, a codominant with Fraser fir in these mountain forests.

Because Fraser fir was a dominant tree of these forests, its sudden loss has resulted in high light levels and reduced soil moisture. Shrub biomass increases in the short term and may cause decreased population sizes of herbaceous understory plants, including rare disjuncts and endemics (Fig. 6). Lichens, mosses, and other species that occur specifically on the bark of Fraser fir may also be at risk. A newly listed species in this ecosystem is the spruce–fir moss

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Fig. 6. Moisture and shade-loving understory species of the southern Appalachian spruce–fir forest are drastically affected by the death of Fraser fir, including the rare northern beech fern, shown here in an undisturbed forest.

spider, a narrowly restricted endemic that has disappeared from several locations affected by the balsam woolly adelgid (K. Langdon, National Park Service, Gatlinburg, Tennessee, personal communication). Changes in populations of other species are probably also occurring. For example, Alsop and Laughlin (1991) showed that decline in the fir population caused a 35% decrease in the density of breeding bird populations, the loss of two forest interior bird species, and the gain of three bird species characteristic of successional vegetation.

The mortality of Fraser fir is an acute problem caused by a nonindigenous insect, whereas air pollution is producing changes that are less dramatic but potentially just as severe (Eagar and Adams 1992). The deposition of pollutants, which is altering soil and stream chemistry (Mulholland and Lenat 1992), increases with elevation and thus has been of particular concern within these high-elevation forests. Biotic effects in streams are being investigated (Mulholland and Lenat 1992).

In the 1970's, red spruce experienced heavy mortality in the Northeast (Eagar and Adams 1992). Mortality in southern Appalachian spruce–fir forests was never high enough to be attributed to pollutant exposure, but growth declines, although not universal, were widely reported (Eagar and Adams 1992). Even though multiple explanations for growth declines are being explored, a leading theory is that pollution causes an increase in the cycling rate for calcium and other cations, and that the increased mobility of calcium will result in its loss to streams (Johnson et al. 1992). This theory predicts a long-term decline in soil fertility in high-elevation forests.

When the first concerns about air pollution effects arose in the late 1970's and early 1980's, there were few baseline data for evaluating change in the spruce–fir ecosystem. We did not know the expected rates of growth or mortality, nor the dynamics of stand composition and structure. Neither did we have an understanding of soil chemistry or its relation to atmospheric deposition or the chemistry of stream waters that drained this system. The decade of research that occurred in southern Appalachian spruce–fir forests (1982–1992) under the National Acid Precipitation Assessment Program (some research continues on individual sites through other sources of funding) has produced a key data set to help evaluate future changes. This program involved remote-sensing imagery on several scales, surveys of pathological fungi and other organisms, permanent vegetation plots, soil analysis, analysis of ecosystem processes, intensive studies of the mechanisms of pollutant exposure, and surveys of terrestrial and aquatic animal populations. The results of this intensive study will aid future assessments of the status and trends of the spruce–fir ecosystem.

Pine Forests

Fire frequency in pine stands on dry topographic positions has decreased during the last 60 years from one fire in 8 to 12 years to one fire in thousands of years (Harmon 1982). Concomitant with this decrease in fire has been the succession from pine to hardwood dominance (Harmon et al. 1983). Four pine species dominated dry sites in the mountains: Virginia pine and short-leaf pine on low-elevation sites, pitch pine on low- to mid-elevation sites, and Table Mountain pine on mid- to high-elevation sites. Table Mountain pine is restricted to the Appalachian Highlands from Pennsylvania to Georgia and Alabama; it has persistent serotinous cones that release seeds only after intense fires (Williams and Johnson 1992; Fig. 7).

After intense fires, these pines become established over several years to a decade, resulting in stands with similar sizes and ages of trees. As these pines age, large patches become vulnerable to outbreaks of a native insect, the southern pine beetle. Although these beetles are a natural part of the system, pine beetle infestations can be alarming and are treated as loss of value in managed forests.

As the pines senesce, they are replaced by hardwoods, among which oaks are usually prominent. As the hardwoods themselves age

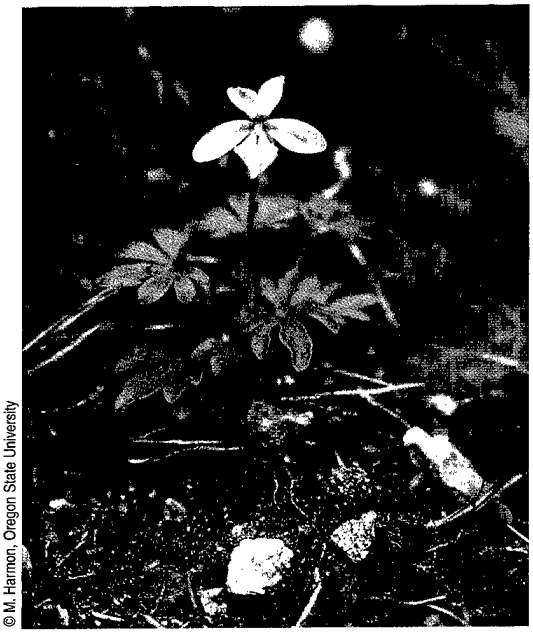

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Fig. 7. Fire is an important natural process on dry slope positions in the southern Appalachian Mountains. Birdfoot violet flowers and fruits heavily after burning on Polecat Ridge in the Great Smoky Mountains. On such sites, pine regeneration, including that of the endemic Table Mountain pine, occurs only after fire.

and grow bigger, they become less vulnerable to fire because of their thicker bark (Harmon 1984). Concurrently, debris produced by the death of overstory pine is reduced by decomposition. Thus, over successional time, fire behavior becomes altered—fires will be less intense and will no longer produce pine regeneration.

Although we know that the southern Appalachians are experiencing a trend from pine to oak dominance on dry ridges (Harmon 1984), the rate of loss of pine ecosystems is the subject of ongoing research. We do not have a quantitative estimate of the number and rate of loss of fire-dependent species, although long-term research on these questions has begun.

Mountain Bogs

Mountain bogs, including true bogs and fens, are small (0.5–10 hectares), isolated wetlands (Richardson and Gibbons 1993). Compared with other mountain wetlands, such as alluvial and levee forests and floodplain pools, they contain high numbers of rare species (Earley 1989; Stewart and Nilsen 1993). These mountain wetlands are much less common in the unglaciated Southeast than in the glaciated north.

Human activity has greatly reduced the number and extent of mountain wetlands. Of the estimated 2,000 hectares of mountain wetlands that historically existed in North Carolina, only about 200 hectares remain. Most remaining mountain wetlands have been affected by timbering, development, and alterations to drainage (Smith 1994). The exact number of remaining bogs is difficult to determine but is most certainly fewer than 150 in the entire Southeast. Few of these are pristine, and most are very small (less than 1 hectare). More than half of the existing bogs are in private ownership and are under serious conversion pressure by private developers. About one-fourth of the remaining bogs are on federal property and are therefore protected, as are those few that are owned or managed by The Nature Conservancy (Richardson and Gibbons 1993).

Bogs have been destroyed by draining, grazing, mining, logging, off-road vehicles, agriculture, and development (Richardson and Gibbons 1993). They are further threatened by water-quality changes—silt loads from surrounding soil erosion and altered chemistry from agriculture (Smith 1994). Alterations to regional hydrological balances (excessive well drilling and pumping, for example) can also destroy bogs (Richardson and Gibbons 1993).

The bog turtle is a threatened species that inhabits mountain bogs and is protected by state laws in only part of its range. The turtle is frequently collected illegally for the pet trade, and collectors have exploited the differential protection status by claiming that they collect bog turtles from states where the species is unprotected. Rare orchids and carnivorous plants often suffer similar fates (Earley 1989). Once a bog has been discovered by a collector, that site is often revisited until all species of commercial value have been removed. As bogs are widely separated from each other, the opportunity for plants and animals to recolonize is minimal, and the site remains permanently diminished.

To date there are almost no quantitative vegetation studies of the Southeast's mountain bogs and fens (Richardson and Gibbons 1993). Intermittent fire and beaver activities are speculated to play a role in the origin and maintenance of these communities (Richardson and Gibbons 1993).

Grassy and Heath Balds

Though the southern Appalachians do not reach a high-enough elevation for a true climatic treeline (Cogbill and White 1991), two kinds of high-elevation treeless habitats occur—heath balds and grassy balds (Fig. 8). Heath balds are stable, low-diversity communities dominated by evergreen broad-leaved shrubs. In contrast, grassy balds are diverse open communities that are unstable and were originally dominated by herbaceous plants (Saunders 1980). Grassy balds do not have distinctive animal communities (however, Otte [1995] suggested that there are undescribed insect species in these habitats) but do support rare plant species, including northern disjuncts and local endemics (Stratton and White 1982).

Although a few grassy balds seem to predate the earliest influence of European settlement, many were created as summer pastures for livestock (Lindsay and Bratton 1979). All the balds have a history of livestock grazing, and when the animals were removed from the 1920's to the 1940's, trees and shrubs began to invade the grassy balds. No known natural processes create or maintain grassy balds—they do not form

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Fig. 8. Mountain laurel is a dominate of heath balds, invades grassy balds during succession, and is a frequent understory shrub in dry forests of the southern Appalachian Mountains.

on distinctive topographies or soils (Stratton and White 1982), and they occupy an extremely small percentage of the sites that are seemingly appropriate for grassy balds, as defined by the extant balds. A few balds may have been created by Native Americans during warmer climates of the past and then were maintained by human-set fires and the native grazing animals that are now extirpated (woodland bison and elk).

The southern Appalachian landscape had 73 grassy balds in the early 1900's (Pittillo 1980; Saunders 1980); the number has been reduced by succession to woody plants, and the size of balds has been reduced by 50% or more of the original surface area. At present, only a few balds are being managed for the open habitat. For example, of 30 original grassy balds in Great Smoky Mountains National Park, only 2 are being managed for the open condition. Although the future will probably bring further reductions in the number of grassy balds in the southern Appalachians, several that are important to rare plant populations are in federal ownership and are being managed for the open condition (R. Sutter and P. White, University of North Carolina, Chapel Hill, unpublished manuscript).

Cliffs and Rocky Stream Gorges

High-elevation rock outcrops support 45 rare plants, including northern disjuncts and southern Appalachian endemics (Wiser 1994). Wiser surveyed these communities at 44 sites, of which 7 were unprotected. Historical population losses are exemplified by mountain avens, a herbaceous perennial species that declined from 16 to 11 populations (Endangered Species Technical Bulletin 1990; Fig. 9). Cliffs are popular hiking destinations and are used by rock climbers. Recreational effects are significant in many areas (Wiser and White 1997), but data sufficient to establish regional trends on mountain avens and other species are not available.

The rocky stream gorges that drain the high mountains also support a number of narrowly restricted endemics, which exist in a tension zone between stream scouring and succession to upland forest. Artificial impoundments eliminate some populations through flooding and result in diminished flood scour for other sites, leading to an increase in plant competition that will reduce the other populations. These sites are also prone to adverse effects because of human recreational activities. One of the plants of these habitats is the narrowly restricted endemic Ruth's golden aster, known from only two rivers in east Tennessee. A multiagency project to monitor and protect this species was begun in 1986; researchers found that the species had declined by some 25%–33% from 1986 to 1995 at two of three populations on one river but appeared to be stable at the third site and on the second river (T. Smith and L. Collins, Tennessee Valley Authority, Norris, Tennessee, unpublished data). Regional data for other endemics or for this habitat in general are not available.

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Fig. 9. The high-elevation endemic mountain avens is found on rock outcrops that harbor some of the South's rarest plants. Scientists are researching the air pollution sensitivity of these rare species in the Great Smoky Mountains National Park.

Ecosystems Found in the Piedmont and Coastal Plain

Bottomland and Floodplain Forest

The Southeast contains 36% of all wetlands and 65% of the forested wetlands of the conterminous United States, even though it makes up only 16% of this area (Keeland et al. 1995). Noss et al. (1995) estimated that 78% of southeastern wetlands were lost between settlement and 1980.

The forested wetlands of the Coastal Plain and Piedmont and the continental interior include bottomland hardwood forests and deepwater alluvial swamps (Sharitz and Mitsch 1993); 12 major forest types have been recognized. The vegetation of these forests varies in composition and structure according to flooding duration (Larson et al. 1981).

Harris (1989) listed characteristics of these ecosystems that are beneficial to wildlife: hard

mast production and a phenology (that is, periodic biological phenomena, such as flowering and breeding, in relation to climate) that is not synchronous with surrounding upland communities, frequent cavity trees, high abundance and biomass of invertebrate wildlife, and a linear distribution throughout the landscape that aids local and regional movement of animals. The seasonal flooding of these habitats makes them less suitable for agriculture; thus, in agricultural landscapes, they are often the only forest refuges available for many mammals, birds, and other species. Bottomland forests were and are very important to many birds in the Southeast, and the extinction of one species, the Carolina parakeet, and the extirpation of another, the ivory-billed woodpecker, are partially the result of fragmentation of this habitat.

Southern floodplain forests may have the largest remaining area of any riparian habitat in the United States (Klopatek et al. 1979; Keeland et al. 1995). Estimates of extent vary widely, however, from 6,600,000 hectares (Klopatek et al. 1979) to 13,000,000 hectares (Abernethy and Turner 1987). This areal extent is decreasing (0.51% per year from 1954 to 1974; Harris and Gosselink 1990), with a total loss of about 63% (Klopatek et al. 1979) to 78% (Noss et al. 1995). These forests have been converted to farmland, industrial parks, and urban areas. Surviving stands are influenced by levee construction, channelization, agricultural runoff, cattle grazing, timber extraction, and invasions of nonindigenous species. Restoration has been attempted, with 65,000 hectares of bottomland forest replanted since 1985, but it is too early to tell if these efforts will be successful (Keeland et al. 1995).

Species and population losses accompany these trends in habitat loss. For example, in Louisiana, Burdick et al. (1989) showed that the number of forest bird species was 15% lower and the number of individual birds 33% lower on transects with 26% forest cover compared with those areas that had 46% forest cover.

Glades, Barrens, and Prairies

Scattered throughout the Southeast are naturally treeless areas that support plants and animals not found in surrounding forests (Fig. 10). These openings have been variously referred to as prairies, glades, and barrens. Historical accounts suggest that at the time of settlement these open habitats were more widespread and adjoined forests with more open understories than the forests of today (Delcourt et. al. 1986; Wilkins et. al. 1991; DeSelm and Murdock 1993; Martin and Boyce 1993). Such open habitats are now rare, occupying only a fraction of 1% of the Southeast's natural landscape because of conversion to agriculture, quarrying, reduced fire frequency, and the loss of two large native grazers, the woodland bison and eastern elk. The naturally treeless areas that remain range in size from 0.25 hectares to as large as 17 hectares and are scattered over the region.

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Fig. 10. Purple coneflower is a species of open glades within closed deciduous forest. These habitats were maintained by frequent fire.

Upland open habitats occur in two settings. First, they are found on the thin soils of bedrock outcrops (hence, they are often treated as rock outcrop communities [Quarterman et al. 1993]). The bedrock itself may have unusual chemistry (the serpentine barrens) or interior drainage (the dry soils over some limestones). These rockier glades had little agricultural value but were used as rough pasture and for homesites, quarries, and dumping areas. The variation in rock types (limestone, diabase, granite, sandstone, shale, and serpentine), topography, climate, and disturbance history produces an array of communities; The Nature Conservancy's national classification includes 40–50 different nonforested, open, herb-dominated communities (The Nature Conservancy and Environmental Systems Research Institute 1994). The most widespread community type is glades over limestone; this community type has been studied since the work of Quarterman in the 1950's (Quarterman et. al. 1993). Twenty-nine endemic plants inhabit this community type, which is one of the highest numbers of endemic plants occurring in any southeastern habitat (Baskin and Baskin 1986, 1989; Sutter et al. 1994). The calcareous glades of Alabama and Tennessee support 21 plant species that are known globally from 20 or fewer locations (R. Sutter, The Nature Conservancy, Chapel Hill, North Carolina, unpublished data). Over half the glade sites have been destroyed, however, with fewer than 30 pristine or only slightly disturbed sites remaining. In Tennessee, 90% of ecologically intact limestone glades and 50% of the total glades area have been lost.

In the glades over limestone, the absence of a canopy allows the ground to be exposed to high temperatures and high amounts of sunlight; thus, the thin soils of some glades often have little water-holding capacity, producing a highly xeric (dry) habitat. In contrast, some glades experience waterlogging and pooling of water in late winter and early spring; these include the limestone cedar glades of Tennessee, Missouri, and Arkansas. These conditions are favorable for some species of winter annuals, such as the six species and four varieties of gladecress that are endemic to southeastern limestone glades (Baskin and Baskin 1986, 1989).

Larger grasslands (prairies and barrens) maintained by fire and grazing are the second kind of open habitat (DeSelm and Murdock 1993); only remnants of this vegetation exist. These larger grasslands (the Big Barrens of Kentucky and the Black Belt of Alabama and Mississippi) had deeper soils and were almost all converted to agriculture.

Although the overall rate of loss is unknown, three areas in Ohio and Tennessee experienced a reduction of this type of open habitat from 1.3% to 3.4% per year for 33 years (DeSelm and Murdock 1993). Prairies occurred in Kentucky (the Big Barrens: greater than 99% loss; Bluegrass Prairie: 100% loss [data from Noss et al. 1995]), Arkansas (the Grand Prairie: greater than 99% loss), Alabama and Mississippi (the Black Belt: greater than 99% loss), Mississippi (the Jackson Prairie: greater than 99% loss), Louisiana and eastern Texas (Coastal Prairie: greater than 99% loss), and Florida (St. John's River Prairie, Kissimmee River Prairie, and prairies west of Lake Okeechobee and in south Florida: virtually all converted to agriculture). Smaller grassland fragments occur throughout the region (DeSelm and Murdock 1993).

Animal species that have been extirpated from prairies and barrens include the greater prairie-chicken, which was extirpated by the early twentieth century from Kentucky grasslands; bison, which was extirpated from North Carolina by 1765, from Maryland by 1775, from Virginia by 1797, and last observed in the Southeast in 1825 (Webster et al. 1985); and eastern elk (Echternacht and Harris 1993). Today, southeastern grasslands are so small and so distant from extensive grasslands to the west that other grassland vertebrate animals do not occur in them, nor do they support locally endemic vertebrates (DeSelm and Murdock 1993). Many eastern animals, though, including rare bird species (Kale 1978; Hamel et al. 1982) and reptiles (Jordan 1986), use these open habitats, and studies of limestone and granite outcrops revealed endemic arthropod species as well (Quarterman et al. 1993). King (1985), for example, found several arthropod species endemic to the exposed rock areas of granite outcrops.

Some of the plant species of open habitats have persisted along roads and under power lines. For example, Schweinitz's sunflower has declined from 21 to 13 populations, all of which are on roads and under power lines (Endangered Species Technical Bulletin 1991). If appropriately managed, these populations can possibly be used to lessen the extinction risk in these species. Populations of smooth coneflower in a power line right-of-way in Granville County, North Carolina, mown at a 1- to 3-year interval by Carolina Power and Light, have thrived (Barnett-Lawrence 1994). Roadside populations, though, are vulnerable to roadway expansion and maintenance activities (Barnett-Lawrence 1994).

The Coastal Plain

Longleaf Pine and Southeastern Pinelands

The pinelands of the Coastal Plain once extended from the James River in southeastern Virginia to the Trinity River in eastern Texas and covered 24 to 35 million hectares (Frost et al. 1986; Stout and Marion 1993). Longleaf pine savanna was the most common community—the trees, which were thinly distributed, flat-topped, and had limbless lower trunks, occurred in a sea of grasses and diverse wildflowers and carnivorous plants. The historical distribution of pineland communities was determined by moisture supply and fire (Frost et al. 1986). Pines were dominant in habitats ranging from pine flatwoods and mesic savannas to the longleaf pine–turkey oak association in the dry Carolina Sandhills. Longleaf pine was the leading species, with slash pine increasing southward. Both species are now outnumbered by loblolly pine because of fire suppression, conversion to farmland, and commercial timber production (Ware et al. 1993).

The most widespread of the pineland communities, the longleaf pine savanna, occurred widely on the moisture gradient from wet areas and mesic savannas to the dry sandhills and turkey oak associations (Fig. 11). The vast, parklike longleaf pine savanna had an herbaceous layer dominated by wire-grass in the southeastern states (Fig. 12) and by bluestems in Louisiana and eastern Texas. At small scales (1–100 square meters), this herb layer is one of the most diverse in the world (40–75 species of vascular plants have been reported for a single 1-square-meter quadrat and 130 for a 0.1-hectare plot [Clewell 1989]). Today, only 14% of the expansive longleaf pine forest remains,

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Fig. 11. Dry sandhill scrub, Emanuel County, Georgia.

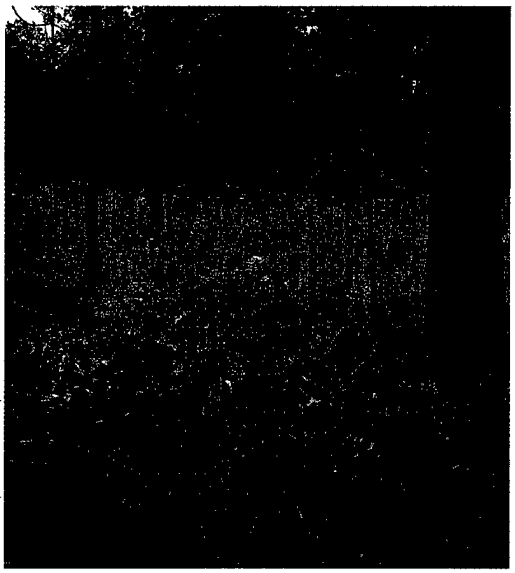
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Fig. 12. Longleaf pine–wire-grass savannah at Piney Bottom Creek, North Carolina. These fire-maintained communities have high plant and animal diversities.

with just 3% surviving as old-growth habitat, a loss comparable with or exceeding that of many of the other unique communities in North America (Noss 1989; Figs. 13 and 14). The dry longleaf pine–turkey oak stands of the sandhills are the most poorly protected areas of this endangered ecosystem (Stout and Marion 1993).

Species that inhabit longleaf pinelands exhibit a high incidence of rarity and endemism. The longleaf pine–wire-grass community includes 191 species of rare plants (Figs. 15 and 16). Although pine communities on the Atlantic Coastal Plain are more diverse and contain a greater number of rare plants, the west Gulf Coastal Plain also has high

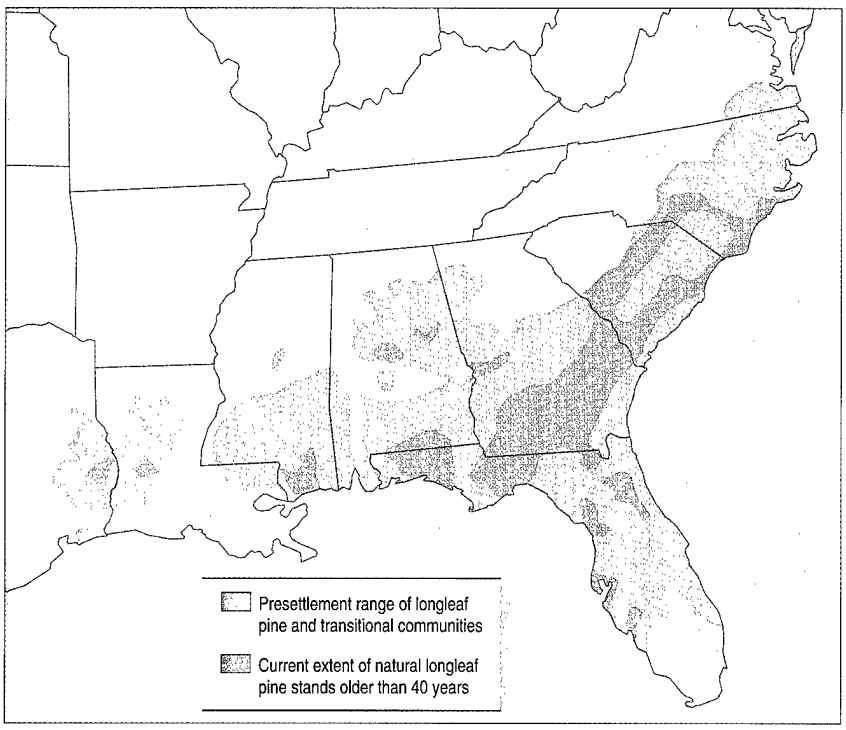

Fig. 13. Former and current extent of natural longleaf pine stands in the southeastern United States (former extent taken from Ware et al. 1993; current extent from Outcalt and Outcalt 1994) Current extent includes old-growth longleaf pine stands and natural second-growth stands older than 40 years.

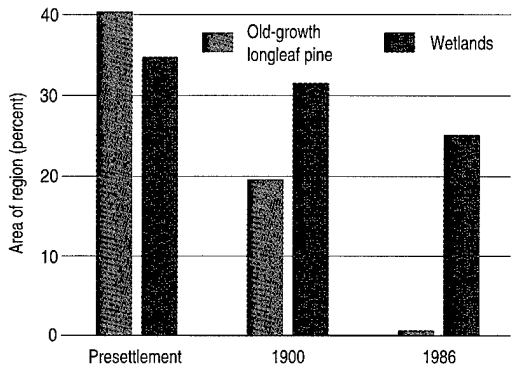

Fig. 14. Percentage of the southeastern Costal Plain composed of longleaf pine and various wetland communities in presettlement time (pre-1880), 1900, and 1986 (redrawn from Noss 1989, as adapted from tabular data in Ware et al. 1993).

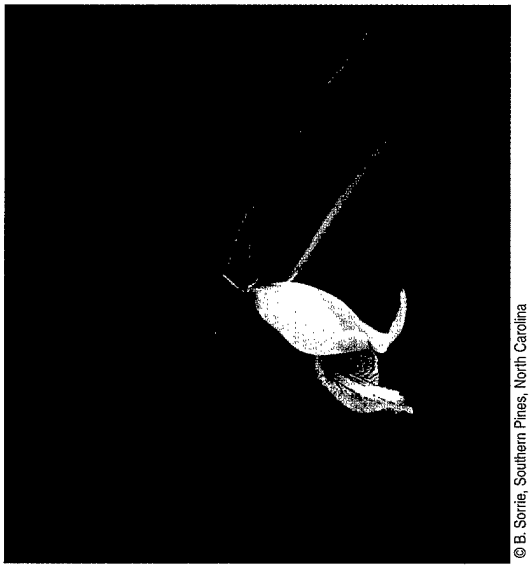
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Fig. 15. Spreading pogonia, a native orchid of longleaf pine–wire-grass communities in the Carolina Sandhills, Fort Bragg, North Carolina.

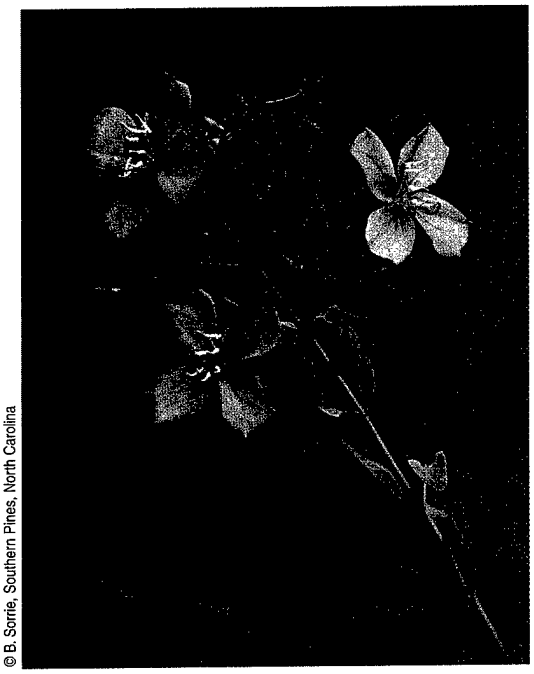

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Fig. 16. Meadow beauty in the longleaf pine–wire-grass communities in the Carolina Sandhills, McBee, South Carolina.

endemism, with 39 endemic species (Bridges and Orzell 1989). The southeastern pineland community harbors large numbers of federally listed species: 18 plants, 4 reptiles, 4 birds, and 1 mammal, as well as 100 candidates for federal listing (Noss et al. 1995). In addition, the pinelands serve as a major corridor for a large number of migratory birds that winter in the West Indies and South America (Stout and Marion 1993), and they support 170 species of reptiles and amphibians (Dodd 1995a). High percentages of these reptile and amphibian species are imperiled (endangered, threatened, or declining): 22% of the salamanders, 15% of the frogs, 34% of the turtles, 31% of the lizards, and 19% of the snakes fall in this category (Dodd 1995a; Fig. 17).

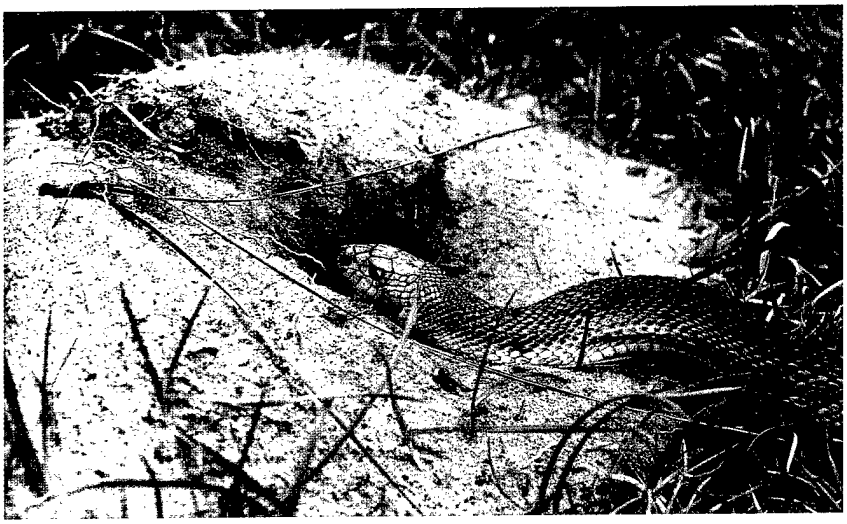

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Fig. 17. Florida pine snake in the sandhills of the Katherine Ordway Preserve—Swisher Memorial Sanctuary.

Lightning fires, occurring at about 1- to 3-year intervals throughout the area, were carried over large areas by wire-grass and pine duff and were stopped only by excessive moisture or abrupt changes in topography. Historically, 10%–30% of the southeastern pinelands burned each year (Ferry et al. 1995); these frequent fires reduced litter accumulation and invasion by competing woody species. Pine seedlings and many of the grasses and forbs present in longleaf pine communities are shade-intolerant, and many require bare mineral soil and reduced competition for germination and early growth. Longleaf pine has several adaptations to minimize fire injury and a large annual needle cast that provides good fuel for future fires (Stout and Marion 1993). The reduction of litter accumulation is essential for the survival of small, rare herbaceous species such as the unique Venus flytrap.

By the time European explorers and settlers arrived in this region, Native Americans had already been augmenting the natural lightning-caused fire regime with annual burning. Set in fall and winter, these fires were used to drive game and improve browse. Early settlers also used fire in winter to improve forage for their livestock, which roamed freely in the forested land.

The longleaf pine forest remained largely intact until the mid-seventeenth century, when the Naval stores industry (that is, products such as turpentine or pitch, originally used to caulk the seams of wooden ships) started to develop in Virginia and then reached its full development in North Carolina in the mid-eighteenth century. Demand then turned to timberland, and despite warnings from late nineteenth-century foresters concerned with regeneration, much of the old-growth forest was cut by the 1920's (Ware et al. 1993).

With much of the timberland being converted to agriculture and much of the wire-grass understory disturbed and fragmented by logging roads and fields, the era of unrestricted ground fires ended. In the absence of fire, other species of pines and woody plants invaded, shading out the regenerating longleaf pine and the sun-loving herbaceous layer. The introduction of livestock also contributed to the end of regeneration by longleaf pine; the nonresinous, carbohydrate-rich meristems of longleaf pine seedlings became favorite livestock forage. In the mesic regions along the coast, extensive areas of longleaf pine were cut, drained, and converted to commercial pine plantations. Finally, the initiation of government-sponsored fire suppression in the 1920's completed the demise of fire-maintained longleaf pinelands in all but a few locations. By 1946 the range of

longleaf pinelands had decreased to one-sixth of their former extent, and today only 14% of the original total remains (Frost et al. 1986).

Much of the remaining 2 million hectares of longleaf pine are fragmented and located near developed areas. Winter burning can actually promote woody invasion of the wire-grass understories, but summer burning (the natural fire regime) is considered hazardous near human property. Prescribed burning relies on firebreaks and roads, which further fragment the herbaceous understory and alter local hydrology (Noss 1989). Even though some rare native species respond to other types of disturbance, fire is the most universally important disturbance (Hardin and White 1989).

Of the animals dependent on longleaf pinelands, the best known is the red-cockaded woodpecker, a federally listed species unique for its use of live old-growth or mature second-growth pine trees for cavity excavation (Costa and Walker 1995). The red-cockaded woodpecker is the prime cavity builder in an environment largely free of snags and natural cavities. This species has declined with the loss of longleaf pine habitat; however, intensive management has stabilized several populations (Costa and Walker 1995). Bachman's sparrow, federally listed as threatened, nests in the wire-grass tussocks. The fox squirrel is dependent on the longleaf pine for forage in late summer (Ware et al. 1993). The gopher tortoise, a species whose populations have declined by 80% in the past 100 years (Auffenberg and Franz 1982), is a keystone species in longleaf pine savannahs—more than 300 species of invertebrates and 65 species of vertebrates use burrows dug by gopher tortoises, the only species that creates this microhabitat (Dodd 1995a). Recent regional trends are not available for this species. A study in Florida showed that gopher tortoise populations had increased on one study site, decreased on another, and remained stable on three others (data from 1987 to 1988 compared with 1978 to 1979; McCoy and Mushinsky 1992).

Carolina Bays

Carolina bays are isolated shallow basins with an elliptical shape and oriented in a northwest to southeast direction. Bays are distributed from New Jersey to northern Florida (Sharitz and Gibbons 1982; Richardson and Gibbons 1993). Estimates of how many of these bays originally existed in the Southeast vary because insufficient inventories have been completed and because development has altered some bays beyond recognition. Recent calculations, however, indicate that there were between 10,000 and 20,000 Carolina bays (Richardson and Gibbons 1993), with an estimated 4,000 bays once occurring in South Carolina (Bennett and Nelson 1991). About 80% of the bays are in North Carolina and South Carolina (Crisman 1992; Fig. 18).

The size of bays varies; for example, length varies from 50 meters to 8 kilometers (Lake Waccamaw in southern North Carolina). The substrate can be clay, sand, or organic material (Richardson and Gibbons 1993). Hydroperiod ranges from short-duration flooding, where evapotranspiration causes complete drying, to sites with permanently saturated soils, to sites with permanently standing water (Sharitz and Gibbons 1982). Carolina bays depend mostly on rainwater for hydrology and nutrients, although some evidence indicates that the hydrology of some bays may have connection with groundwater (Sharitz and Gibbons 1982). This dependence on precipitation results in large fluctuations in water levels during a year and in variation between years (Sharitz and Gibbons 1982), causing the year-to-year variation in composition and biomass observed in Carolina bay communities (Sutter and Kral 1994). Like many southeastern Coastal Plain ecosystems, most Carolina bay communities historically had regularly occurring fires, but fire regime varied with hydroperiod and vegetation.

Given this range of substrates, hydrology, and fire history, bays are, not surprisingly, biologically variable. Richardson and Gibbons

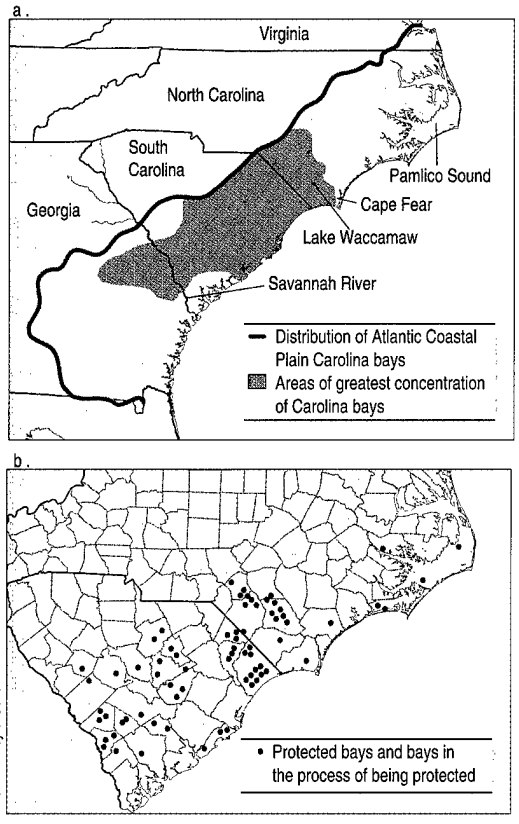

Fig. 18. Distribution and protection of Carolina bays. a) South Atlantic Coastal Plain showing distribution of Carolina bays larger than 246 meters in length (based on Richardson and Gibbons's 1993 interpretation of a map in Prouty [1952]). b) Carolina bays that have been protected or are in the process of being protected as of June 1995 (data for South Carolina are from Bennett and Nelson [1991]; data for North Carolina are from M. Schafale, Natural Heritage Program, Raleigh, North Carolina, unpublished data).

(1993) listed plant communities that occur in bays: pine forest or savanna, herbaceous marsh, shrub bog, deciduous forest dominated by blackgum, evergreen bay forest, and pondcypress swamp with herbaceous understories. Bennett and Nelson (1991) added xeric sandhill scrub, oak–hickory forest, swamp forest, depression meadow, shrub border, and open-water lake.

Sutter and Kral (1994) estimated that nonalluvial wetlands (of which Carolina bays are a major portion) support more than one-third of the rare plants that occur in the Southeast. Bennett and Nelson (1991) listed 23 species of rare, threatened, or otherwise noteworthy plants in bays in South Carolina.

Carolina bays represent a major portion of the freshwater habitat in the southeastern Coastal Plain. Animals that depend on bay habitat include amphibians, the American alligator, freshwater turtles, snakes, and birds (Sharitz and Gibbons 1982). Because of their fluctuating water levels, few bays can support fishes, but bay lakes do support permanent fish populations (Sharitz and Gibbons 1982). Some bays that lack fish populations are important predator-free breeding sites for amphibians. Several animal species are endemic to particular bays; Lake Waccamaw, for example, supports at least two and possibly four endemic fish species and three endemic mollusk species.

Carolina bays are threatened by ditching for agriculture (the most common disturbance), silviculture, and grazing; changes in local and regional hydrology; development for recreation, residence, and industry; and fire suppression (Sutter and Kral 1994). Bennett and Nelson (1991) surveyed 2,651 bays (Fig. 19) in South Carolina and found that 97% had undergone some form of alteration, and 81% had experienced two or more kinds of human disturbance. Out of the 4,000 original bays in South Carolina, they estimated that 400–500 are still relatively intact. Wetland regulations have protected many privately owned bays on the Coastal Plain, but fewer than 2,000 hectares of this community are protected in North Carolina (Richardson and Gibbons 1993).

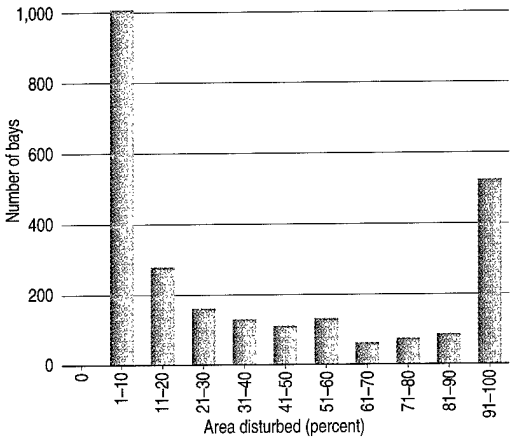

Fig. 19. Number of Carolina bays negatively affected (percent of surface area disturbed) by human factors. Percentages based on surveys of 2,651 Carolina bays in South Carolina (redrawn from Bennett and Nelson 1991).

Pocosins

The word *pocosin* comes from an Algonquin word meaning "swamp-on-a-hill" (Tooker 1899), referring to the position of this wetland community in upland interstream areas. Pocosins are freshwater wetlands dominated by a dense cover of broad-leaved evergreen shrubs or low-growing trees with highly organic soils developed in areas of poor drainage (Sharitz and Gibbons 1982; Christensen 1988). The soils are low in pH and available nutrients, with phosphorus often a limiting factor (Richardson and Gibbons 1993). Vegetation is separated from the underlying mineral soils by the organic layer and is isolated from runoff because of its landscape position in broad divides and flats without much watershed to feed water onto the site. In extreme circumstances, the only nutrients available to plants come from rainfall.

The most nutrient-limited pocosins are those where peat is deep (more than 1 meter [Christensen 1988]), which results in lower productivity and shorter vegetation (less than 6 meters); these areas are commonly referred to as short or low pocosin. Where peat is shallower (0.5–1 meter deep), vegetation is taller, and the area is referred to as tall or high pocosin. High pocosin usually surrounds low pocosin (Richardson and Gibbons 1993). Short pocosin develops from tall pocosin because peat accumulation eventually prevents roots from reaching the mineral soil, a condition that continues until fire burns the peat so that mineral soils are accessible again (Christensen 1988).

Pocosins are fire-maintained ecosystems. In addition to being adapted to flooded and low-nutrient conditions, plants in pocosins either tolerate fire or depend on it to complete their life cycles (Sharitz and Gibbons 1982). Without fire to maintain or generate openings in the dense shrubs and to open serotinous fruits, some species cannot continue to persist. Vegetative production in pocosins is highest in the first two growing seasons following a fire (Christensen 1988).

Several plant species depend on pocosin habitat, including whitewicky, arrowleaf shieldwort, spring-flowering goldenrod, and roughleaf yellow loosestrife. Others, such as the Venus flytrap, dwarf witchalder, sweet pitcherplant, and whitebeaked rush, depend at least in part on pocosins or associated habitats (Richardson 1983).

No vertebrate animals are endemic to pocosins, but for many species pocosins are key

habitat and refuge from the development of the surrounding landscape (Richardson and Gibbons 1993). Although information on fauna remains limited, Clark et al. (1985) found 41 species of mammals inhabiting 12 pocosin and Carolina bay sites in North Carolina.

Pocosins also store and regulate fresh water for regional ecosystems (Richardson and Gibbons 1993). In addition, their other valuable functions are input of organic matter to streams and rivers and filtering of dissolved nutrients and suspended materials, thereby reducing eutrophication (Richardson 1983).

The presettlement distribution of pocosins has been estimated at 1.2 million hectares (Richardson 1983). Of the 907,933 hectares of pocosin that existed in North Carolina in 1962, by 1980, 33% had been entirely developed, 36% had been partially developed, and only 31% (281,180 hectares) remained in a more or less natural state (Richardson et al. 1981). From 1980 to 1989, the amount of surviving area that was protected increased from 5% to 22% (Richardson and Gibbons 1993). In 1989, about one-third of the unprotected pocosin area was owned by major timber companies; other large landholders included corporate agriculture (14%) and federal and state agencies (18%; Richardson and Gibbons 1993; Fig. 20). Alteration and conversion of pocosins have been primarily due to timber production, agriculture, and peat mining. Recent changes in the enforcement of the Clean Water Act in North Carolina have reduced the amount of development in pocosins (Richardson and Gibbons 1993).

As sites are lost, the isolation of carnivorous plant wetlands is increasing, which may cause species to fail to disperse among sites. Gibson (1983) described the loss of area and increased isolation as factors that will cause a collapse of carnivorous plant diversity in these habitats. The most important causes of loss of habitat have been fire suppression and the draining of wetlands for agriculture and forest plantations. Other commercial effects are flooding caused by construction of fish ponds and changes in water quality due to fertilizer runoff (plant carnivory is an adaptation to low-fertility soils). In addition, private and commercial plant collectors seek out the rarest species. Over the last 100 years such collecting has removed millions of plants; a new collection pressure has come from the use of the Venus flytrap as a source of an herb medicine, Carnivora, produced in Europe.

The number of populations of this unique and narrowly restricted endemic plant has decreased from 21 to 12 in the last century (Figs. 23 and 24). The collection of the Venus flytrap on public land is now regulated by the state of North Carolina.

Examples of ongoing population loss come from 2 federally listed species of pitcher-plants. Jones' pitcher-plant has declined from 26 to 10 populations, all of which are small and 8 of which occur on private land (Endangered Species Technical Bulletin 1988). Likewise, the Alabama pitcher-plant has declined from 28 to 12 populations, of which only 4 are significant (Endangered Species Technical Bulletin 1989).

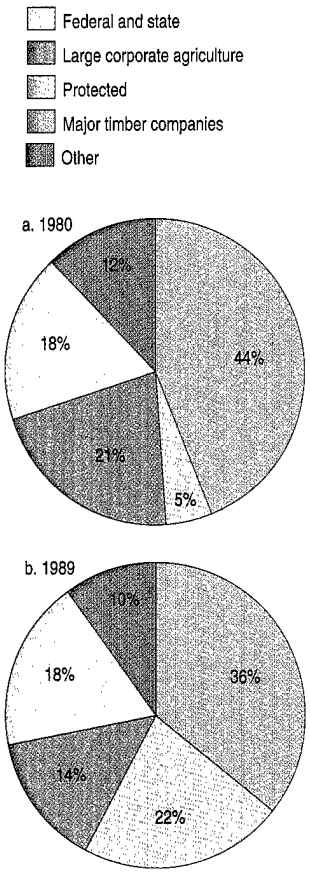

Fig. 20. Ownership patterns, by percent, of North Carolina pocosin wetlands in a) 1980 and b) 1989 (redrawn from Richardson and Gibbons 1993). © John Wiley & Sons

Carnivorous Plants

The Southeast possesses the highest diversity of carnivorous plants in the world (Fig. 21). As many as 20 species occur in a single site, and 54 species in five genera and three families occur across the region (Gibson 1983). These plants obtain nutrients from animals, particularly insects, via elaborate adaptations, such as sticky leaves, hollow tubular leaves, and traps. Vast wet meadows once covered hundreds of hectares on the outer Atlantic Coastal Plain and Gulf Coastal Plain, with smaller hillside seepage bogs inland. Gibson (1983) reported two centers of diversity, one in North Carolina and the other in Alabama (Fig. 22). The highest diversities are found in regions where wetlands (longleaf pine savannas and pocosins) are most numerous and closest together. However, there has been a dramatic loss of area for these habitats—less than 3% remains as degraded habitat, and less than 1% remains as pristine habitat (Folkerts 1982).

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Fig. 21. Yellow pitcher-plants in a seepage bog in the North Carolina Sandhills. The southeastern Coastal Plain is a world center for the diversity of carnivorous plants, with 54 species in 5 genera and 3 families. Carnivory provides an added source of plant nutrients on sandy sites that are often acidic and nutrient-poor. Diversity of carnivorous plants, as well as other herbaceous species, is promoted by fire in these habitats.

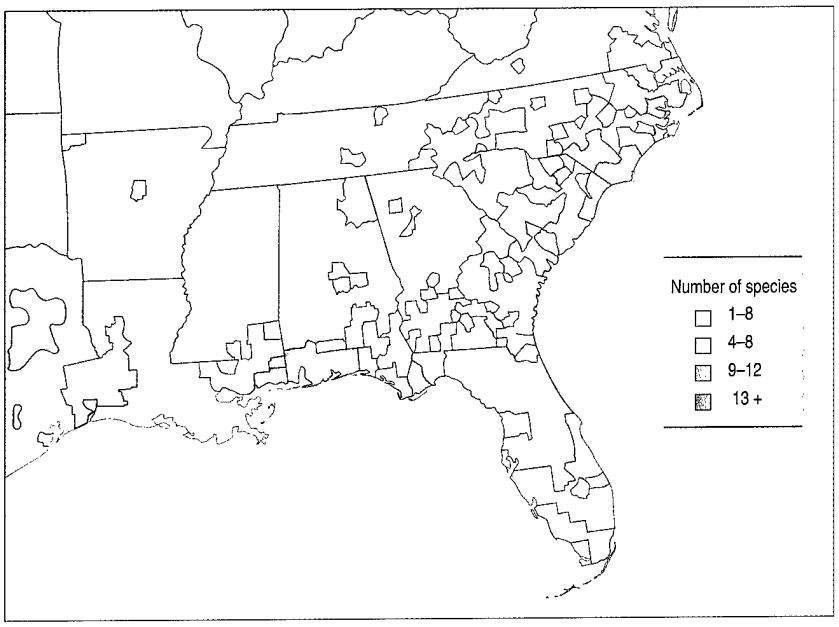

Fig. 22 . Two major centers of diversity in the carnivorous plant community: the Atlantic Coastal Plain and the Gulf Coastal Plain. Data are from numerous sources, including herbarium records (Gibson 1983).

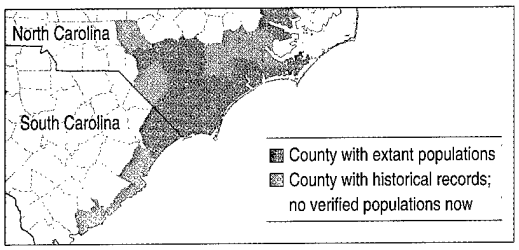

Fig. 23. Distribution of Venus flytrap in the Carolinas (redrawn from Boyer 1995). Only 12 of 21 historical county locations are extant.

© K. Moore, North Carolina Botanical Garden

Fig. 24. The Venus flytrap is a carnivorous plant whose image is known the world over but which is restricted in the wild to an extremely small part of North Carolina and South Carolina. This plant, which is subject to exploitation, depends on habitat protection and fire management.

Atlantic White-Cedar Swamps

Atlantic white-cedar swamps are unique communities adapted to variable hydrological regimes, fire, and acidic, nutrient-poor peat soils (Levy 1987). Fire removes competitive vegetation and clears the seedbed for white-cedar regeneration (Laderman 1989). White-cedar, though, is not a fire-resistant species and can be severely damaged in prolonged hot fires. Although white-cedar is not tolerant of prolonged flooding, brief, frequent flooding reduces competing species and is essential for white-cedar reproduction. Thus, white-cedar stands require frequent, light fires in the dry season and waterlogged soils subject to a variable hydroperiod (Laderman 1989).

Because of the difficulty and expense associated with exploiting these communities, white-cedar stands often represent some of the only forested land in a region of intense agricultural and developmental pressure. Atlantic white-cedar wetlands provide habitat and essential cover for many species, including black bear, deer, rabbits, and other fauna (Laderman 1989). Unique species occur as well, including Hessel's hairstreak, a butterfly that feeds exclusively on Atlantic white-cedar (Laderman 1989). The diversity of bird species is relatively high in Atlantic white-cedar swamps (Terwilliger 1987).

Much of the original Atlantic white-cedar community was destroyed during European colonization and the timbering and draining for agriculture that occurred during the last two centuries. Road construction and the ditching and damming of natural waterways continue to diminish this habitat, as does suburban encroachment, agricultural and industrial runoff, and pollution. Those white-cedar stands not protected by law are threatened by these continuing activities (Laderman 1989).

Historically, Atlantic white-cedar was found in the South in a nearly continuous band from southeastern coastal Virginia to the interior sandhills region of Georgia, and from the Florida Panhandle across the Gulf of Mexico coast to Mississippi (Frost 1987). Now Atlantic white-cedar swamps are restricted to inaccessible or protected freshwater wetlands in small, isolated stands (Laderman 1989). Drainage, development, and logging have reduced Atlantic white-cedar to 10% of its original extent (Frost 1987).

Barrier Island Communities and Maritime Forests

The Southeast supports over 200 individual barrier islands with a total area of over 610,000 hectares (Bellis and Keough 1995). The ecosystems (Fig. 25) of these islands are diverse and

dynamic, a product of regional climate, geomorphology, local sediment deposition, and the forces of ocean currents, tides, wind, salt spray, erosion, and violent ocean storms (Bellis 1992; Stalter and Odum 1993; Bellis and Keough 1995). The islands are grouped into five geographical categories: the mid-Atlantic region, extending from New Jersey to Cape Hatteras, North Carolina; the Sea Islands, bordering the coasts of South Carolina and Georgia; the Florida Atlantic; the eastern Gulf of Mexico coast; and the Louisiana–Texas Gulf of Mexico coast (Stalter and Odum 1993).

Human activities have only had a major effect on the barrier islands in the past 50 years (Fig. 26). Eighteenth- and nineteenth-century settlements were small, scattered, and difficult to reach. Most activities were confined to forestry, livestock grazing, and subsistence agriculture, except in the Georgia and South Carolina Sea Islands, where cotton and rice plantations were widespread. The construction of bridges and causeways and the improvement of transportation in the early part of this century brought new opportunities for recreation, tourism, and second-home development. Development has meant the construction of jetties and sea walls, filling and draining of marshes, and extensive dune stabilization and beach nourishment programs, all of which obstruct the natural fluctuations of the barrier island communities. Despite limited fresh water and the constant threat of storm damage, development continues at an accelerating pace (Stalter and Odum 1993). Barrier island development in the Southeast has increased more than 300% in the past 50 years (Johnson and Barbour 1990), and coastal Florida's development proceeds at a rate nearly twice that of the entire Atlantic and Gulf of Mexico coasts combined (Johnson and Barbour 1990). Although there are stretches of protected barrier island beaches and dunes and intact salt- and freshwater marshes, close to half of the area of these communities is estimated to have already been lost (Noss et al. 1995).

Development, of course, has many effects. Beach traffic disturbs nesting birds and sea turtles, compacts the soil, and disrupts dune-building activities. Jetties, sea walls, inlet stabilization, and artificial dunes disrupt normal overwash activities, altering normal dune development and increasing erosion in some areas and sand deposition in others. Development within the foredune zone and forest clearing destroy natural protective barriers to salt spray and wind damage. Pollution of marshes, estuaries, and creeks is a common result of inputs of treated and untreated sewage, fertilizer runoff from developments such as golf courses, and numerous contaminants from marinas, fish-processing plants, highways, and small industries (Stalter and Odum 1993). Finally, fragmentation of vegetation interferes with natural migration patterns.

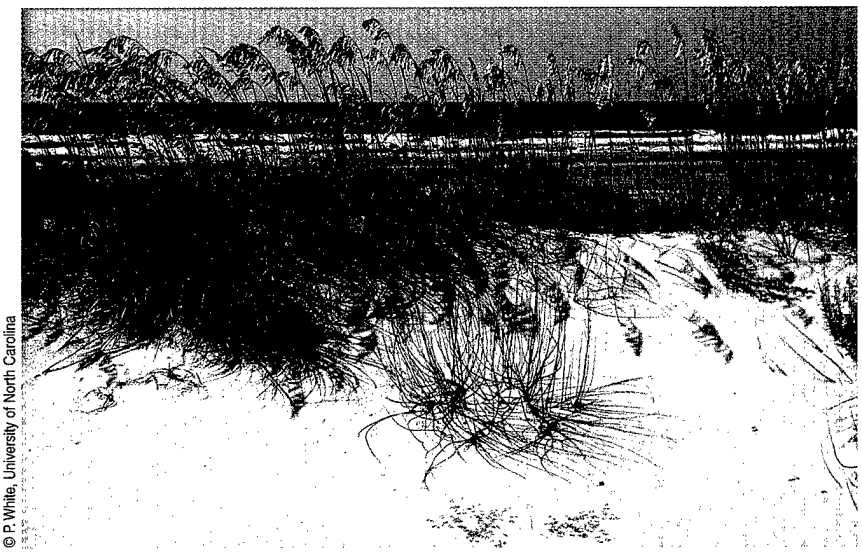

Fig. 25. Sea oats dominate the primary dunes along the North Carolina coast.

Experience with severe storm damage on coastal structures has modified development activities to some extent. Today, setback requirements in effect in many areas prohibit the destruction of the foredunes and reduce effects on beach areas. Existing structures, however, still require protection from beach migration, as well as regular, costly, beach nourishment projects (Johnson and Barbour 1990). About one-third of the barrier islands lining the Atlantic and Gulf of Mexico coasts have been protected by being set aside as parks, wildlife management areas, and national seashores (Stalter and Odum 1993). Areas that are open for development, however, are largely at risk for continued severe habitat degradation and other environmental losses. Most of the Atlantic coast of Florida is unprotected and very little natural coastline remains.

Maritime communities have decreased in areal extent since settlement, but the magnitude is known only for local areas. For example, coastal wetlands around Tampa Bay have decreased by 44% (Johnston et al. 1995). From 1950 to the present, the area of coastal wetlands along the Gulf of Mexico decreased by 20%–35% (Johnston et al. 1995); the largest losses were in Louisiana, where coastal impoundments flooded wetlands (Fig. 27). In general, freshwater wetlands have decreased to a much greater extent than estuarine wetlands. In 1982 the Coastal Barrier Resources Act restricted the use of federal funds for development of barrier islands. An extensive monitoring system has shown that the area of undeveloped barrier islands has been stable since that law was passed (Williams and Johnston 1995).

Bellis and Keough (1995) estimated that 39,000 hectares of maritime forest occurred in

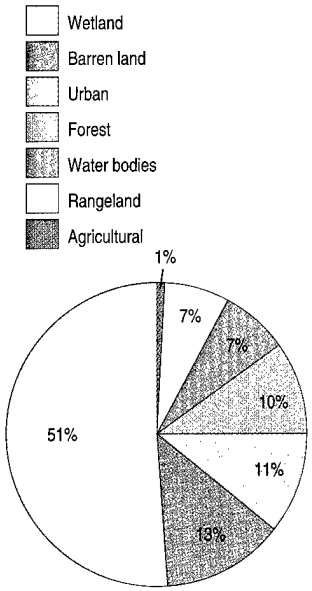

Fig. 26. Barrier island land use (redrawn from Stalter and Odum 1993; data from Lins 1980).

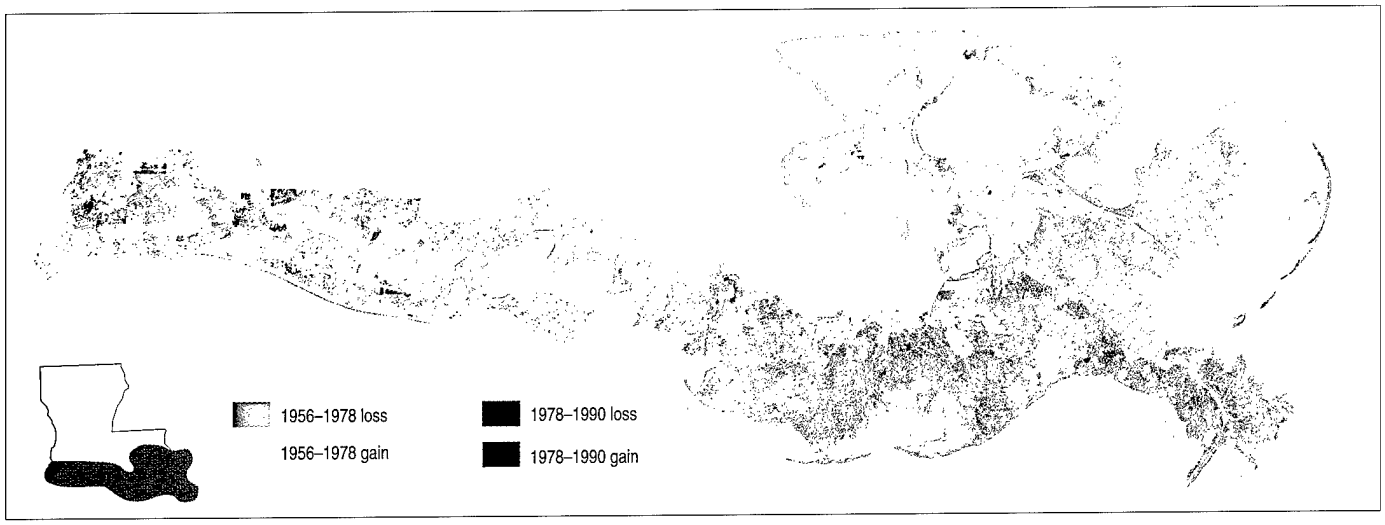

Fig. 27. Coastal land loss and land gain in Louisiana, 1956–1990 (Johnston et al. 1995).

North Carolina, Georgia, and Florida, the three states with the best inventories. This represents an unknown fraction of the original extent of these forests. About half of the remaining forests are unprotected and likely to be developed within the next decade (Bellis and Keough 1995; Table 9). The degree of human disturbance and changes within the small forest fragments that remain (for example, edge effect and the fact that fragments may not be large enough to support a population big enough to convey long-term persistence) produce declines in the numbers and species of many animals (Gaddy and Kohlsaat 1987; Bellis and Keough 1995).

Several investigators noted the inadequacy of existing data for detection of trends. Bellis and Keough (1995) suggested the need for a complete survey and assessment of maritime forests. Besides effects of development and nonindigenous species, maritime communities will probably be influenced by sea-level rise and drawdown of freshwater supplies (Bellis and Keough 1995). Daniels et al. (1993) modeled the influence of sea-level rise on endangered species in South Carolina and showed that 52% of the regionally endangered species were found within 3 meters of current mean sea level and that several scenarios of sea-level rise would drastically reduce the habitat for these species.

Overgrazing is also a problem on barrier islands, not only because of a large white-tailed deer population but also because of the large numbers of feral animals introduced to the islands, including horses, cattle, goats, pigs, and sheep (Stalter and Odum 1993). Eradication of some of the larger feral species has been successful on some islands, but other introduced animals, especially feral dogs and cats, negatively affect small mammal populations. Other introduced species include European rats and nutria (Stalter and Odum 1993).

Large numbers of migratory and nesting bird species are found on barrier islands (Stalter and Odum 1993); for example, 350 species have been recorded on barrier islands in North Carolina alone (Parnell et al. 1992). Coastal marshes are critical to overwintering populations of many waterbirds. In addition, migration routes of many raptor species include southeastern barrier islands. Neotropical migrants use the islands as a point of departure and arrival in their travels to and from their winter habitats in the tropics (Stalter and Odum 1993).

Many birds have been negatively affected by development and human encroachment. Species that nest in bare sand can be disturbed by pedestrian and off-road vehicle traffic and by the construction of artificial dunes. Harrington (1995) reported that for 27 species of eastern shorebirds, 12 had stable populations, 1 was increasing, and 14 were decreasing. Surveys initiated off the North Carolina coast in the early 1970's tracked the fluctuations in nesting bird populations (Parnell et al. 1992; Table 10). Eight species were increasing strongly (brown pelican, cattle egret, white ibis, glossy ibis, laughing gull, herring gull, royal tern, and Sandwich tern), three were increasing (yellow-crowned night-heron, great black-backed gull, and caspian tern), four were declining (gull-billed tern, common tern, least tern, and black skimmer), and seven were presumed stable. Some of the species have even shifted locations; Parnell et al. (1992) suggested that cutting of coastal swamps during the last 50 years resulted in movement to the estuaries. Further, creation

Table 9. Development and maritime forests on the Southeast's Atlantic Coastal Plain (from Bellis 1992). NA = data not available.

State	Shoreline (kilometers)	Undeveloped maritime forest (hectares)	Developed maritime forest (hectares)	Undeveloped, unprotected maritime forest (percent, 1992)
Florida	690	NA	NA	NA
Georgia	155	156,165	21,418	35
South Carolina	295	68,740	45,000	71
North Carolina	480	15,558	NA	55
Virginia	225	NA	NA	NA

of new habitat from dredged material may have caused populations to shift from one estuary to another.

Stalter and Odum (1993) listed nine endangered species of birds that are wholly or partially dependent on habitat on southeastern barrier islands: whooping crane, Eskimo curlew, bald eagle, Arctic peregrine falcon, eastern brown pelican, Cape Sable seaside sparrow, Bachman's warbler, Kirtland's warbler, and red-cockaded woodpecker. These species use the barrier islands in a variety of ways: nesting (five species), migration (four species), wintering (five species), feeding (seven species), and resting–roosting (seven species). Stalter and Odum (1993) attributed population losses in these species to development (direct loss of nesting, resting, and foraging habitat), dredging and filling of marshlands (loss of community structure and composition used by the birds), pollution, and direct disturbance on recreational beaches.

Five species of sea turtles are found in the open ocean and coastal waters of the Southeast, and all nest on open beaches: the green sea turtle (status: endangered/threatened; U.S. Department of Commerce 1994), the hawksbill (endangered), Kemp's ridley (endangered), the leatherback (endangered), and the loggerhead (threatened). Sea turtles are difficult to census in open waters and, because of the concentration of female turtles nesting on the beach strand and the apparent faithfulness of their return to specific beaches, the number of nesting females is considered the single best indicator of population trends (Committee on Sea Turtle Conservation 1990). The Kemp's ridley nests annually, but the other species nest less regularly. Long-term data sets (that is, over a decade of observations) are essential to detecting trends (Committee on Sea Turtle Conservation 1990). The dependence of sea turtle species on the narrow beach strand also makes them vulnerable to a host of human-caused problems, including beach development and recreation, artificial lighting (which disorients hatchlings), and increases in nest predators such as raccoons. Recently, federal law has mandated that shrimp trawlers use turtle exclusion devices, which should decrease mortality in a critical life stage for reproduction (Committee on Sea Turtle Conservation 1990).

Population estimates are available for only two of the five species of sea turtles (U.S. Department of Commerce 1994): 20,000–28,000 loggerheads and 400–500 green sea turtles nest in the United States. Although the number of nesting loggerheads has declined by 3% annually at a site in Georgia and by 26% during the 1980's at a site in South Carolina, it has increased at several sites in Florida (Committee on Sea Turtle Conservation 1990; Dodd 1995b; Fig. 28). Summed across the Southeast, loggerheads increased from 1982 to 1990 and decreased from 1990 to 1993 (Dodd 1995b), although the recent decline has been relatively mild, leaving the species at higher levels than in the early 1980's. A recent review concluded that the overall status of loggerhead population size was stable (U.S. Department of Commerce 1994). This study also concluded that there was inadequate data to report an overall trend in green sea turtle populations, but numbers at one Florida site had increased from 1971 to 1989 (Fig. 28), and the species is presumed to be recovering. The green sea turtle was drastically reduced by fishing (it was served in turtle soup) during the early 1900's.

At one study site in Mexico, Kemp's ridley is presumed to have declined sharply from 1947 to 1990, to 1% of original levels (Committee on Sea Turtle Conservation 1990). Data collected at that site from 1977 to 1990 suggested a continued but much less drastic downward trend (Fig. 28). Very few hawksbills and leatherbacks nest in the United States, and data are inadequate for precise statements of trends of these species, although expert opinion holds that the hawksbill is declining (U.S. Department of Commerce 1994).

Table 10. Trend data for nesting coastal waterbirds in North Carolina (from Parnell et al. 1992).

Species	Pre-1900's	Early 1900's	Current status	Current trend
Black-crowned night-heron	Rare	Common	Common	None
Black skimmer	Unknown	Abundant	Common	Declining
Brown pelican	Unknown	Absent	Abundant	Increasing
Caspian tern	Unknown	Absent	Uncommon	Increasing
Cattle egret	Absent	Absent	Abundant	Increasing
Common tern	Unknown	Abundant	Common	Declining
Forster's tern	Absent	Absent	Common	None
Glossy ibis	Absent	Absent	Common	Increasing
Great black-backed gull	Absent	Absent	Common	Increasing
Great blue heron	Unknown	Common	Uncommon	Unknown
Great egret	Abundant	Rare	Common	None
Green heron	Unknown	Common	Sparse	None
Gull-billed tern	Absent	Rare	Common	Declining
Herring gull	Absent	Absent	Common	Increasing
Laughing gull	Absent	Common	Abundant	Increasing
Least tern	Abundant	Sparse	Common	Declining
Little blue heron	Common	Abundant	Common	None
Royal tern	Common	Abundant	Abundant	Increasing
Sandwich tern	Unknown	Sparse	Common	Increasing
Snowy egret	Unknown	Rare	Common	None
Tricolored heron	Common	Common	Common	None
White ibis	Absent	Absent	Common	Increasing
Yellow-crowned night-heron	Rare	Rare	Sparse	Increasing

Central and South Florida

Everglades

Nowhere in the Southeast does the conflict between natural diversity and the needs of a growing human population occur on such a large scale as in the Everglades of south Florida (Davis and Ogden 1994b). The

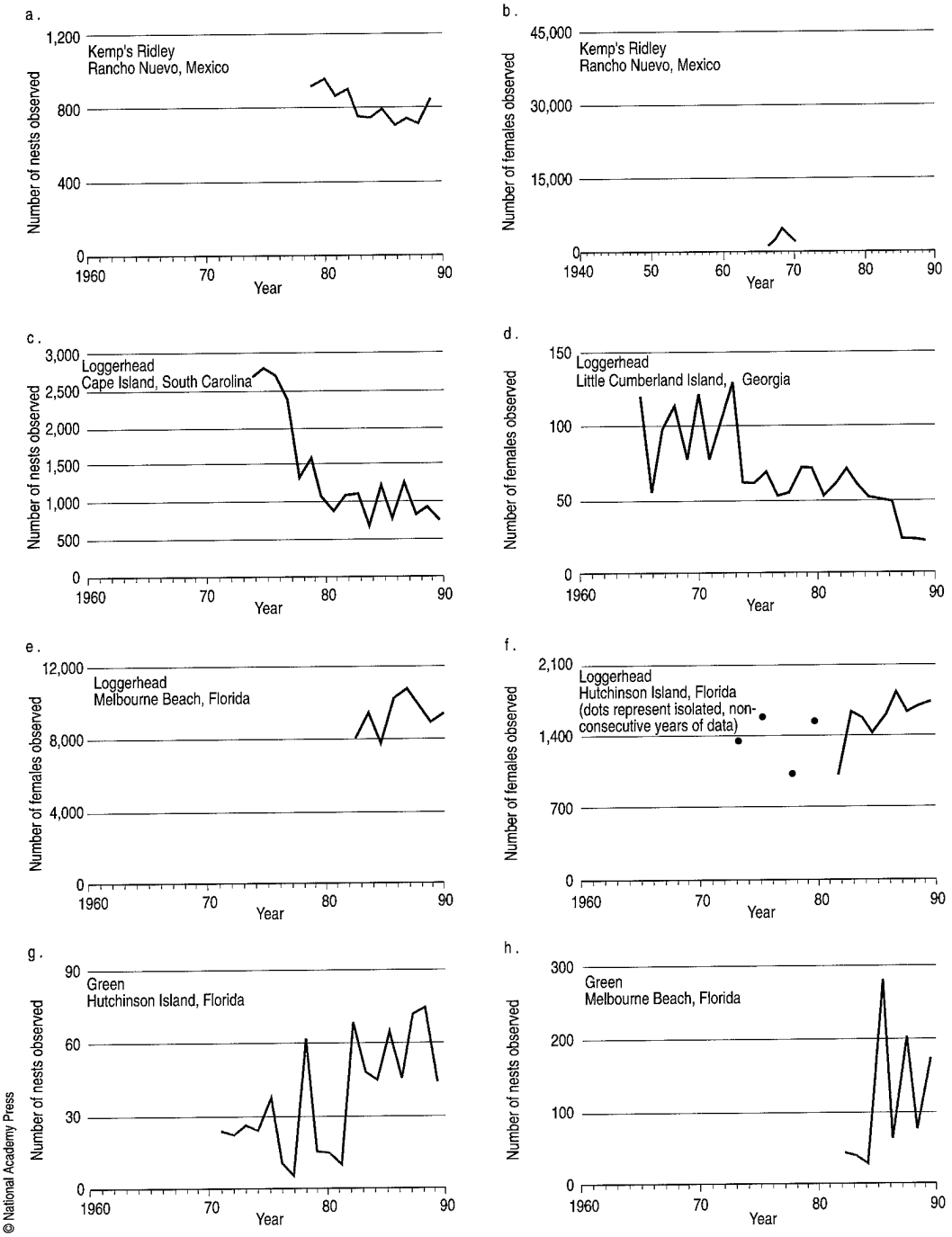

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Fig. 28a-h. Trends in sea turtle populations (from Committee on Sea Turtle Conservation 1990).

Everglades consist of a broad river of sawgrass with pools of open water and scattered islands of shrubs and trees. Historically, the system extended from Lake Okeechobee to Florida Bay.

The Everglades are bordered by the Everglades Agricultural Area to the north and west and by urbanization on Florida's east and west coasts. The flow of water in the northern part of the Everglades system, between Lake Okeechobee and Everglades National Park, is regulated in a series of impoundments to control flooding and provide water for agriculture and human populations. The amount, seasonal variation, and chemical composition of the water supply is critical to the ecosystems of the Everglades.

Everglades National Park has been called the first U.S. national park established for its biological diversity rather than for its scenic grandeur, for it was the preservation of the tremendous diversity of wading birds and other wildlife that was prominent in the founding documents. Everglades National Park, however, protected less than 20% of the sawgrass marsh for which the Everglades are named, and the

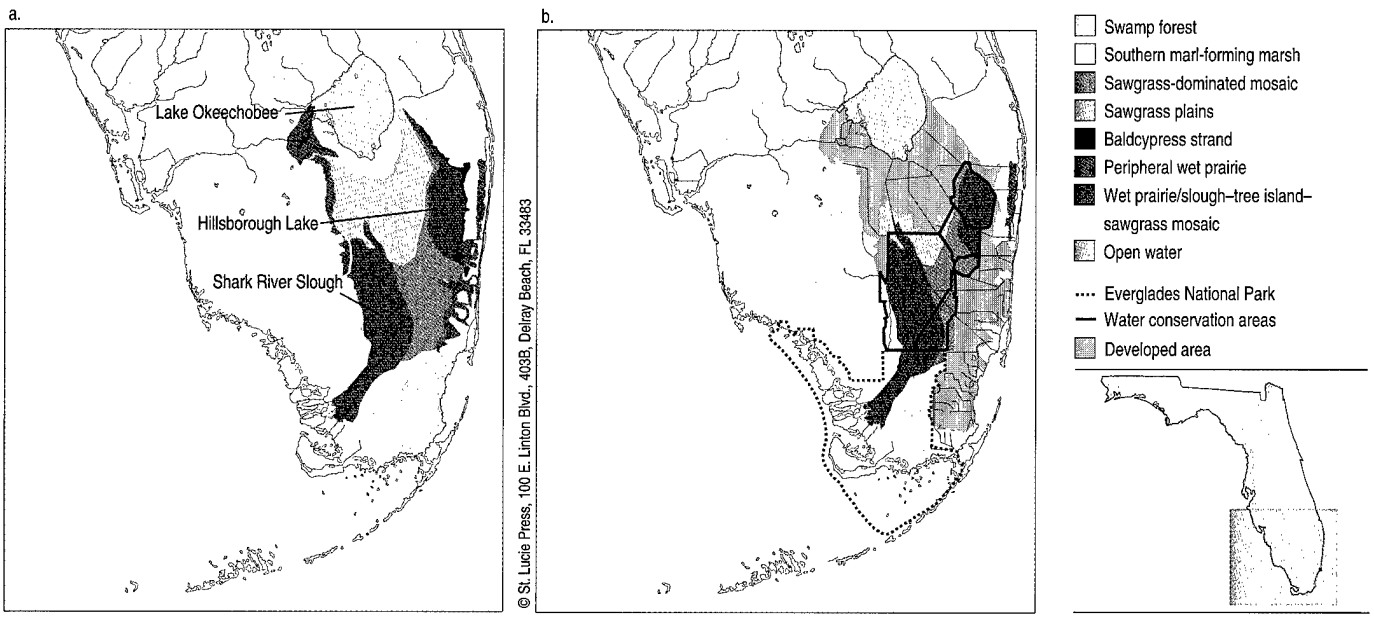

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Fig. 29. a) Former (around 1900) and b) current (1990) extent of Everglades vegetation (redrawn from Davis and Ogden 1994a,b).

area protected is the lowest portion of the watershed and thus is vulnerable to upstream manipulation of water supply (Davis and Ogden 1994a). Although the full extent of the Everglades *river of grass* was one million hectares (Fig. 29), 50% of this original wetland area has been drained and used for agriculture and development. The balance, 30%, is within impoundments of the South Florida Water Management District (Davis and Ogden 1994a).

A mosaic of unique and interacting ecosystems (Fig. 30) exists in the Everglades (Gunderson and Loftus 1993): ponds, sloughs, sawgrass marshes, wet prairies on peat (including three types), wet prairies on marl, bayhead swamp forests, pond-apple forests, willow heads, baldcypress forests, and hardwood hammocks. Two critical variables in this mosaic are hydrology and fire regime, although tropical storms, sea-level rise, habitat fragmentation, alterations to nutrients in drainage waters, and invasions by nonindigenous species (including one tree species, Australian melaleuca, that greatly influences ecosystem function in the Everglades) are also important (White 1994).

Since 1900 water flow to Everglades National Park has followed eight different hydrological regimes under human influence (Davis and Ogden 1994b). The dominant theme from 1920 until increased attempts at restoration in 1985 was reduction in the extent and duration of inundation in the park (producing a secondary effect of lower relative elevation of sites through higher oxidation rates of organic muck), the pooling of waters behind levees north of the park, the loss of transitional glade communities, a change from attenuated to pulsed flows, and a reduction of freshwater flows to Florida Bay (Fennema et al. 1994; Light and Dineen 1994).

Over the same period, wading bird populations within the park decreased to 10%–20% of original densities (Bennetts et al. 1994; Davis and Ogden 1994a; Light and Dineen 1994; Ogden 1994). In addition, the Everglades now have no nesting colonies of white ibis, have fewer than 1,000 pairs of great egrets, and fewer than 500 pairs of snowy egrets (Light and Dineen 1994). Robertson and Frederick (1994) noted that Everglades National Park was once a source of wading birds for other areas but since 1900 has become a sink for birds produced elsewhere. The declines within the park were accompanied by spatial shifts in the populations within the park (Ogden 1994), as well as shifts for some species to areas outside the park. The Everglade snail kite would seem particularly vulnerable because of its restricted distribution,

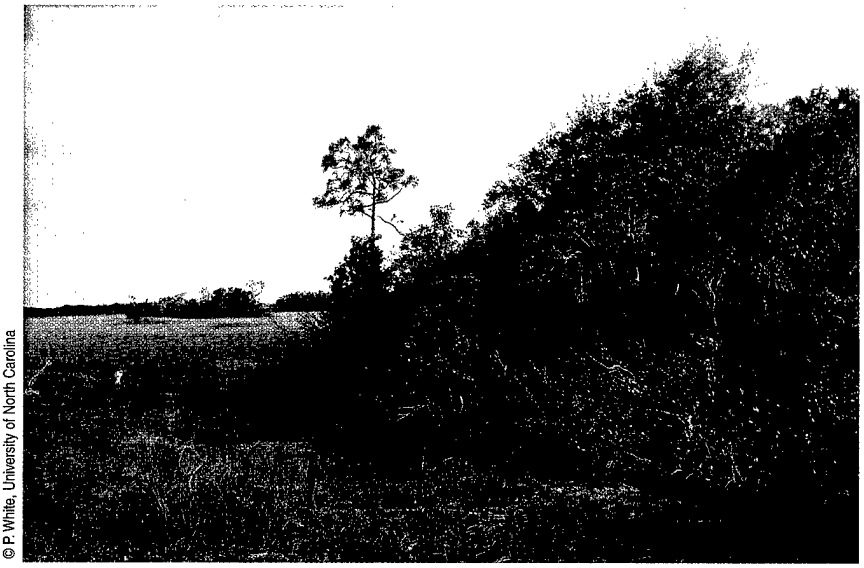

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Fig. 30. Relatively low elevations and underlying rock formations produce the mosaiclike nature and abrupt boundaries of many plant communities in the Everglades.

small and fluctuating population size, and dependence on a single food item, the apple snail.

The changes to the wading bird populations are a result of decreases in the extent of the wetland foraging habitat (Ogden 1994), particularly of the early dry season habitat (Davis et al. 1994). With this loss in area there were also decreases in the connectivity, heterogeneity, and total productivity of the sawgrass marsh, which already has one of the lowest productivities for wetlands (Davis et al. 1994). These changes are well established and universally associated with changed hydroperiod. Robertson and Frederick (1994) noted, however, that there are relatively few good quantitative studies, that data on animals other than birds are lacking, and that uncertainty exists about the specific ecological mechanism behind the trends (that is, about the availability and productivity of prey for the wading birds and how these populations are affected by hydroperiod). Loftus and Eklund (1994) noted not only the widespread report of downward trends in fish populations but also the lack of consistent long-term studies of these populations. They also described the problem of detecting trends given a lack of understanding of natural variability and that some populations may shift spatially (thus, a local decline might not be a global decline).

Davis et al. (1994) produced an exemplary study of landscape change in the historical Everglades. They depicted change on two scales. First, they used historical vegetation maps to reconstruct the predrainage landscape of the Everglades and compared this with a modern vegetation map for the area. Next, they mapped plant communities in greater detail on 25 randomly selected study areas, each a square mile (259 hectares), by using imagery from 1965 to 1971 and from 1984 to 1987. On the regional scale, three of seven physiographic landscapes had been entirely eliminated (swamp or custard-apple forest, peripheral wet prairie, and baldcypress stand), and other landscape types had been reduced by 74% (sawgrass plains), 47% (sawgrass-dominated mosaic), 24% (southern marl-forming marshes), and 13% (wet prairie/slough–tree island–sawgrass mosaic). On the local scale, wet prairie and slough decreased by 25%, and sawgrass marsh increased by 33%, a change attributed to lower water levels. Davis et al. (1994) discussed functional losses related to these changes: loss of total aquatic production due to reduction in spatial extent, loss of aquatic production in the southern Everglades due to shortened hydroperiod and interrupted flows, loss of habitat diversity at small scales, and reduction of dry-season feeding habitat of wading birds. Davis et al. (1994) concluded that the factors responsible for the historical configuration of habitats were extended hydroperiods and slow water flow caused by the presence of extensive sawgrass marshes, punctuated by drought years with severe fires.

The Everglades are facing additional threats: nonindigenous plant invasions and sea-level rise. Dominance of Australian melaleuca is estimated to be in the tens of thousands of hectares (Bodle et al. 1994; also see chapter on Nonindigenous Species), and sea-level rise is occurring at a rate 6 to 10 times higher than in the past 3,200 years, possibly affected by global warming (Light and Dineen 1994). Light and Dineen (1994) reviewed the role of agriculture in causing peat subsidence through increased oxidation of organic matter and suggested that the late 1900's may well have been the high point of agricultural production in the area because of the eventual loss of peat soils.

Pine Rockland and Tropical Hardwood Hammocks

Upland outcroppings of limestone in south Florida support pine rockland and tropical hardwood hammocks (Fig. 31) that are unique in the continental United States (Snyder et al. 1990). These ecosystems have been greatly reduced in extent by development and conversion to agriculture. Although wetlands have decreased by 40%–50% since 1900, the more restricted

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Fig. 31. Peperomia vines and bromeliads show tropical growth forms on a live oak in a tropical hardwood hammock in Everglades National Park.

upland pine forests have decreased by 80% (Robertson and Frederick 1994). This loss of area brought with it increasing fragmentation—Robertson and Frederick (1994) estimated that distance between forest patches increased from 25 to 40 kilometers in the original landscape to 100–200 kilometers today. Not including Long Pine Key in Everglades National Park, only about 2% of the original pine rocklands persists, and only three of the extant tracts are more than 50 hectares (Snyder et al. 1990). The upland hardwood hammocks of peninsular Florida fared somewhat better; although many important and large stands were lost, about 50% of the original area is extant (Snyder et al. 1990). Most of the remaining stands of pine rockland and tropical hardwood hammocks in peninsular Florida are protected in Everglades National Park or by state or local governments. In contrast, most of the remaining undeveloped land in the Florida Keys is privately owned and likely to be developed (Snyder et al. 1990).

The upland forests of south Florida had higher rates of endemism of plants (42 plant taxa, including 12 species listed by Florida or the U.S. Fish and Wildlife Service as endangered or threatened) and animals (20–25 animal taxa, including 9 species listed by Florida or the U.S. Fish and Wildlife Service) than wetlands (no endemic plants and 2–3 species of vertebrates) (Snyder et al. 1990; Gunderson and Loftus 1993; Robertson and Frederick 1994). Further, the wetlands still retained their historical complement of vertebrates, although the uplands lost 26% of their breeding birds between 1920 and 1990 because of habitat fragmentation (Robertson and Frederick 1994). One plant species is presumed extinct from these habitats, three plant species have been extirpated, several color forms of the unique tree snails have been lost, and many of the endemic species are threatened (Snyder et al. 1990).

Even where upland vegetation is protected, species survival is not guaranteed. Fire is essential to the management of pine rockland vegetation, and pine and tropical hardwood hammocks are severely threatened by invasions of nonindigenous animal species (Snyder et al. 1990). Established nonindigenous animal species include 7 mammals, 30 birds, 4 amphibians, and 25 reptiles (Snyder et al. 1990). More research is needed before we know what effects these introductions are having on native species. Likewise, there are many plant invaders, several of which not only displace native species but also alter fire behavior and thus change the way the pine rockland ecosystem functions (Snyder et al. 1990).

The pine forests of the Florida Keys are low-lying and have limited supplies of fresh water. Ross et al. (1994) showed that pine coverage on Sugarloaf Key decreased from 88 to 30 hectares from 1935 to 1991, a loss they attributed to sea-level rise, documented at 15 centimeters over the last 70 years and thought to be accelerating now. Soil and groundwater salinity and the importance of salt-tolerant plants were higher where pines had died. Consequently, mangroves are likely to increase, and the landscape diversity of ecosystems and the number of terrestrial species will decrease in the coming decades (Ross et al. 1994).

Florida Scrub

A unique landscape of dense shrub thickets and taller pine forests occurs on the upland sands of the central ridge of the Florida peninsula (Myers 1990). The upland, or *high pine,* is related to the sandhills and longleaf pine flatwoods found broadly on the southeastern Coastal Plain. The scrub communities, dominated by oaks, rosemary, and pines, are more restricted to Florida and adjacent states, and those dominated by sand pine are restricted to Florida (Myers 1990). The distinctiveness of the scrub ecosystem is underscored by its high levels of endemism: scientists believe that 40%–60% of the species are endemic (Myers 1990).

Only scattered islands of these communities are extant. The Lake Wales ridge is an example of the biological importance of these remnants; it possesses the highest number of unique species, presumably because it has been above sea level for the longest period. This ridge contains a flora of which 30% is endemic, as well as the greatest concentration of federally listed species in eastern North America (Martin 1993). Federally listed plants number 13 and state-listed number 22 (Myers 1990). Sixteen plant species occur in 20 or fewer sites (Martin 1993). Five vertebrates are restricted to the Florida scrub, of which three are listed as threatened by the U.S. Fish and Wildlife Service (Florida scrub-jay, Florida sand skink, and blue-tailed mole skink; Myers 1990).

Even though fire causes natural regeneration of scrub vegetation, this vegetation does not return to areas cleared for citrus (expanding southward in Florida because of recent freezes), homes, and businesses; in addition, scrub vegetation is greatly depleted when fire is excluded for long periods. As in all parts of Florida, the human population is rapidly growing in this region. Less than 10% of the natural scrub habitat is still found on the Lake Wales ridge, some in large tracts but much in small pieces scattered among housing developments and shopping centers. Although the trend is downward, several groups (U.S. Fish and Wildlife Service, The Nature Conservancy, Archbold

Biological Station) are working to protect the remaining scrub through acquisition and management (Martin 1993).

Mangroves

In the continental United States, well-developed mangrove forests occur only in south Florida (although mangrove species do occur in Louisiana) in areas where tidal waters produce saline conditions for all or part of the year (Fig. 32). Gilmore and Snedaker (1993) described four types of mangrove communities determined by the salinity regime, which, in turn, is determined by topography and surficial hydrology. Mangroves exist in a tension zone between saltwater flows and freshwater flows from inland areas; in addition, these forests are frequently battered by tropical storms, resulting in an ecosystem often dominated by patches of trees with different age classes.

There are about 202,000 hectares of mangrove forests in Florida (Gilmore and Snedaker 1993). Odum and McIvor (1990) reviewed data that indicated a loss of about 2.5% of the mangrove habitat between 1943 and 1970 in the three counties with the highest original total. They noted, though, that the rate of loss was quite uneven from place to place; for example, in Tampa Bay, 92% of the mangrove forest habitat was lost to impoundment between 1955 and 1974, and 44% of the estuarine areas have been lost (Gilmore and Snedaker 1993). Overall areal extent of this habitat has been reduced by development (draining and filling for urban areas and mosquito control), by reductions in freshwater flow because of diversion of runoff from inland areas (these reductions change salinity and alter productivity within the mangrove forests), and by invasion of nonindigenous species. Coastal mangrove forests dominated by red mangrove were protected by Florida law starting in the 1970's, but Gilmore and Snedaker (1993) reported continuing losses due to poor enforcement and disregard of this protection, as well as to legal but detrimental pruning of mangrove trees. Moreover, mangrove forests that are more inland have no protection on private land and thus are currently dependent on public lands for their survival. The large stands on public lands in the Everglades National Park have been affected in unknown ways by past reductions in freshwater flows and by other human influences (Gilmore and Snedaker 1993). In the future, sea-level rise (10–15 centimeters per century and probably accelerating) may increase the area dominated by mangroves in areas with a low topographic gradient (Odum and McIvor 1990).

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Fig. 32. Mangrove forests dominate the dynamic coastlines of southern and central Florida.

Although plant species richness is not high in these ecosystems, the habitat is highly productive and diverse in other groups. Gilmore and Snedaker (1993) listed seven guilds of animals determined by spatial position. Mangrove forests are extensively used by larval and juvenile fishes and invertebrates and probably play critical roles in the survival of many species of tunicates, crustaceans, mollusks, insects, and fishes. Mangrove forests provide habitat for species that are important in regional fisheries, as well as for eight species that are listed as threatened or endangered by the U.S. Fish and Wildlife Service (Odum and McIvor 1990).

Aquatic Ecosystems

Freshwater habitats in the Southeast include standing and flowing waters (Fig. 33). Rivers and streams range from the fast and clear high-elevation streams of the southern Appalachians to the slow and often opaque rivers of the Coastal Plain (Adams and Hackney 1992). In areas of karst topography, *lost* or *disappearing streams* are aboveground only during high water, and underground drainage in cave systems is important. Although few large lakes occur naturally in the Southeast, there are thousands of small ponds (Crisman 1992). In addition, many lentic ecosystems (ponds, reservoirs, and impoundments) were made by humans.

Rivers and Streams

Isphording and Fitzpatrick (1992) described the Southeast's rivers and streams as an evolutionary laboratory. There are 30 major river systems that drain to the Gulf of Mexico or the Atlantic Ocean. Long isolation of these waters has produced high species richness and local endemism. Continental high points in diversity occur in fishes (535 species), salamanders (51 species in 19 genera), aquatic insects

(Wallace et al. [1992] suggested that undescribed species equal described species in some groups), crayfishes (300 species in 11 genera), and many mollusks (for example, mussels with 270 species and subspecies in 49 genera [Isphording and Fitzpatrick 1992], and freshwater snails with 118 species in 9 families in the Mobile River basin [Bogan et al. 1995]). Taxonomic revision is ongoing in these groups, and new species are still being discovered. Systematic and genetic relatedness among the species has been used to describe biogeographic provinces and evolutionary histories (for example, Sheldon 1988). Six broad geographical provinces were based on several animal groups (fishes, mollusks, and crayfishes): the Atlantic Coastal Plain, the eastern Gulf Coastal Plain, the southern Appalachians, peninsular Florida, the Great River (Ohio–Mississippi) systems, and the trans-Mississippi region (Isphording and Fitzpatrick 1992). The faunas of the Atlantic Coastal Plain and the eastern Gulf Coastal Plain had their origins in different parts of the southern highlands. The southern Appalachians have a high degree of endemism in isolated headwater streams.

Southeastern stream systems have been altered by human activities, including impoundment, channelization, lowering of water tables, increased runoff, acid mine drainage, air and water pollution, sedimentation, recreation, and introduced species (including mussels, fishes, and aquatic plants). Many examples of effects on stream biota can be cited (Hackney et al. 1992)—nearly all major stream systems have been channelized or dammed (Adams and Hackney 1992). In the Southeast, 144 major reservoirs have been built (Soballe et al. 1992), and one-third of all Florida rivers have impoundments. The closing of the Norris Dam on the Clinch River in Tennessee in 1936 caused a loss of 45 mussel species below the dam within 4 months (Soballe et al. 1992). The creation of the Tennessee–Tombigbee Canal is allowing mixing of formerly isolated native biota; Sheldon (1988) predicted this mixing will result in species loss through competition and interspecific hybridization. Between 1930 and 1971, 2,017 square kilometers were surface-mined in the Appalachian Highlands, leading to acidification of nearby streams and reductions in aquatic species diversity and biomass (Mulholland and Lenat 1992). Water hyacinth, a nonindigenous plant first introduced to New Orleans in 1884, had become a problem locally by 1890 and covered 80,000 hectares in Florida by 1975 (Crisman 1992).

Only 20% of the nation's freshwater communities are protected by federal laws, and of these, only 10% are east of the Mississippi (Benke 1990). Despite having the highest diversity of fish species in the United States (McAllister et al. 1986), the rivers and streams of the Southeast are little understood and only minimally protected. Lotic species (those that live in moving water), especially those of higher elevations, are most seriously affected, as their specialization to clear, fast-moving streams renders them unable to adapt to conditions caused by dredging or impoundment (Hackney and Adams 1992).

Courtesy, N. Burkhead, USGS

Fig. 33. Virginia's Roanoke River is home to an endangered fish, the Roanoke logperch.

Caves

The Southeast has about two-thirds of all U.S. caves that are more than 3 kilometers long, one-half of the 49 deepest U.S. caves, and a total of some 20,000 individual caves, including Mammoth Cave in Kentucky, the world's largest cave system (Hobbs 1992). These caves are distributed over several physiographic provinces but are most abundant in the Interior Low Plateaus of Kentucky and Tennessee, the Ozarks, and the Coastal Plain of Florida and adjacent Georgia. Springs, including thermal springs in Arkansas, Georgia, Maryland, North Carolina, Virginia, and West Virginia, are often associated with areas where cave systems are common.

The caves and springs of the Southeast have a diversity of unique organisms, including 10 federally listed endangered species and 140 state-listed species (Hobbs 1992). All 6 species of the cavefish family are largely confined to the Southeast. Many of the larger species, such as blind fishes and salamanders, are vulnerable to extinction because of narrow physiological tolerances, long-delayed reproduction, and low reproductive outputs, traits that may have been selected because of their historically stable cave environments.

Although 62 cave complexes are protected (Hobbs 1992), survival of cave ecosystems depends on successful management of terrestrial systems and water quality. Caves depend on outside sources of detritus (plant material) for energy flow and are threatened by changes in the quantity and quality of water flowing from terrestrial sources. The late 1980's organization of an International Biosphere Reserve around Mammoth Cave National Park seeks to develop cooperative management of water resources among public and private partners to protect that cave system.

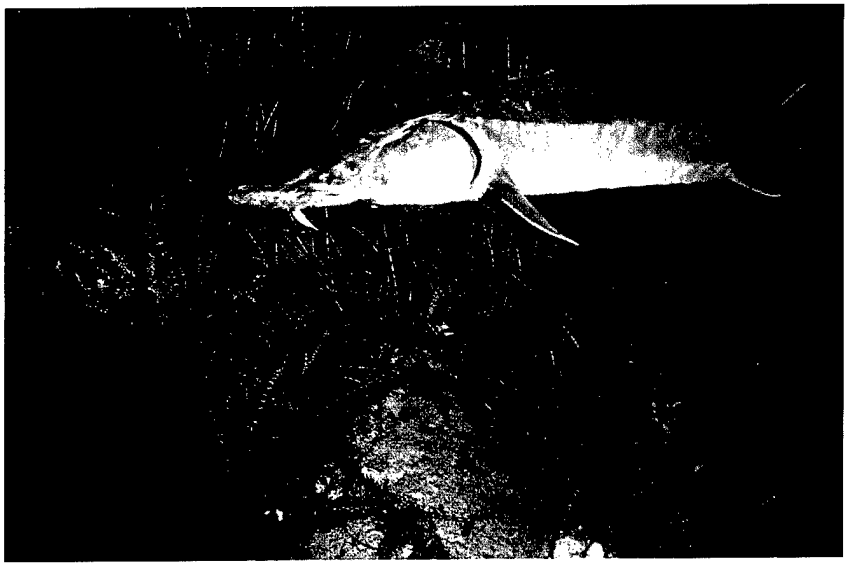
Natural Lakes and Ponds

Natural lakes and ponds in the Southeast are mostly small and were formed because of special characteristics of landform and geology. The two most common lake types are the Carolina bays and Florida solution ponds on carbonate bedrock (Crisman 1992). In addition to numerous ponds in Florida, solution of carbonate bedrock has produced sagponds in the southern Appalachians and the limestone sinkhole ponds of the Interior Low Plateaus (Crisman 1992).

In addition to Carolina bays and solution ponds, there are five other lake types in the Southeast (Crisman 1992): oxbow ponds and other ponds formed by the dynamics of erosion and deposition in river valleys, coastal ponds formed when streams are blocked by dunes and longshore deposition of sands or when basins are created by storm surge (most common in the Florida Panhandle), lakes formed by landslide blockage of mountain streams (for example, Mountain Lake in Virginia), lakes formed by local subsidence of the land surface (for example, Reelfoot Lake in Tennessee), and lakes formed by uplift of marine basins (for example, Lake Okeechobee in Florida). Most lakes and ponds are small, although the large lakes include Lake Okeechobee in Florida, the second-largest lake wholly within the United States, and Reelfoot Lake in Tennessee, formed by the New Madrid earthquake in 1811 (Crisman 1992).

Beavers were historically important in creating ponds on stream basins in the Southeast. Although the native subspecies of this animal became extinct in the Southeast by about 1900, recently a northern subspecies of beaver has spread through the Southeast after several releases by game managers between 1930 and 1950. The beaver was important in the natural dynamics of rivers and in maintaining habitat diversity. In some areas now, however, this species is entering a predator-free and fragmented landscape and may be threatening remnant natural areas.

Principal threats to natural ponds and lakes include eutrophication, acidification, drainage, control of water-level fluctuation, and invasions by nonindigenous species. Crisman (1992) noted that a serious hindrance to documenting these effects is the lack of an understanding of the composition, dynamics, and natural variation in these systems.



Courtesy N. Burkhead, USGS

Fig. 34. A Gulf sturgeon, a threatened species, swims in a spring on the Suwannee River. Sturgeons, which are one of the oldest existing fish species, were once common on Gulf of Mexico rivers, which these fish ascended in the spring to spawn. Dams and pollution have severely reduced Gulf sturgeon populations.

Status and Trends of Fishes, Freshwater Mussels, and Macroinvertebrates

Freshwater Fishes

The Southeast has 535 native freshwater fishes in 31 families (Lee et al. 1980; Echternacht and Harris 1993; Fig. 34; Table 11), making this region the richest of any temperate area of comparable size in the world. The total number of species represents 65% of the freshwater fishes of the United States, with 48% (257 species) of the southeastern species found nowhere else in the country. Fifty additional species are marine fishes that occasionally invade fresh water. Ten additional species live in the sea but spawn in fresh water, and one species, the American eel, lives in fresh water but spawns in the sea. Thirty-five nonindigenous species have become established in this region. Diversity is also high at smaller sampling scales. Cells of one-degree latitude and longitude typically have 25–50 species, and some have as many as 73. Elsewhere in North America the number at this scale is typically 5 to 15 (McAllister et al. 1986).

The high species richness is the result of diverse aquatic habitats and historical factors

that have permitted longer periods of isolation with sporadic interbasin dispersal (Sheldon 1988). Sea-level change during the Ice Age affected the distance between the mouths of rivers, which provided alternating periods of isolation and opportunities for dispersal. Stream capture in the highlands also allowed rare but significant opportunities for interbasin dispersal. Geographical differentiation in fishes has been used to define seven faunal regions: southern Appalachians, Interior Plateau, Lower Mississippi River, Lower Mobile River basin, Atlantic Slope, Lower Appalachicola River basin, and peninsular Florida (Walsh et al. 1995; Table 12).

Sheldon (1988) demonstrated that there is a strong species–area relationship for freshwater fishes but that, in a given basin area, the isolated rivers that flow directly to the Atlantic Ocean or Gulf of Mexico had fewer fish species than comparable river segments (similar basin area and habitat diversity) within larger, more-branching river systems (for example, the Mississippi and its large tributaries). Sheldon also showed the importance of separate evolution in isolated drainage basins in increasing the number of regional species. He predicted from species–area relationship that the Tennessee–Tombigbee Canal, which links two long-isolated and species-rich basins, will eventually result in a decline in the number of species—the connected system will not be able to support as many species as the two systems could support when isolated.

Human-caused changes to rivers and streams have greatly imperiled the Southeast's rich fish fauna (Johnson 1995; Williams and Neves 1995). About 19% of the region's species are endangered or threatened, and this percentage has increased through time (Johnson 1995). At present, there are 30 fish species listed by the U.S. Fish and Wildlife Service, 23 of which are narrowly restricted endemics. The high percentage of imperiled species in the southern Appalachians (Table 12) reflects the presence of narrowly restricted endemics (Fig. 35) in headwater streams, the dependence of many species in that region on good water quality in small rivers and streams, and the vulnerability of such streams to disturbances in their watersheds. The high percentage of imperiled species in the Interior Plateau region reflects the presence of species endemic to cave systems (Fig. 35).

There are many examples of fragmentation of the range of fishes and the extirpation of others from entire river systems. The loss of individual populations is probably the most significant change now occurring but is not well documented until a species is on the verge of extinction. Three species have become extinct:

Table 11. Federally listed vertebrates. The numbers of native, endemic, extinct, and extirpated species are taken from Echternacht and Harris (1993). The numbers of narrowly restricted endemics (species limited to only one or a few states and a narrow habitat breadth) and listed species are from U.S. Fish and Wildlife Service (1994).

Group	Number of species listed as					
	Native	Endemic	Extinct	Extirpated	Narrowly restricted endemics	Listed endemics
Fishes	535	257	3	2	30	23
Reptiles and amphibians	242	83	0	0	12	8
Birds	237	0	2	3	13	4
Mammals	101	7	0	5	22	13

Faunal region	Percent of species endangered or threatened
Southern Appalachians	18.3
Interior Plateau	11.4
Atlantic Slope	7.1
Lower Appalachicola River basin	6.3
Lower Mississippi River	6.0
Lower Mobile River basin	4.9
Peninsular Florida	4.1

Table 12. Imperiled fish species as a percentage of the total number of species by faunal region (from Walsh et al. 1995).

Maryland darter, harelip sucker, and whiteline topminnow (Miller et al. 1989; Walsh et al. 1995). The least darter has been extirpated in the Southeast but populations persist elsewhere, and only a few individuals of the slender chub have been seen since the mid-1980's (Walsh et al. 1995; Fig. 36).

Narrowly restricted endemics, short-lived species, and species dependent on good water quality are particularly vulnerable. Nearly all of the 30 species that are federally listed are narrowly restricted endemics with limited tolerance for habitat modification. The extinct whiteline topminnow is an example of a narrowly restricted endemic; it was found only in a single Alabama spring that was used to supply

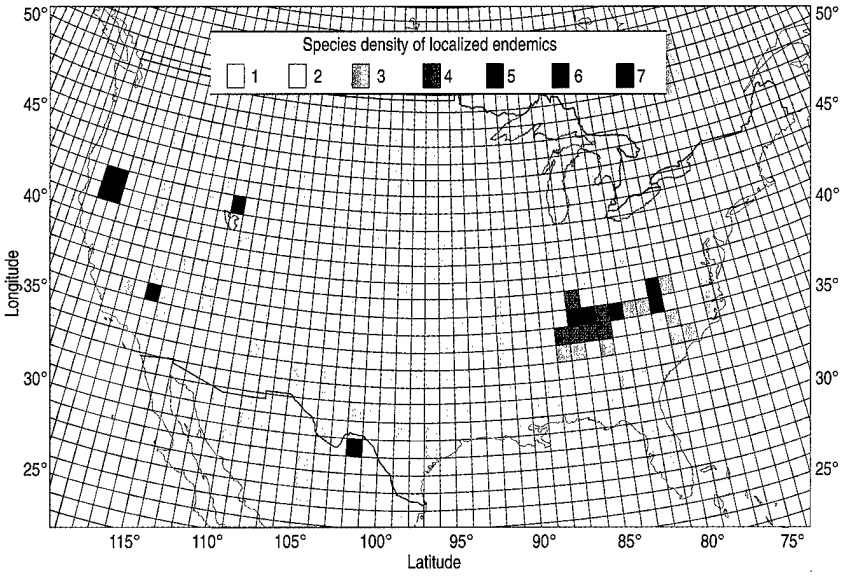


Fig. 35. Distribution of endemic fish species in the Southeast, as compared with the rest of the contiguous U.S., on a grid of one-degree latitude by one-degree longitude (redrawn from McAllister et al. 1986).

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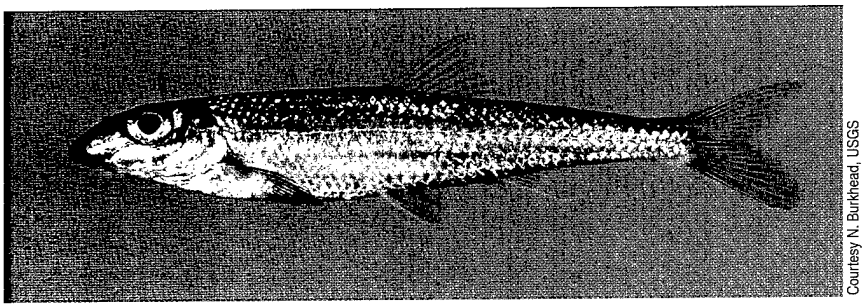


Courtesy N. Burkhead, USGS

Fig. 36. Only a few individuals of the threatened slender chub have been observed since the mid-1980's despite intensive surveys by scientists. More effort is needed to determine if this small minnow is still extant.

water for the city of Huntsville. The Waccamaw silverside, confined to a single Coastal Plain lake in North Carolina, is vulnerable because of its narrow range and short-lived nature (it is an annual species). Other endangered species are not so restricted, however; for example, the harelip sucker was found in eight states. This species, last collected in 1893 but probably persisting to the early 1900's, appears to have been restricted to clear-water pools with rocky substrates in moderate to large streams, a habitat vulnerable to siltation and agricultural runoff (Miller et al. 1989).

A recent assessment of the habitats of threatened fish species in Tennessee found that medium-sized rivers were especially important (Etnier and Starnes 1991). Only 14% of all fishes reported in Tennessee occur in medium-sized rivers, but 41% of the fish species on the state's threatened and endangered species list depend on the habitat medium-sized rivers provide. These fishes are threatened because of impoundments already constructed or pending and because they are sensitive to the loss of coarse substrates caused by sedimentation. However, the imperiled species were distributed across a variety of habitats: large creeks and small rivers (21% of threatened species), streams (16%), springs (13%), and big rivers (9%).

Many investigators have suggested the need for long-term monitoring to detect trends and natural fluctuations in fish populations. Bass (1990) reported that fish trends in Florida from 1983 to 1987 revealed some flux of species in individual rivers during this period but no statewide decline. Bass (1990) concluded that monitoring is critical to understanding natural fluctuations and to detecting long-term trends.

Freshwater Mussels

The Southeast's freshwater mussels include 270 species and subspecies in 49 genera, representing 90% of the freshwater mussel fauna of all of North America north of Mexico (Williams et al. 1993). Ten genera are endemic to the Southeast. Of 93 species and subspecies limited in the United States to one or two states, 91 occur only in the Southeast. The species richness of freshwater mussels in the Southeast is attributed to habitat diversity (including substrates of attachment), evolution within isolated river basins, stream capture over geologic time (which produces new patterns of dispersal and isolation), and high richness in fish species (larval forms use fish as hosts).

Forty-eight percent of the freshwater mussels of the Southeast are endangered, threatened, or possibly extinct (Williams et al. 1993; Williams and Neves 1995). An additional 25% are of special concern, resulting in 73% of this diverse fauna being at risk. Only 25% of the fauna is considered stable (Williams et al. 1993). Of 21 species that are now potentially extinct, 14 were endemic to the Southeast (Williams et al. 1993). Declines in freshwater snails and other mollusk groups are probably also occurring in the Southeast, but surveys of these groups are less complete.

Declines in mussel faunas have affected river basins regionwide, including those with higher and lower amounts of endemism. Historically, diversity of mussels increased from headwaters to the mouths of rivers; pollution and other human influences also increase in this direction. Hence, declines in diversity have been most significant in the lower reaches of rivers. Habitat specialists (those requiring, for example, a particular kind of hard substrate) have declined more than habitat generalists.

Factors that are important in declines in mussel richness and abundance are sedimentation, pollution, changes in river flow due to dams and channelization, invasions of nonindigenous species (for example, the zebra mussel and Asian clam), and loss of fish hosts. In addition, commercial harvest of mussels is causing unknown effects on target and nontarget species (Williams et al. 1993). As with other aspects of aquatic diversity, retention of natural vegetation in floodplains and along riverbanks is a key element in the protection of water quality and mussel populations. Many southeastern states still have areas with high mussel diversity and abundance, such as the Clinch River in Virginia, Swift Creek in North Carolina, Stephens Creek in South Carolina, and the Ogeechee River in Georgia. These waters tend to be tributary and headwater rivers within drainage basins of several hundred square kilometers in which silviculture is the dominant land use and agricultural and urban areas are limited.

No regionwide monitoring or conservation plan exists for freshwater mussels. Conservation efforts will require cooperation of many public and private groups because mussel populations ultimately depend on water quality that is affected by human activities over large areas. The growing human population and its

need for sources of clean drinking water will increase the pressure for the creation of additional reservoirs, which in turn will further imperil this distinctive element of the southeastern fauna.

Benthic Macroinvertebrates and Water-Quality Trends

The Clean Water Act directs the U.S. Environmental Protection Agency to evaluate, restore, and maintain the chemical, physical, and biological integrity of our nation's waters. In response, state environmental protection agencies have implemented water-quality monitoring programs that are chemically based and that have successfully addressed water-quality issues (U.S. Environmental Protection Agency 1990). Chemical monitoring alone is not adequate for describing water-quality changes, however. Spills and rapid fluctuations in effluent characteristics can go undetected in routine monitoring of water chemistry. Pollution from nonpoint sources can arrive with rain and runoff between routine sampling dates. To address these concerns, most state programs have supplemented chemical monitoring programs with biological monitoring programs, which often include the assessment of benthic macroinvertebrate (aquatic insect larvae) populations but may also include fish, periphyton, and phytoplankton populations. All but four states conduct some form of biological water-quality monitoring (U.S. Environmental Protection Agency 1991). Used together, chemical and biological water-quality monitoring programs provide a comprehensive, integrated approach to water-quality assessment.

Benthic macroinvertebrates are sensitive to subtle changes in water quality. Because many species have life cycles of 6 months to 1 year, the effects of a short-term pollutant (such as a spill) will not be overcome until the next generation appears (Lenat 1993; Patrick and Palavage 1994). Benthic macroinvertebrate communities have also been shown to respond differently to different water-quality problems. Typical responses include declines in richness and increases in abundance of tolerant taxa as a response to nutrient enrichment, decreases in richness and abundance in response to toxic effluents, and stability in richness and declines in abundance in response to sedimentation (Lenat 1993; Patrick and Palavage 1994).

Biological surveys typically fall into two primary categories: network trend monitoring and intensive surveys at selected locations to assess effects from specific sources. In trend monitoring, biological data are collected from fixed stations over set intervals. For example, in North Carolina before 1990, the Division of Environmental Management maintained a Benthic Macroinvertebrate Ambient Network by using stations of the ambient water-quality monitoring program. North Carolina and many other states have been conducting monitoring programs organized around river basins (Fig. 37). In this system, sampling is concentrated in one large river basin or in as many as six smaller ones each year so that all river basins are eventually surveyed during a 5-year period. The basinwide program uses many of the original stations of the ambient water-quality program.

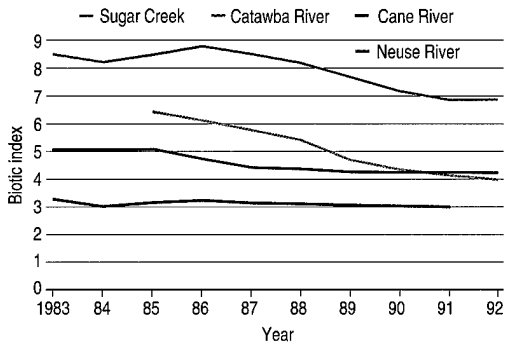


Fig. 37. Trends in water quality for four North Carolina river systems, as indicated by benthic macroinvertebrate monitoring. The North Carolina Biotic Index (Lenat 1993) is a summary measure of the tolerance values of specific macroinvertebrates relative to their abundance; the index serves as a measure of the general level of pollution regardless of source or stream size. A high biotic index indicates poor water quality. In this figure, Sugar Creek, in the Piedmont of South Carolina, and the Catawba River, near Mt. Mitchell in western North Carolina, both show improvement in water quality over the past decade. The Cane River, north of Mt. Mitchell, and the Neuse River, southeast of Raleigh in the Piedmont, North Carolina, have shown little change in water quality (D. Penrose, North Carolina Department of Environment, Health, and Natural Resources, unpublished information).

Although most states have collected biological data for fewer than 10 years, nonetheless, evaluation of water-quality trends has been possible. In North Carolina, improvements in biological communities have been detected as a response to a phosphate ban and upgrades to wastewater treatment plants. Macroinvertebrate communities also improved after an upgrade to a pulp and paper mill that was polluting a section of the Pigeon River, a problem that resulted in the state of Tennessee suing the state of North Carolina.

Patrick and Palavage (1994) argued that surface waters have improved the most where they have had the greatest degree of regulation. Unregulated sources, such as runoff from agricultural and urban areas, appear to play the major role in stream degradation in the Southeast (Duda et al. 1979; Benke et al. 1981; Lenat and Crawford 1994). Agricultural activities result in greater concentrations of most dissolved substances, greater levels of sedimentation, and higher concentrations of nutrients (Lenat and Crawford 1994). Urban runoff, on the other hand, can be a mixture of different pollutants, including enrichments, sediments, and toxic metals.

The scarcity of long-term biological data from streams and rivers has sparked interest in monitoring; most state and federal agencies have programs to address biological integrity. Federal programs include the U.S. Geological Survey's National Water Quality Assessment Program, a nationwide program designed to

assess the status and trends in the quality of surface-water and groundwater resources of entire river basins (Gurtz 1993). Ten of the 60 river basins included in this program are in the Southeast. If this project continues, it will provide a much-needed basis for the future assessment of aquatic trends in the country.

Status and Trends of Reptiles, Amphibians, Birds, and Mammals

Reptiles and Amphibians

Reptiles and amphibians are present in virtually all natural habitats in the Southeast. All the turtle species nest on land, some aquatic turtles and snakes hibernate on land, and dozens of species of southeastern frogs and salamanders are terrestrial as adults but require wetlands for breeding and development of young. Also, terrestrial corridors among aquatic habitats are essential for reptile and amphibian dispersal during unfavorable periods such as drought.

Of the more than 450 species of reptiles and amphibians native to North America, more than half (242 species) occur in the Southeast (Conant and Collins 1991; Echternacht and Harris 1993; Gibbons 1993; Table 11). The Gulf Coastal Plain is the most significant area of endemism in reptiles and amphibians in the United States (Dodd 1995a)—40% of southeastern amphibians and 29% of southeastern reptiles are endemics. In addition, there are 4 species of introduced amphibians and 20 species of introduced reptiles in the Southeast, most of which are found in the Coastal Plain and Florida.

Courtesy of Savanna River Ecology Lab

Fig. 38. The Appalachian salamander, an endemic species of the southern Appalachians.

The Southeast has the highest regional total (130 species) of amphibians in the United States (Echternacht and Harris 1993), including 38 species of frogs and toads (12 of these are endemic to the Southeast) and 92 species of salamanders (45 of which are endemic to the Southeast; Fig. 38). The southern Appalachians are a world center of diversity for salamanders and have 68 species of a unique group of lungless salamanders that evolved in this region of well-oxygenated streams and high rainfall. The Southeast has 6 species of large, fully aquatic salamanders and the Coastal Plain has 32 species of frogs and toads, of which 11 are endemic.

There are 52 species of snakes in the Southeast, of which 11 are endemic (Conant and Collins 1991; Echternacht and Harris 1993). Of the 91 species of lizards native to the United States (the only group of U.S. herpetofauna concentrated more heavily in another geographic region—the Southwest [Stebbins 1966]), 21 occur in the Southeast, and 6 of these are endemic. The Southeast has 36 species of turtles, 13 of which are endemic; the Coastal Plain possesses North America's highest diversity in this group. One of the two greatest concentrations of freshwater turtle species in the world (the other is in Asia) is in the Mobile River basin (Iverson 1992; Lydeard and Mayden 1995).

The only crocodilians in the United States, the American alligator and American crocodile, are restricted to the Southeast. From northeastern North Carolina southward, the American alligator is recovering from past population declines (Stalter and Odum 1993; Woodward and Moore 1995). Woodward and Moore (1995) estimated increases in Florida populations of 1.9% per year since the mid-1970's and concluded that reproduction is probably sufficient to balance the recent revival of legal hunting. The ecological role of the American alligator is highly significant: the reptile creates pools in the marshes that serve as habitat for many other species.

Although there have been no documented extinctions in these groups, 12 species are listed as endangered or threatened by the U.S. Fish and Wildlife Service: American alligator, American crocodile, blue-tail mole skink, Florida sand skink, Eastern indigo snake, gopher tortoise, 4 turtle species, and 2 salamander species. All of these except one mountain salamander species occur on the Coastal Plain. Eight of the 12 species—the 4 turtles, 2 skinks, and 2 salamanders—are narrowly restricted endemics. The gopher tortoise has become threatened in part because of the loss of longleaf pine habitat (Bury and Germano 1994). The American alligator is a wide-ranging animal

that was formerly reduced by hunting and human alteration of aquatic habitats and now has recovered so that hunting has been reinstituted in some areas (Woodward and Moore 1995).

The greatest threat to reptiles and amphibians comes from habitat loss and changes in water quality. Numerous examples can be given of population declines in individual wetlands as a consequence of human activities. Drainage and destruction of temporary ponds have resulted in the reduction of striped newts in Georgia (Dodd 1995a), the extirpation of the flatwoods salamander from a portion of its range, and apparent declines of gopher frogs in Alabama and Mississippi (Dodd 1995a).

Species that are adapted to terrestrial habitats have also suffered. Of the 242 native reptiles and amphibians in the Southeast, 170 (74 amphibians, 96 reptiles) are native to longleaf pine–wire-grass ecosystems (Dodd 1995a). The near loss of this natural community, through timbering, development, and fire suppression, has had a significant, though largely unquantified, effect on reptiles and amphibians.

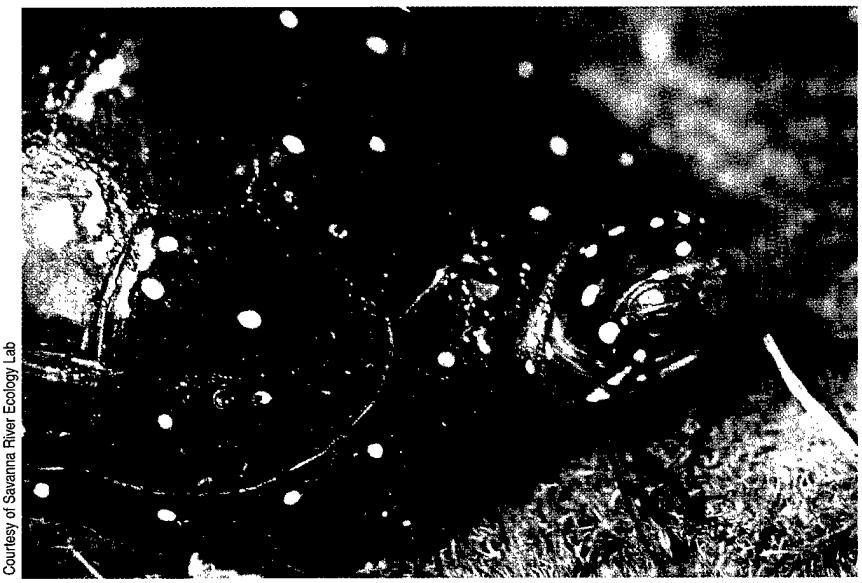
Several species of map turtles, which are native to large southern rivers, have presumably been severely affected by impoundments. The ecological status of some of these turtles has also been affected by the removal of dead trees and the dredging of river bottoms, which harbor mollusks that the turtles eat. The opportunity has passed for us to measure the effect on historical population levels, even within the last century, but most scientists agree that many populations of map turtles are declining (Buhlmann and Gibbons 1996).

Some musk turtles are restricted to stream systems; the flattened musk turtle from Alabama, for example, represents a species whose very existence has been jeopardized by water-quality degradation. The negative effects have been not only from direct health effects on these turtles but also from the elimination of their basic food supply, the freshwater mollusks that live in the streams (Lydeard and Mayden 1995; Buhlmann and Gibbons 1996).

Spotted turtles (Fig. 39) are a clear example of how humans can cause a reduction in a species' population sizes and numbers. Destruction of small wetlands is one obvious assault on this species; spotted turtles have special habitat requirements and do not persist in other aquatic habitats, such as farm ponds, once their wetland homes are destroyed. In addition, the spotted turtle is threatened because of legal collection by commercial collectors (for example, more than 500 turtles were collected in North Carolina in 1993; A. Braswell, North Carolina State Museum, Raleigh, personal communication). For a species that lives in small, isolated wetlands, usually in low numbers, removal of several adults from a habitat can be devastating to a population (Congdon et al. 1993).

Commercial collecting for the restaurant trade has also had an effect on some reptile populations. For example, the alligator snapping turtle and the common snapping turtle are severely and negatively affected by commercial enterprises that remove many individuals of these long-lived species.

It is critical to realize that in one major respect, most reptiles and amphibians are not like game species such as deer or northern bobwhite—their populations are not sustainable if adults are removed. Individuals of most reptile and amphibian species take years, often more than a decade, to reach maturity. Populations are often disjunct and the numbers of individuals small. Such species are sensitive to abrupt reductions in population size and cannot replace themselves when subjected to harvest (Congdon et al. 1993).



Courtesy of Savanna River Ecology Lab

Fig. 39. A spotted turtle, which is one of the Southeast's 36 species of turtles and one whose numbers are declining.

Highway deaths also deplete the numbers of many species of reptiles and amphibians that travel overland. A 2-meters-long indigo snake, for example, does not move fast enough to safely get across today's highways.

Some ecologists have reported declines in amphibian populations and related these to specific threats, such as acid rain, destruction of the ozone layer, global warming, or other forms of nonpoint pollution (Blaustein 1994). It is unclear if any of these factors are responsible for amphibian declines in some regions (Pechmann et al. 1991; Pechmann and Wilbur 1994), but habitat destruction is the primary threat to most species of reptiles and amphibians in this country and probably in most countries in the world today. Timber harvest, for

example, dramatically reduces amphibian populations in the southern Appalachians (Petranka et al. 1993). Habitat destruction may take more subtle forms, though, and what may appear to be protected and pristine habitat may actually be experiencing degradation because of changes in hydrology, pollution, herbicide and pesticide runoff, the introduction of competitive nonindigenous species, the introduction of disease organisms, or the loss of important breeding sites such as temporary ponds (Blaustein 1994; Dodd 1995b).

No modern extinction of a reptile or amphibian species has yet occurred in the Southeast, but there are many examples of long-term declines in the numbers of individuals and populations. Amphibian declines are difficult to assess because of natural population fluctuations; more long-term information is needed to better interpret trends in amphibian populations and to discern natural and anthropogenic causes (Pechmann et al. 1991; Blaustein 1994; Pechmann and Wilbur 1994).

Insufficient knowledge of the distribution and ecology of native reptiles and amphibians is a major shortcoming in any national effort to detect change and avoid loss in this group. An example of the difficulty that ecologists face in confirming the presence of herpetofauna is apparent from studies by investigators at the Savannah River Ecology Laboratory and from studies by other investigators on the Savannah River Site in South Carolina. This site is the largest tract of land (750 square kilometers) in North America with high herpetofaunal species diversity and a long-term record of intensive ecological research and survey. Since the 1950's, herpetologists have collected data on more than a million individual reptile and amphibian specimens representing more than 100 species (Gibbons and Semlitsch 1991). Nonetheless, despite intensive surveys, the presence of new species has been verified on the Savannah River Site at a rate of more than five species per decade.

Birds

The Southeast originally had 237 native species of birds, none of which were strictly endemic to the region (Echternacht and Harris 1993; Table 11). Three species are nearly restricted to the Southeast: Bachman's warbler (which may be the rarest vertebrate in the region), Swainson's warbler, and the brown-headed nuthatch. Twenty-six percent of the total (61 species) is associated with water. Of these, 19 are large wading bird species, a group for which the Southeast has the continent's highest total. The greatest species richness of birds occurs in the coastal wetlands. Thirty-one species (13.4%) are restricted to the high mountains. Echternacht and Harris (1993) estimated that there are 17 established nonindigenous bird species in the Southeast, but they warned that the number may be an underestimate, considering that other species have been released in the area.

Land clearing and hunting were responsible for the extinction of two bird species in the Southeast: the passenger pigeon (last reported in the wild in 1899) and the Carolina parakeet (last reported in the wild in 1913). Passenger pigeons were hunted for their market value whereas Carolina parakeets, birds of old wetland forests, were hunted to protect fruit crops.

Three species have been extirpated from the Southeast: ivory-billed woodpecker (last seen in the 1950's and thought to persist in Cuba), which was dependent on large-cavity trees in extensive and old riparian forests; and the Zenaida dove and the Key West quail-dove, which were rare Caribbean species restricted to Florida— the reason for their extirpation is not known (Echternacht and Harris 1993). An additional subspecies, the dusky seaside sparrow, became extinct because of poor fire management of its marsh habitat in coastal northern Florida.

Fourteen species and subspecies of birds are federally listed, of which 12 are Coastal Plain species: crested caracara, Mississippi sandhill crane, Florida scrub-jay, brown pelican, piping plover, Cape Sable seaside sparrow, dusky seaside sparrow (now extinct), wood stork, least tern, Bachman's warbler, ivory-billed woodpecker, and red-cockaded woodpecker. The fate of these species is largely tied to habitat loss, including reductions in longleaf pine savannah, Florida scrub, wetlands, and beach communities. Two other federally listed species, the bald eagle and the peregrine falcon, were formerly wide-ranging species sensitive to pesticides; these species are now recovering.

The Southeast is important not only for summer breeding populations but also for birds that winter in the Southeast and for birds that migrate farther distances (for example, to the Caribbean and Central and South America) after passing through the South in spring and fall. Coastal habitats, maritime forests, and longleaf pine savannah are all important to migrating species. Threats to bird species include land-use changes, forest fragmentation (which often results in increased nest predation and cowbird parasitism), tropical deforestation (for Neotropical migrants), elimination of wetlands, and coastal development.

Several investigators have published summaries of trend data for bird species in the United States. By using the Breeding Bird Survey data for 1966 to 1992,

Peterjohn et al. (1995) reported that birds of grassland and shrubland experienced the most significant and consistent declines; fully 82% of grassland species declined over this period. General results indicate that there were declines in specialist species and those that depend on natural habitats, whereas there were increases in generalist species that adapted well to use of agricultural landscapes.

Hunter (draft report) used the same data base to support this conclusion for the Southeast: of 14 bird species that occur in grassland habitats (including coastal prairies in Texas and Louisiana and longleaf pine savannahs), 8 significantly declined, and only 1 significantly increased. Average population declines per year varied from 1% to 6% (vesper sparrow). These habitats harbor 10 endangered bird species and 5 candidate species. Hunter also showed that of 24 bird species in successional shrub–scrub vegetation, 14 species experienced significant population declines ranging from 1% to 5.8% per year. The eastern Bewick's wren (5.8% per year) and the golden-winged warbler (5.4%) experienced the greatest declines.

Root and McDaniel (1995) studied trends in 27 species of songbirds by using the Christmas Bird Count data from 1959 to 1989. They found that in the United States, the largest decreases of these species were in the Southeast. On a per state basis, 10%–30% of the 27 species were declining in southeastern states, whereas, with the exception of South Carolina (25% of the birds increasing), 0% to 5% of the species showed increases. They also found that birds of open habitats that depended on the seeds of grasses and herbaceous plants (for example, sparrows and meadowlarks) experienced the greatest declines.

In these data sets, about half of the Neotropical migrants showed increases and half decreases (Peterjohn et al. 1995). Declines of about 1%–2% per year have also been observed in area-sensitive woodland birds such as the wood thrush and veery (Peterjohn et al. 1995; Root and McDaniel 1995). The loggerhead shrike declined by 3.2% per year (Yosef et al. 1993; Peterjohn et al. 1995).

Some bird species, though, have increased in the last several decades, pointing to significant conservation success stories. For example, the brown pelican population has increased by 3.8% each year, at least in part because of the banning of DDT (Erwin 1995). Several species of raptors have also increased because of the banning of DDT, protection, and habitat management (Fuller et al. 1995). The endangered Mississippi sandhill crane, originally found from Alabama to Louisiana but now known from only one site in Mississippi, has increased because of intensive conservation management (Gee and Hereford 1995; Peterjohn et al. 1995). That species reached a low point of 13 individuals in the wild in 1985; there are now 20 individuals in the wild, with an additional 115 birds released from captive breeding (Gee and Hereford 1995). Egret populations were drastically reduced in the early 1900's because of hunting for the plume trade; populations are recovering and have increased by an average of 2% per year (Erwin 1995).

Critical information for the conservation of bird species includes understanding the relationship between reproductive success and habitat size and quality. Hunter (draft report) stated that to create populations that will endure and that will generate excess individuals to colonize new sites, some birds species (for example, the ivory-billed woodpecker) require 2,000 to 40,000 hectares of unbroken habitat. Further, we have to understand the relation between reproductive success and such microhabitat variables as forest-age structure. Hunter also reported that species that require large areas can act as umbrella species for species with smaller area requirements. If we understand the habitat area each bird species needs, it will help us determine optimum block sizes and rotations for harvested forests. The need for large habitat areas is another argument for reforestation of marginal farmlands and the retention of wetlands. Because the southeastern landscape is so heavily in private ownership, land used for agriculture and forestry must play a large role in the survival of bird species diversity. Erwin (1995) suggested that recent increases in great blue heron populations resulted from this bird's practice of feeding in aquaculture ponds. Finally, regional monitoring of bird populations is essential because of geographic movements of species. For example, white ibis and wood stork populations have declined in south Florida but are stable in the Southeast as a whole because of population shifts northward to northern Florida, Georgia, and the Carolinas (Erwin 1995).

Mammals

Terrestrial and freshwater habitats in the Southeast are home to 101 mammal species (Echternacht and Harris 1993; Table 11). Of these, 5 are extirpated, all of them ecologically important species of either large carnivores or grazers: jaguar, ocelot, gray wolf, elk, and bison (Echternacht and Harris 1993). Two other large carnivores are on the verge of extinction: the Florida panther, the only remaining subspecies of mountain lion in the eastern United States, and the red wolf.

Endemic species represent a relatively small percentage of the mammals. According to

Echternacht and Harris (1993), eight small mammal species are endemic to the Coastal Plain province of the Southeast: southeastern pocket gopher, colonial pocket gopher, Sherman's pocket gopher, Cumberland Island pocket gopher, oldfield mouse, Florida mouse, Perdido Key beach mouse, and round-tailed muskrat. The region also has eight species of introduced mammals, four of which have many adverse effects on native communities: coyote, pig (feral domesticated pigs and wild boar) in the mountains and Coastal Plain, and nutria and horse in the Coastal Plain. Beavers were extirpated in the Southeast but have become reestablished in the last 20 years. Although beavers were historically important in the maintenance of habitat diversity, beavers of today inhabit landscapes with reduced predation and where the remnant habitats may themselves be vulnerable to loss from flooding.

There are 22 federally listed mammals in the Southeast: eastern mountain lion and the Florida panther, Key deer, gray wolf, red wolf, Louisiana black bear, 4 species of bats, 9 small mammal species restricted to the Coastal Plain in Florida or Alabama, a shrew restricted to Virginia and North Carolina, and 2 species of flying squirrels restricted to the mountains (Lee et al. 1982; Humphrey 1992). The eastern mountain lion and the gray wolf are already extirpated in the Southeast. In the following sections we discuss these and other species representative of trends in southeastern mammals.

Small Mammals

Small mammal species that are most at risk in the Southeast have narrow distributions. Most of the threats to these species come from development and subsequent loss of habitat. In isolated communities, such as beach habitats, feral cats represent a significant threat. Shrews and other insectivorous mammals suffer from the concentrated effects of residual pesticides. Fleming and Holler (1989) described ongoing efforts to reintroduce the endangered Perdido Key beach mouse to a site in Gulf Islands National Seashore.

The future of the fox squirrel is linked to that of its habitat, the longleaf pine savannah. A long-lived species with low reproductive rates, the fox squirrel has not been well studied or understood, but timbering, fire suppression, and development are all limiting its range and reducing its population sizes.

Bats

Of the 39 bat species listed for the United States, 17 occur in the Southeast (Di Silvestro 1989). Widespread pesticide use, resulting in poisoning as well as loss of food sources, is responsible for significant declines in bat populations since the 1960's (Di Silvestro 1989; Humphrey 1992; Drobney and Clawson 1995). This threat has diminished with regulations on pesticide use. The greatest threat to bats now comes from habitat destruction and disturbance. Few caves meet the temperature and humidity requirements bats need for hibernation, and these caves are occupied by large numbers of bats, making these bats particularly vulnerable to disturbance. The slow rate of reproduction among bats (often only one offspring per year) means that a population can be quickly destroyed, with little opportunity for recovery (Di Silvestro 1989).

The Indiana bat ranges over a huge area of the eastern United States, but the winter habitat for 85% of the species is limited to just seven caves, with over half of the population using just two caves (Di Silvestro 1989). Human disturbance has caused numbers of this species to drop from 330,000 to 49,000 in Kentucky alone (Di Silvestro 1989). Nationally, the decline in the Indiana bat population has reached 22% in the past 10 years (Drobney and Clawson 1995). Missouri has experienced the greatest decline (34%), whereas bat numbers in Indiana have somewhat increased and Kentucky's population is now stable.

The gray bat has suffered a similar fate. Guano collection during the Civil War caused heavy losses initially because of disturbances to nursery caves and habitats, but the gray bat recovered, only to be decimated by the popularity of cave exploration in the 1960's and 1970's. Between 1970 and 1976 the population of some colonies dropped more than 50%. Though only a handful of caves are suitable for the gray bat, this species is showing signs of recovery, largely due to the protection of four critical caves (Di Silvestro 1989).

River Otter

The river otter inhabits slow-moving streams, ponds, and other wetlands (Di Silvestro 1989). Historical threats included trapping and hunting. As a result of overtrapping in the 1970's, the otter was given protection through the Convention on International Trade in Wild Species of Endangered Flora and Fauna. Trapping pressure continues, however, as otters are frequently caught in traps intended for beaver.

The future of the river otter is inextricably linked to the future of wetlands, which are disappearing at the rate of 200,000 hectares per year (Di Silvestro 1989). Otter reintroduction programs are under way in Kentucky and Tennessee. Reintroduction in the Great Smoky Mountains National Park, where the

otter population was completely extirpated by 1936, began in 1986. This program is showing some signs of success; juvenile otters are seen on a regular basis.

Wolves

The gray wolf has long been extirpated from this region. The red wolf, once a dominant predator of bottomlands and hardwood forests, was listed as endangered in 1967 and is now the focus of reintroduction programs (Rees 1989).

As the red wolf neared complete extinction in the mid-1970's, the remaining red wolves, reduced in range to the swamps of southern Louisiana, were captured to initiate a breeding program. Of the 400 animals captured, only 14 were considered true wolves; these became the basis of the breeding stock. Today there are 201 red wolves in captivity and about 80 in the wild; these were released in the Alligator River National Wildlife Refuge in eastern North Carolina, Great Smoky Mountains National Park, and protected areas on barrier islands of South Carolina, Florida, and Mississippi (G. Henry, U.S. Fish and Wildlife Service, unpublished data).

Red wolves have suffered from loss of habitat and intentional trapping, poisoning, and hunting. More recently, their greatest threat has been genetic dilution because of hybridization with wild dogs and coyotes, which have invaded the Southeast. A lack of mates may increase the chances of hybridization, so only mated pairs of red wolves have been released (C. Lucash, Great Smokey Mountains National Park, Gatlinburg, Tennessee, and University of Tennessee, Knoxville, personal communication).

Florida Panther

The Florida panther, the only subspecies of mountain lion remaining in the eastern United States, was once found throughout the southeastern Coastal Plain from Arkansas east to South Carolina (Humphrey 1992). This subspecies is now limited to the woodlands of the southern tip of peninsular Florida. Although other subspecies of mountain lion were extirpated by hunting and habitat loss in the early part of this century, the Florida panther's numbers were not only reduced by hunting but also by development, agricultural expansion, and degradation and fragmentation of habitat.

Today the Florida panther's numbers are estimated at between 30 and 50, and declining. Loss of habitat is the greatest threat the panthers face, as well as illegal shootings and highway collisions, which slowly remove more individuals than can be replaced naturally. Each individual loss represents a loss of genetic diversity, which results in inbreeding and increased numbers of abnormalities. Florida panthers are now estimated to have only half of the genetic diversity of western mountain lions (Humphrey 1992). The panther's continued presence in southern Florida is due to the existence of large interconnected blocks of public and private woodland and areas in successional stages, which support populations of deer and feral pigs, their most important prey (Humphrey 1992).

Scientists and resource managers have taken many measures to preserve the remaining Florida panthers. Highway underpasses, constructed for panther migration, have shown signs of panther use. A captive breeding program began in 1991, with a goal of 130 breeding animals by the year 2000 (Fergus 1991). A vigorous public education program has resulted in the panther being named the state mammal by popular vote of Florida's school children (Humphrey 1992).

Key Deer

The Key deer is the smallest of the eastern races of white-tailed deer and is endemic to south Florida. Hunting in the early part of this century brought their numbers down to between 25 and 80 animals by 1951 (Humphrey 1992). After hunting was banned in 1939, the deer's numbers returned to nearly 400 by 1974. The numbers have since dropped again, however, as a result of habitat loss, illegal poaching, traffic accidents, attacks by feral dogs, and loss of freshwater supplies (Humphrey 1992).

White-Tailed Deer

White-tailed deer populations have fluctuated dramatically with changing human influence and land use. We can identify four periods of contrasting trends and influence on native ecosystems. Before 1500, deer populations were moderate in size—Native Americans hunted deer extensively, and large native predators of deer were also present. Between 1500 and 1800, deer populations probably increased in some areas and decreased in others. Increases occurred because of reduced hunting by Native Americans and the increase in old-field habitats as Native American farms and villages were abandoned after Europeans displaced the native populations. Decreases were the result of exploitive hunting for trade by Native Americans and European colonists. Between 1800 and 1930 deer populations were reduced to near extirpation in many areas because of increased hunting, widespread agricultural clearing, and also other causes such as draining of wetlands. Since 1930 deer populations have rebounded vigorously because of farm

abandonment, lower hunting pressure, and the near-absence of natural deer predators. Deer populations are still increasing in the Southeast and in some areas are drastically altering the composition and density of understory stems in forests. Deer are a major issue in forest and conservation management.

Black Bear

Black bears once occupied the entire southeastern United States (Fig. 40). This omnivorous, intelligent, and adaptable carnivore can survive in a diversity of forested habitats. Over the past 150 years, however, intensive human activities, primarily urban development and land clearing for agricultural crops, have reduced the species to less than 10% of its former range (Fig. 40). Black bears have been virtually eliminated from the Piedmont physiographic region and now occur only in the Coastal Plain and in mountain areas of the Appalachians, Ouachitas, and Ozarks. Bears occur in the Coastal Plain from the Dismal Swamp in Virginia, along parts of the Atlantic and Gulf of Mexico coasts to Louisiana, and sporadically up the Mississippi River delta to the White River National Wildlife Refuge (Wooding et al. 1994; Vaughan and Pelton 1995). More than 80% of the high mountain habitat of black bears occurs on public lands, but coastal habitats are predominantly on private lands (77% private, including the holdings of large timber companies; M. Pelton, University of Tennessee, Knoxville, unpublished data).

Black bears in the Ouachita and Ozark national forests have a unique history. Before 1950 no bears remained in these large areas of northwestern Arkansas, southern Missouri, and eastern Oklahoma. In the 1950's, more than 250 black bears were trapped and translocated from Minnesota to the Ouachitas and Ozarks. Since then, the black bear population has expanded to more than 3,000 individuals. This success story is in contrast to the recent designation of the Louisiana and western Mississippi black bear population as threatened (U.S. Fish and Wildlife Service 1994). This population exists on remaining small tracts of bottomland hardwoods. Likewise, the Florida black bear is categorized as authorized for listing on the U.S. list of endangered and threatened species and may be listed soon. The Florida subspecies suffers from the same problems of bottomland hardwood loss to agricultural crops and expanding human populations.

Bear population health within the region ranges from good to questionable. In areas such as the southern Appalachians of Georgia, North Carolina, South Carolina, and Tennessee, more than 3,000 bears reside on four national forests, one national park, and some private lands; this area encompasses nearly 2.5 million hectares. Four hundred to 600 bears are legally harvested from this population annually. Almost 500,000 hectares of this land are in designated or de facto sanctuaries or refuges. On the other hand, on some sites in the Coastal Plain only 20 to 60 bears may exist in the relatively isolated bottomland hardwood tracts that remained after extensive clearing of forests for agriculture.

Managers have translocated black bears from occupied habitats to areas in which large blocks of forest occur. For example, an experimental black bear population has been reintroduced into the Big South Fork region in the Cumberland Mountains of Kentucky and Tennessee; so far, this experimental reintroduction has been successful. This area encompasses more than 80,000 hectares, consisting primarily of the Big South Fork National River and Recreation Area and the Stearns Ranger District of the Daniel Boone National Forest. In the Coastal Plain, researchers estimate that more than 1.5 million hectares of unoccupied, potential bear habitat exist.

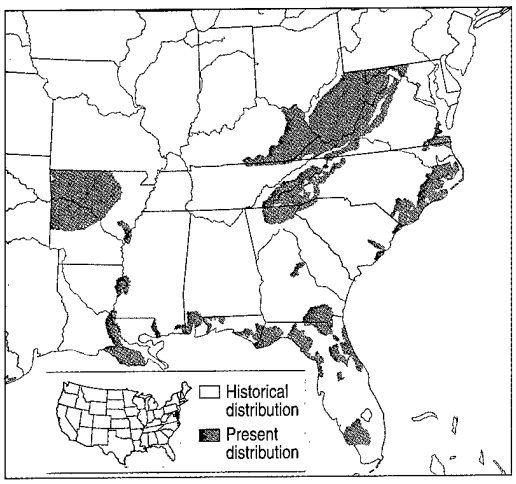


Fig. 40. Present distribution of the American black bear in the southeastern United States. Distribution is based on 1993 survey responses (M. R. Pelton, University of Tennessee, Knoxville, unpublished data).

Information Needs

We write at a time when the first attempts are being made to understand trends in the Southeast's rich biological diversity. Adequate information exists only for selected species and ecosystems—recent work on wetland loss provides the single best documentation of change at the ecosystem level. A number of endangered species are adequately monitored, but birds are the only widely distributed group for which there is a regular comprehensive regional monitoring program. Research has often focused on birds, but we are also much in need of regional inventory and monitoring schemes for other

groups that play critical ecosystem roles, such as fungi (Mueller 1995; Rossman 1995), or are likely indicators of environmental change, such as lichens (Bennett 1995), amphibians, mussels, butterflies and moths (Powell 1995), and diatoms (Charles and Kociolek 1995).

Even in the best cases, however, spatial and temporal variability can make detection of trends difficult, as we have recently seen with attempts to detect trends in amphibian populations. Monitoring must be carried out in a regional and national context. For example, spatial shifts in bird populations have shown us that species can increase in one area and decrease in another (Erwin 1995). Such shifts are even to be expected if climate change occurs. Clearly, we must do a better job of monitoring so that we will be able to describe, understand, and predict trends.

Although the potential loss of a species is so dramatic that it attracts our attention, the single-most important regional trend is one that is occurring around us all the time but is rarely noted—the loss of populations and the fragmentation of range for species not yet endangered. There are many reasons to believe that this is a general phenomenon in the Southeast: changes in ecosystems due to fire suppression, outright conversion of natural habitat to forest plantations and agriculture, and changes in hydrology and water quality. Scientists presume that the loss of populations reduces genetic diversity, interrupts gene flow and dispersal, and destabilizes species originally dependent on metapopulation dynamics.

Biological monitoring should be developed in a way that allows us to address the ecological and landscape context of populations. Population change may be the result of such community properties as succession and the invasion of nonindigenous species or physical variables such as weather and pollutant exposure. Population change in one habitat may be the result of changes in another (for example, the loss of nearby wetlands). Although we may broadly monitor populations spatially, ecological and landscape variables also should be monitored, at least in intensively studied sites, if we are to understand the trends we detect.

Monitoring should include periodic mapping of ecosystems, ground-based monitoring of ecosystem dynamics, analysis of ecosystem processes, and simulation modeling for prediction. Work on the Everglades is perhaps the best example of a comprehensive and multidisciplinary approach to monitoring (Davis and Ogden 1994b). Other sites that have included several, if not all, of these elements are the southern Appalachian spruce–fir forests (Eagar and Adams 1992), Coweeta Hydrologic Laboratory (a National Science Foundation Long-Term Ecological Research site), and the Savannah River Ecology Laboratory.

Even in these areas, though, researchers often note the short period of data collection and the resulting difficulty of separating trends from natural fluctuation. The danger of inadequate information is the confusion and conflict that often occur when a loss of biological diversity is first suspected. To see this situation in the Southeast we need only turn back the clock some 15 years; when the first concerns about acid rain effects in the southern mountains were raised, there was little understanding of expected growth and mortality or of soil chemistry, ecosystem processes relating to nitrogen transformations, or fluctuation in streams that drained high-elevation watersheds. We must design monitoring and research strategies to deal with an ever-lengthening list of suspected regional trends in biological diversity such as the recent reported declines in Neotropical migrants, amphibians, and tree growth rates.

We also argue for a bioregional approach to monitoring and research: intensive multidisciplinary work on regional landscapes. Such an approach is used in the Everglades, Chesapeake Bay (Pendleton 1995), the Appalachicola River basin (Livingston 1992), the Savannah River Ecology Laboratory, and the Biosphere Reserve programs in the southern Appalachians, the Mammoth Cave area in Kentucky, and the Land-Between-the-Lakes region in Tennessee. All of these projects not only include strictly preserved areas but also recognize the inevitable presence of humans in the Southeast and seek to protect biological diversity while allowing some areas to be intensively used by people. These projects also include multiple public and private partners.

We critically need better information on a range of key issues that will help us maximize the biological diversity that can persist in the Southeast. These issues include better understanding of

- the sensitivity of species to habitat fragmentation and the persistence of species in agricultural landscapes of various types;
- the roles of hydrological regimes and fires of various intensities and in different seasons;
- the ways to avoid future nonindigenous species problems and to control the problems that already exist;
- sustainable methods and levels of harvest, both for target species and for nontarget species that are affected by harvest;
- the ways to propagate species taken directly from the wild to avoid damage to surviving natural areas;

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- the ways to develop off-site gene and species banks as last resorts for the rarest and most threatened species;
- the ways to restore natural processes and whole systems on the ubiquitous degraded lands in the Southeast;
- and the ways to predict the varying sensitivities of ecosystems and species to sea-level rise and climatic change.

Acknowledgments

We gratefully acknowledge the patient help of the many people who have helped us produce this chapter. We thank three anonymous reviewers and many biologists and resource managers who furnished ideas and information. The latter included P. Beaty, M. Boyer, A. Braswell, L. Collins, C. Frost, S. Hall, P. Hamel, W. Hunter, K. Langdon, C. Lucash, J. Peschmann, J. Rock, M. Schafale, I. Smith, T. Smith, B. Sorrie, R. Sutter, A. Weakley, E. Wilds, and R. Haven Wiley.

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Caribbean Islands

The thousands of islands and cays composing the Greater and Lesser Antilles are among the most biologically interesting areas of the world. Centrally located in the West Indies, Puerto Rico and the Virgin Islands are in the eastern extreme of the Greater Antilles at 18° north latitude, about halfway between the southern tip of Florida to the north and the Caribbean coast of Venezuela to the south (Fig. 1). Although Puerto Rico and the Virgin Islands are in the tropics (south of the Tropic of Cancer), the seas around the islands keep them cooler than tropical mainland Central America. Because the mean annual temperature of the region at sea level is lower than 24°C, the lower limit of the tropical region, these islands are actually classed as subtropical (Ewel and Whitmore 1973).

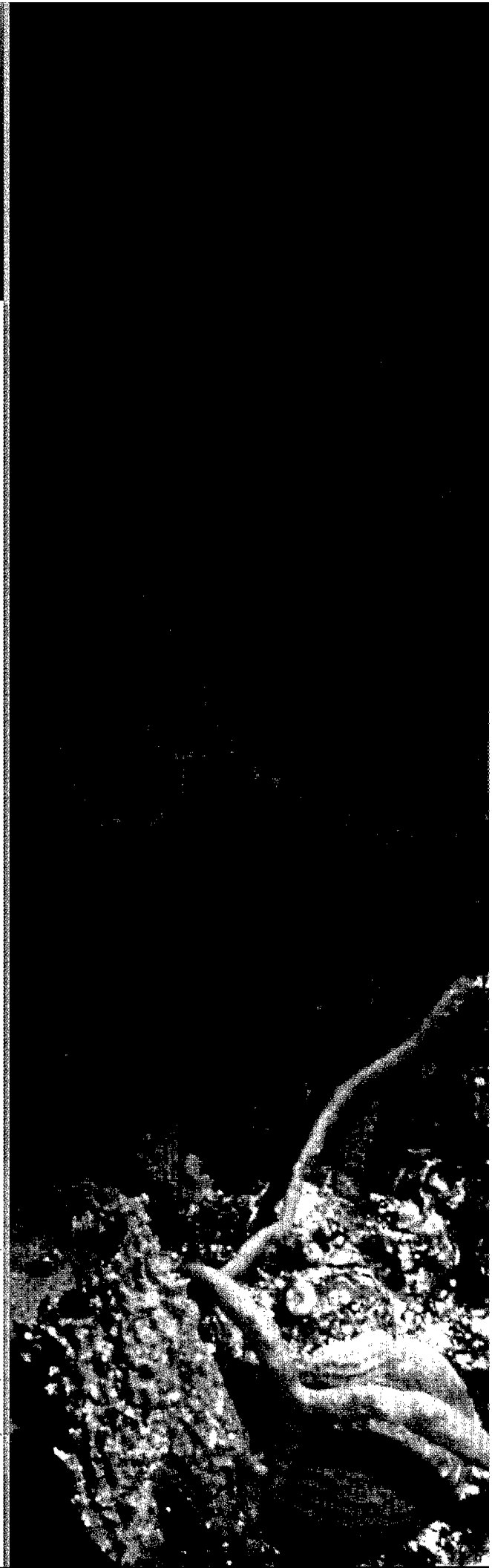
Columbus visited Puerto Rico on his second voyage in 1493; the island remained a Spanish colony until it passed to the United States after the Spanish–American War of 1898. The island has been in a commonwealth relationship with the United States since 1952. The Virgin Islands have been governed by several countries, including France and Denmark. After the United States purchased the islands of St. John, St. Thomas, and St. Croix from Denmark in 1917, they became an unincorporated territory of the United States. The remainder of the Virgin Islands are possessions of Great Britain.

The many islands that make up the Virgin Islands and Puerto Rico are separated by water today, although at the time of maximum lowering of the seas during the ice ages, Puerto Rico and most of the Virgin Islands, including St. John, St. Thomas, and the British Virgin Islands, were one piece of land called the Puerto Rican Bank (Pregill 1981). The islands of Mona (Puerto Rico) and St. Croix (U.S. Virgin Islands), though, were never connected to the Puerto Rican Bank because they were separated by channels of deep water. At the end of the last Ice Age (about 8,000 years ago) and after sea levels rose, the Puerto Rican Bank fragmented and separated into Puerto Rico and the Virgin Islands. Because the small islands were connected with most other land masses in the Puerto Rican Bank until fairly recently in evolutionary terms (Pregill 1981), none of them have more than a few unique species. In contrast, Mona Island and St. Croix have higher numbers of endemic animals and plants because these islands have been isolated from Puerto Rico for a longer time and may never have been connected to other islands of the Puerto Rican Bank.

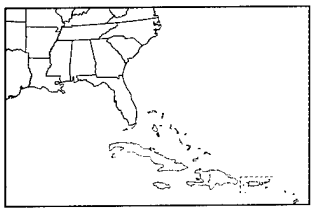
General Description of Puerto Rico

The main island of Puerto Rico is roughly rectangular in shape, 178 kilometers long by 58 kilometers wide, with an area of 8,802 square kilometers. The three principal geographic regions of Puerto Rico are the mountains and foothills of the Cordillera Range (highest elevation 1,353 meters), which transects the island from east to west; a discontinuous fringe of mostly flat Coastal Plain; and rugged limestone or karst regions occurring in the north-central and northwestern part of the island.

The Commonwealth of Puerto Rico consists of the main island and several satellite islands, including Mona Island (5,517 hectares) and its satellite, Monito (15 hectares); Desecheo Island (122 hectares); Caja de Muerto (202 hectares); Vieques Island (13,606 hectares); and the Culebra archipelago (Culebra Island, the main island, is 2,696 hectares; Fig. 1). The Cordillera de Fajardo stretches from eastern Puerto Rico toward



Courtesy V. Vincente, National Oceanic and Atmospheric Administration



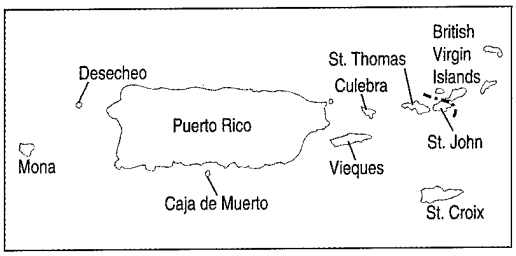


Fig. 1. Puerto Rico and the U.S. Virgin Islands.

Culebra and Vieques islands and consists of many small cays (islets). Numerous other small cays lie offshore of Puerto Rico.

Average annual rainfall varies widely in the different areas and indicates the range of local climates and associated plant communities. Southwestern Puerto Rico is the driest region and receives about 75 centimeters of rain each year, whereas more than 700 centimeters fall annually in the eastern Sierra de Luquillo.

General Description of the U.S. Virgin Islands

Although the U.S. Virgin Islands are on the same submarine bank as Puerto Rico, they are relatively low and have little rainfall compared with Puerto Rico. The fewer numbers of life forms in the Virgin Islands are the result of the smaller size, the lower relief, and the restricted variety of habitats of these islands. Annual rainfall averages about 140 centimeters, with wetlands expanding and contracting considerably depending on the amount and frequency of rain. Animals and plants that live in these wetlands experience population changes related to the amount of rainfall.

St. Croix is physically similar to the other Virgin Islands but is separated from them by a sea passage more than 3,600 meters deep, whereas the other islands are separated from each other by relatively narrow passages only a few meters deep. Aside from the main U.S. Virgin Islands, 54 small islands flank St. Thomas, St. Croix, and St. John. These cays are particularly important for native reptile species and nesting seabird colonies (Tolson 1988; Dammann and Nellis 1992).

St. Croix is the largest (34 kilometers long by 9.6 kilometers wide; 219 square kilometers) and most southern of the U.S. Virgin Islands; it is about 64 kilometers south of St. Thomas and St. John. The highest point on the island is Mount Eagle, with an elevation of 355 meters. As a consequence of this relatively low elevation and the forest clearing that has occurred on St. Croix, the area is much drier than most of the Greater Antilles, averaging only 102 centimeters of rain in the west and about 76 centimeters in the east. The average mid-island temperature is 26°C, with a variation of only 3°C to 5°C between the warmest and coolest months.

St. Thomas is about 19 kilometers by 5 kilometers (90.3 square kilometers), with a maximum elevation of 477 meters. Although little agricultural activity has occurred on St. Thomas in the recent past, it does suffer from high urban and tourist developmental pressure.

St. John is about 13 kilometers long, with an area of 53 square kilometers, and a maximum elevation of 392 meters. This island has a relatively small human population compared with St. Thomas and St. Croix.

Status of Ecosystems

Terrestrial Ecosystems

Virgin Forests

Recent environmental change in the West Indies has been dramatic. In contrast to the warm and moist climate of the region today, dry, cool climates prevailed 15,000–20,000 years ago, and savannas and other ecosystems adapted to this climate were probably widespread (Pregill 1981; Olson and Hilgartner 1982). Plants and animals of the islands' lowlands and lower montane areas were typical of a dry, savannalike habitat until about 13,000 years ago, when a shift to the current moister conditions occurred. As a result, the animal and plant communities gradually evolved toward their present composition (Pregill 1981).

The environmental shifts resulting from human activities have been just as dramatic as these earlier climatic changes (Garcia-Montiel and Scatena 1994). A human population that is too large for its supporting resources and a broad array of associated environmental problems have greatly changed the ecosystems and native plants and animals of Puerto Rico and the Virgin Islands.

Several kinds of natural processes are important in shaping the environments of islands, including earthquakes, landslides, fires, and hurricanes (Guariguata 1990; Larsen and Torres-Sanchez 1990; Reilly et al. 1990; Scatena and Larsen 1991). Puerto Rico and the Virgin Islands were covered with luxuriant forests that consisted of more than 500 tree species when Columbus arrived (Little and Wadsworth 1964). Extensive cutting and modification of natural forests, widespread agriculture, and introduction of many nonindigenous plants from other parts of the tropics have fragmented the original plant associations into remnants of the once-extensive tracts of forest.

Typical mountain forests are confined to Puerto Rico. The most magnificent of these forests probably occurred from 150 meters to

650 meters in elevation in the eastern mountains, known as the Sierra de Luquillo, and up to 920 meters in the central mountains, the Cordillera Central. At this forest's maximum development, its trees reached 33 meters in height, with some trees 2.5 meters in diameter. Three forests of distinctive size and composition grew together, each forming a separate plant layer. Probably about 170 tree species grew throughout this forest.

Life Zones

Biologists divide Puerto Rico and the Virgin Islands into six regions, each characterized by an association of certain animals and plants. These life zones range from dry forest to rain forest in the Coastal Plain, and wet forest and rain forest in the mountain areas (Ewel and Whitmore 1973; Fig. 2). Subtropical lower montane rain forest occupies the smallest area, accounting for only 0.1% of the islands, whereas subtropical moist forest is the most extensive life zone, covering about 60% of the area.

Subtropical Dry Forest

The subtropical dry forest is the driest life zone of the six (mean annual rainfall, 60–110 centimeters), and it covers substantial areas in the Virgin Islands, Vieques Island and southwestern Puerto Rico, and all of Mona, Culebra, and Desecheo islands. The vegetation of the subtropical dry forest zone tends to form a complete ground cover, and on most soils the trees are almost entirely leafless during the dry season, even though vegetation in the Virgin Islands is mostly evergreen. Many of the tree species common on the north side of Puerto Rico were excluded by the harsher climate on the island's dry, southern side. Instead of the more common trees found on the island's north side, this life zone supports a few other species adapted to such arid conditions. Palms are usually absent. Plants often have small, succulent or leathery leaves, and plants with thorns and spines are common. Trees are usually less than 15 meters tall and their crowns are broad, spreading, and flattened, with sparse foliage. Fire is common on the better soils where the successional vegetation includes many grasses, and large amounts of organic debris accumulate on the soil surface during the dry season (generally December–April). Agriculture is marginal at best and is only possible with irrigation. Pasturing of livestock (mainly cattle and goats) has been extensive. In the past, charcoal manufacturing and nonindigenous livestock took their toll on the native dry forests. Growth of cities has proceeded rapidly but is limited primarily by water supplies.

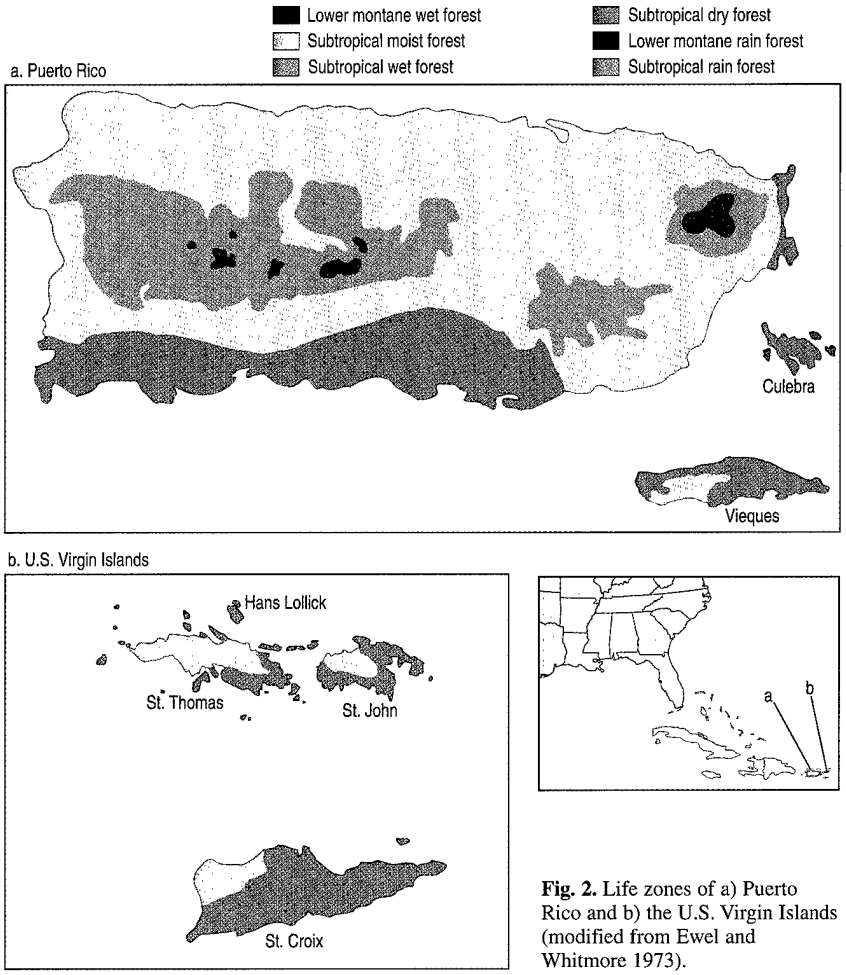


Fig. 2. Life zones of a) Puerto Rico and b) the U.S. Virgin Islands (modified from Ewel and Whitmore 1973).

The dry coastal forests of Puerto Rico support many species of animals and plants. Of 700 plant species (including 246 tree species) in the Guánica Forest, informal evaluations suggest that 45 (6.4%) are considered rare and endangered (Hill 1975; Woodbury et al. 1975; Lugo 1983; Fig. 3). The trees of the dry coastal forest include gumbo limbo, mesquite, oxhorn bucida, common lignumvitae, red manjack, and indio (see Table 1 for a more complete list). Mangroves line the coasts of this zone, but the trees do not attain the height of mangrove species in the subtropical moist forest zone. Forests of this life zone have more bird species than the wetter life zones (Kepler and Kepler 1970), although lizard and frog populations are comparatively larger in wetter zones (Rivero 1978).

Excessive soil drainage accentuates the dryness in the inland limestone region of the southern coast of Puerto Rico, as it does on the northern coast. These extreme conditions exclude some kinds of vegetation, and hardier species take their places. The trees of the dry limestone forest include corcho bobo, guayacán blanco, willow bustic, and alelí (see Table 1 for a more complete list).

Courtesy F. J. Vilella, USGS

Fig. 3. *Epidendrum krugii*, an endemic orchid of dry limestone forests of Puerto Rico at Guánica Biosphere Reserve. Although limestone forests are not as well known by the general public as rain forests, tropical dry forests are characterized by high species richness and are hot spots of biodiversity.

Subtropical Moist Forest

The subtropical moist forest zone is characterized by a mean annual rainfall of 100–220 centimeters and a mean temperature of 18°C–24°C. Most of the subtropical moist forest zone has been cleared of forest because the region's climatic conditions and soils are generally favorable for agriculture. Only small, scattered pieces of the original forest remain. Historically, the species composition of vegetation varied with locality but included a mixture of many species, with at least 200 kinds of trees. On the northern Coastal Plain of Puerto Rico, trees grew to 35 meters or more in height. In contrast, on the southern Coastal Plain and in the moist limestone region of Puerto Rico and the Virgin Islands the forest trees grew only 13 to 20 meters tall. Characteristic trees in the moist forest of the coasts include the endemic Puerto Rican royal palm (found only in Puerto Rico), ausubo, false mastic, roble blanco, box-briar, and white prickle (Table 1). Many of the characteristic trees, shrubs, and lianas are leafless during the dry season. Epiphytes are common. Grasses, in both natural and improved pastures, dominate the landscape today in this Puerto Rican zone. Mangroves, which line the coasts in the subtropical moist forest zone, are under heavy developmental pressure (Lugo 1988; U.S. Department of the Interior 1994). In addition, human activities have extensively altered this zone's coastal freshwater swamps, which may be Puerto Rico's most endangered ecosystem (Cintrón 1983; U.S. Department of the Interior 1994).

Inland from the coastal forest is the moist forest of the limestone hills. This forest is similar to the subtropical moist forest along the Coastal Plain and includes many of the same species. Drier soils on the well-drained limestone hills and the greater humidity in protected areas among the hills caused most of the chief differences between the inland moist forests and the Coastal Plain forests, especially in the southern part of Puerto Rico close to the central mountains. Common trees in this forest include palma de lluvia, uvilla, cupey, and white prickle (see Table 1 for a more complete list).

Subtropical Wet Forest

The subtropical wet forest zone occupies most of the higher mountains of Puerto Rico but is not found in the Virgin Islands or Puerto Rico's outlying islands. Rainfall is high, averaging 200–400 centimeters each year, and accounts for a rich flora with more than 150 species of trees. Forests are diverse, and the second-growth trees grow rapidly. Epiphytic ferns, bromeliads (air plants), and orchids are common. Remnants of mature forest remain in three protected areas. The plant community of this zone is sometimes called the *tabonuco* type after the dominant tree, which is also known as candlewood. Other prominent trees include the common tree-fern, motillo, and ausubo (Table 1). The natural forest forms a closed canopy at about 20 meters. Mahogany and teak have been successfully established in plantations; the International Institute of Tropical Forestry has carried out extensive research on the tabonuco forest type and on the plantations (Mosquera and Feheley 1984).

Much of this life zone in Puerto Rico is covered by second-growth vegetation as a result of farm failures and abandonment. Formerly, much of this zone in western Puerto Rico was converted to shade coffee plantations, but the coffee crop, as is typical of most agriculture in Puerto Rico, has greatly declined since about 1950 (Birdsey and Weaver 1987). As in all other zones, land use has shifted toward grazing livestock. On abandoned lands, higuillo, yagrumo macho, yagrumo hembra, and balsa are early successional species. Sierra palm is common in the wetter parts of the zone.

Table 1. Characteristic plants of life zones in Puerto Rico and the U.S. Virgin Islands (from Ewel and Whitmore 1973).

Life zone	Characteristic plants
Subtropical dry forest	Alelí, bitter-ash, calambreña, common lignumvitae, corcho bobo, Royen's tree cactus, Florida fiddlewood, guayacán blanco, gumbo limbo, indio, leadtree, mesquite, oxhorn bucida, pricklypear, red manjack, sarrasuela, silk cotton tree, Spanish lime, sweet acacia, tachuelo, tamarind, willow bustic
Subtropical moist forest	Ausubo, box-briar, common guava, cupey, false mastic, guaba, guama, gumbo limbo, matchwood, mountain immortelle, palma de lluvia, palo de pollo, Puerto Rico acrocomia, Puerto Rican royal palm, roble blanco, shortleaf fig, Spanish cedar, trumpet tree, tulipán africano, uvilla, West Indian locust, white prickle
Subtropical wet forest	Ausubo, balsa, giant tree-fern, higuillo, Honduras mahogany, matchwood, motillo, sierra palm, tabonuco, teak, trumpet tree
Subtropical rain forest	Ausubo, giant tree-fern, motillo, sierra palm, spiny tree-fern, tabonuco
Subtropical lower montane wet forest	Caimitillo, caimitillo verde, guayabota de sierra, jusillo, nemocá, oreganillo, palo colorado, roble de sierra
Subtropical lower montane rain forest	Similar to lower montane wet forest, but with greater abundance of epiphytes

Subtropical Rain Forest

The subtropical rain forest zone occupies only 13.2 square kilometers and is restricted to the windward faces of the Sierra de Luquillo in Puerto Rico (Fig. 4). It is the wettest of the sea-level belt of subtropical life zones, with an annual rainfall of about 380 centimeters. Plant species are essentially the same as those found in the surrounding subtropical wet forest, with the main features the high frequency of sierra palms and a superabundance of epiphytes. The spiny tree-fern is more abundant here than in the subtropical wet forest. Much of this zone has remained intact, originally under the protection of the Spanish Crown lands, then within the federally protected Caribbean National Forest.

Courtesy J. Wiley, USGS

Fig. 4. Upper Luquillo Forest, Puerto Rico.

Subtropical Lower Montane Wet Forest

Of the two lower montane life zones in Puerto Rico, the subtropical one is by far the most extensive, occurring in both the eastern and central parts of the island from about 700 meters to the summits of most mountains above 1,000 meters. Annual rainfall ranges from about 170 to 340 centimeters. The palo colorado, the dominant tree in the colorado forest zone, is the species that endangered Puerto Rican parrots use most often for nest sites (Fig. 5). This forest has fewer species of animals and plants than the adjacent subtropical wet forest; only about 53 tree species have been recorded (Wadsworth 1950). Other characteristic plant species include nemocá, caimitillo, and caimitillo verde (Table 1). This zone includes the elfin (dwarf) forest association and the palm brake, consisting of pure stands of sierra palm. The vegetation of this zone has been extensively altered from cutting and agriculture; the best-preserved tract occurs within the Caribbean National Forest.

Subtropical Lower Montane Rain Forest

This zone occurs only on the windward slopes of the Sierra de Luquillo, just above the subtropical rain forest, and has the smallest area of any Puerto Rican life zone. Average annual rainfall is 450 centimeters, and the mean annual temperature is 18.6°C. The plants of this zone are similar to those of the lower montane wet forest but with a greater abundance of epiphytes, palms, and tree-ferns (Little and Woodbury 1976). The steep slopes and poor timber quality of the tree species in the subtropical lower montane rain forest zone have not attracted agriculture or timber interests. Because this zone is within the Caribbean National Forest, it has been protected from most human-caused disturbances.

Reforestation and the Natural Habitat of Today

Although Puerto Rico was covered with various kinds of forests when Europeans arrived in 1493, by 1912 nearly all of the island had been clear-cut for agriculture (Murphy 1916). Although considerable secondary forest cover exists today, only about 0.2% of the original forest remains. With these sweeping changes in the environment, many plants and animals declined or disappeared. Despite the near-complete ruin of natural habitat, only a few species are known to have been completely lost from the island's ecosystems. Other species, though, may have been eliminated before they were recorded by naturalists.

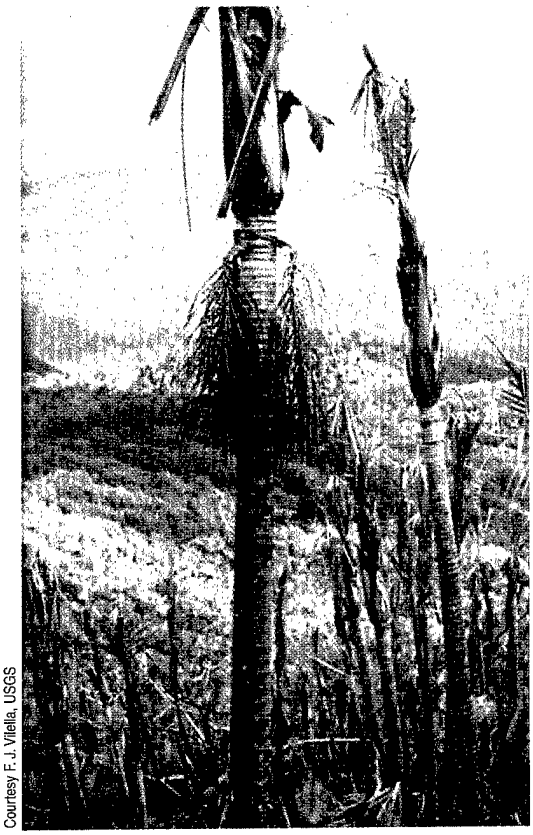
Nevertheless, this extreme habitat fragmentation has placed many species at great risk. Several species survive only as tiny clusters of a few individuals separated from other small groups by inhospitable expanses of unsuitable habitats. Not only are such populations at risk of extinction because of their small sizes and

Courtesy J. Colón, U.S. Fish and Wildlife Service

Fig. 5. Puerto Rican parrot perched on the entrance vine of its nesting cavity in a tabonuco tree. This is the first record of parrots nesting in this tree species since the Puerto Rican parrot project began in 1968 (see Vilella and García 1995). These trees dominate the overstory of lower elevation forests in the Sierra de Luquillo (in the subtropical lower montane rain forest zone).

their lack of genetic interchange, but they are also more susceptible to any chance natural or unnatural events such as fires, diseases, or hurricanes. Extinction could be caused by random events that often have little effect on larger, more continuous populations.

The severe tropical storms that strike these islands at fairly frequent intervals are the most powerful forces shaping the ecology of the West Indies. In the past, such fierce storms had only moderate, and usually short-lived, effects on most island ecosystems. Some of the islands' ecosystems are largely determined by these storms. For example, such storms flush the debris from mangroves, making way for aquatic communities, particularly fish nurseries. In addition, these storms open mature forest canopies, which allow succession of plants and animals (Fig. 6). However, as human activities have substantially fragmented habitats of the West Indies and reduced their size, hurricanes have posed more serious threats to the survival of organisms and communities (reviewed in Askins and Ewert 1991; Walker et al. 1991; Wiley and Wunderle 1993). For example, the Puerto Rican parrot was historically widespread and abundant throughout the main island, Culebra Island, and probably other Puerto Rican satellite islands. Even the strongest of hurricanes would have cut a damaging swath through only a relatively small part of these islands, allowing the parrot to survive. Now that the parrot is limited to the Sierra de Luquillo, though, a direct hit by a hurricane poses much more serious consequences: when such a hurricane did strike the Luquillo Forest in 1989, about half the wild parrot population was destroyed (Vilella and García 1995; Fig. 7).



Courtesy F.J. Vilella, USGS

Fig. 7. Damage by Hurricane Hugo to sierra palm forest in the Sierra de Luquillo. Puerto Rican parrots synchronize their breeding activities to coincide with the fruiting peaks of this forest palm. Sierra palm fruit was scarce during 1990, the year after the hurricane, and only one pair of wild parrots successfully fledged two young that year.

Courtesy F.J. Vilella, USGS

Fig. 6. View of Hurricane Hugo's damage to the Caribbean National Forest. Hurricane damage was not evenly distributed—notice the ridge on the right side of the photograph. The right side of the ridge (facing northwest) suffered severe damage, whereas the left side of the ridge (facing northeast) suffered little damage.

Effects of Human Activities

Humans probably had little real effect on the region's forests until the colonial period. The cutting of the islands' forests, partly to harvest timber but more generally to clear land for farming, took place primarily in the nineteenth century. That cutting eliminated tree growth from the more fertile and accessible lands, but left small forest remnants on steep slopes, rocky mountain summits, or poor soils. Thus, the best-developed forests are gone, and the remaining forests are quite different from those seen by the early explorers. The most valuable trees, both in terms of species and size, have been removed. Few trees exceed 30 centimeters in diameter, and those that do generally have little timber value. Even within the best-preserved examples of original forest, selective harvesting of some species has altered forest structure and species composition.

In the second half of the twentieth century, Puerto Rico shifted away from an agrarian-based economy to a modern industrial and tourism-based economy (Fig. 8). Considerable areas of agricultural land, particularly the least

productive, were abandoned as people migrated away from rural areas to cities. Those abandoned croplands have subsequently reforested, either through management programs to improve watersheds or through natural succession. Today, about 38% (284,000 hectares) of Puerto Rico's surface area (9,000 square kilometers) is forested, with secondary forest and abandoned coffee plantation shade accounting for 76% of all forestland (Birdsey and Weaver 1987; Ortiz 1989; Fig. 9). Along with second-growth reforestation of abandoned agricultural lands, many nonindigenous species became established in the island. Some of these, such as teak and mahogany, were established in timber plantations, whereas others were imported as ornamentals for gardening and landscaping.

The natural plant cover in the Virgin Islands suffered the same fate as did the forests in Puerto Rico. Uplands that were originally covered with seasonal deciduous or evergreen forests were clear-cut to cultivate the land. Distribution and composition of vegetation were completely controlled by large-scale cultivation, heavy grazing by goats and sheep, and the periodic burning of "brush." St. Thomas and St. Croix still have large human populations and considerable agriculture and grazing; consequently, these islands remain extensively deforested. In contrast, St. John was gradually abandoned by people after 1848, and vegetation has again covered more than 75% of the island (Robertson 1962).

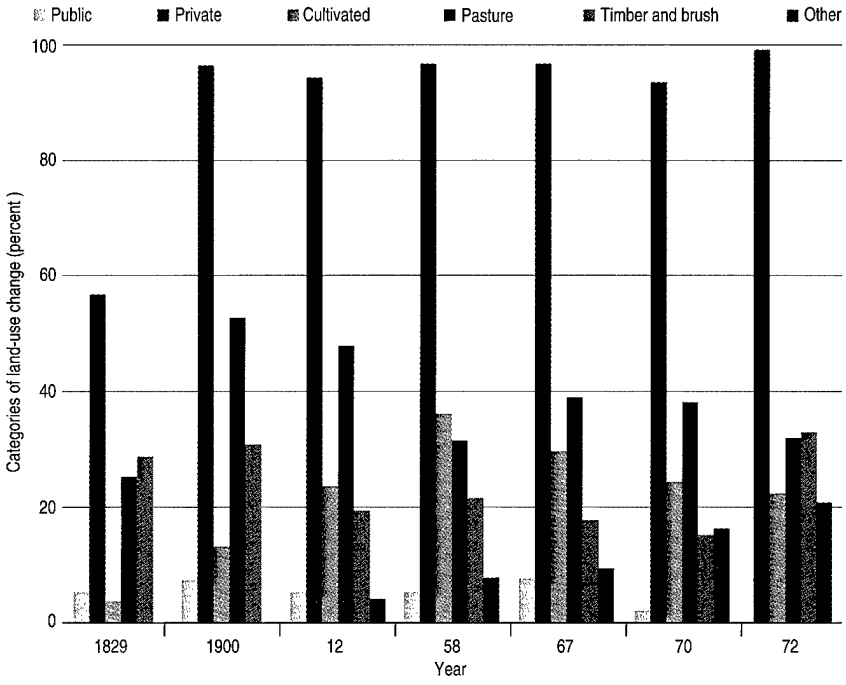


Fig. 8. Historical land-use changes (in percentage of area) in Puerto Rico, 1829–1972 (modified from Lugo 1983).

Aquatic Ecosystems

Marine Environments

Like most of the Caribbean, the islands in the Puerto Rican Bank often share the following confining physical and biological coastal scenario: a limited coastline extension, a restricted shelf dimension, a permanent temperature gradient, oligotrophic waters, and a sparsity of upwelling zones. Nonetheless, the littoral systems surrounding the islands of the Puerto Rican Bank are nuclei of biodiversity and are responsible for coastal organic production. St. Croix and Mona islands are surrounded by deep water on all sides and have comparatively narrow shelves. The shelf and its adjacent coastal fringe support several important ecosystems.

Coral Reefs

Coral reefs support small island fisheries, protect the shoreline from erosion, create or nourish sandy beaches, and represent perhaps the most valuable coastal resource of the islands in the Caribbean. Although coral reefs generally have low biomass (280 grams of organic carbon per square meter per year), they are highly productive (2,900–4,200 grams of organic carbon per square meter per year) and support a wide diversity of taxa, many of commercial or recreational importance (Goenaga and Boulon 1991; Bohnsack 1992; Fig. 10).

These reefs provide homes for most of the islands' fishes and marine invertebrates. Patch reefs are scattered all around the islands but are most abundant behind major reef formations. The best-formed reefs are in the shallow waters surrounding the drier islands or adjacent to those parts of Puerto Rico where few rivers deposit sediments on coral formations.

Coral reefs are subjected to many natural disturbances. Hurricanes frequently and intensely weaken coral reefs in the Caribbean through the physical destruction caused by storm wave activity and through sediment runoff from the surrounding coastal areas. However, random events such as storms may

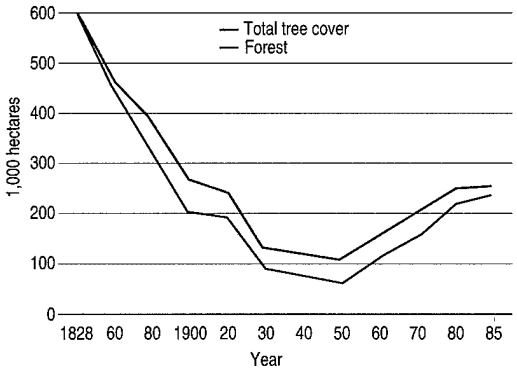


Fig. 9. Area with tree cover in Puerto Rico, 1828–1985. Forest does not include nonstocked forestland (modified from Birdsey and Weaver 1987).

Fig. 10. Coral reef community featuring gorgonian corals and calcareous and tubular sponges.

Coral Reefs of the U.S. Virgin Islands

Most of the coral reefs around St. Thomas, St. John, and St. Croix are shallow fringing reefs that parallel the islands' coastlines. Many of them are true coral reefs, established on a framework of coral skeletons deposited over thousands of years. Elsewhere, coral reef organisms grow on submerged boulders and rock ridges near shore. Submerged bank reefs are also found in deeper water, some with spur and groove formations. Reef-building organisms grow on the walls of Salt River Canyon, a drowned river valley on the north shore of St. Croix. Extensive barrier reefs with well-defined lagoons do not occur around St. John or St. Thomas, but such reefs are found around Buck Island Reef National Monument north of St. Croix and along the island's southeastern shore. In some locations, fringing reefs extend out from rocky headlands at bay entrances, cutting off back-reef areas and eventually leading to the formation of salt ponds. More than 40 species of scleractinian corals have been found on U.S. Virgin Islands reefs (Beets and Lewand 1986; C. Rogers, U.S. Geological Survey, Virgin Islands National Park, St. John, personal observation). The total coverage of living coral on U.S. Virgin Islands reefs is typically less than 40%, although some reef zones have higher coverage (Beets et al. 1986).

Coral reefs in the U.S. Virgin Islands face the same pressures as reefs elsewhere in the Caribbean (Rogers 1985; Beets et al. 1986). Hurricanes and other major storms, higher than normal water temperatures, and coral diseases, together with destruction caused by boat anchors and boat groundings, careless land use, dredging, pollution, and overfishing, cause reef deterioration. Within the last 15 to 20 years, the amount of live coral cover has declined, while the abundance of algae has increased (Fig. 1). The increase in algae probably reflects both the increase in substrate available after the death of coral and the inability of the herbivorous fish and sea urchins to keep the algal growth in check.

Long-term monitoring of reefs around St. John began in 1989 with the establishment of five permanent transects at depths of 12 to 14 meters in Lameshur Bay off the island's southern coast (Fig. 2). Similar transects were established off Buck Island at the same time. In 1991 other long-term sites were established around St. John in Newfound and Francis bays. These sites have provided detailed information about the effects of storms and the recovery of reefs from storms and anchor damage (Rogers et al. 1991; Rogers 1992). Maps of the major benthic habitats around St. John and early studies at Buck Island provide valuable baseline information about U.S. Virgin Islands reefs (Gladfelter et al. 1977, 1979; Beets et al. 1986).

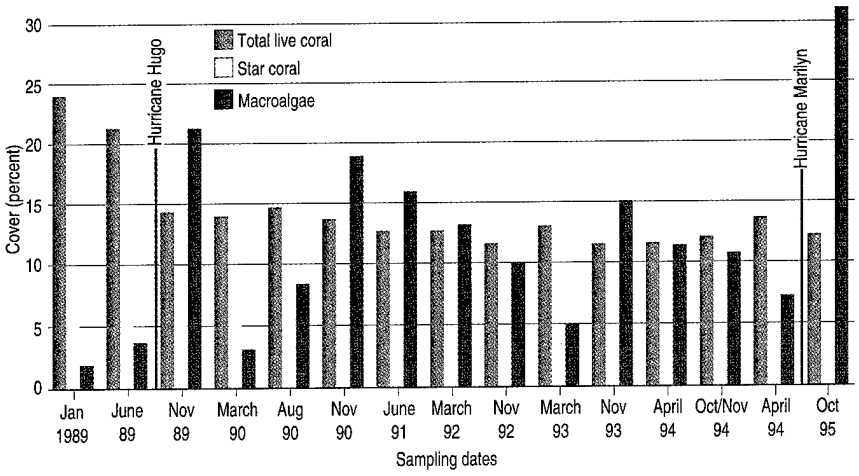
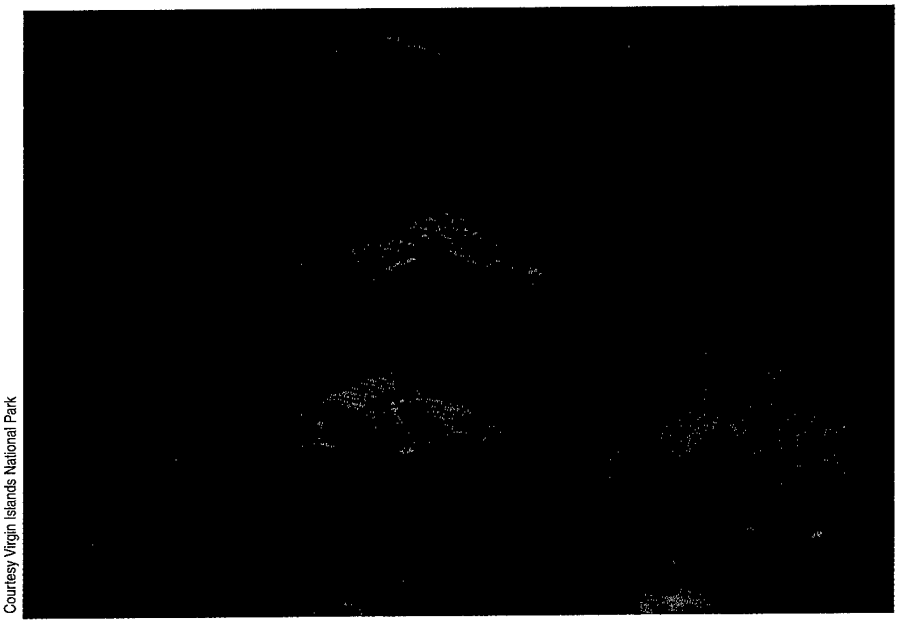


Fig. 1. Percent of cover of total live coral, star coral, and macroalgae at Yawzi Point, St. John, from January 1989 to October 1995.

Perhaps the most conspicuous change on U.S. Virgin Islands coral reefs over the last few decades is the decline in elkhorn coral, one of the primary reef-building corals in the Caribbean (Fig. 3). Elkhorn corals often form shallow crests near the water's surface, creating physical barriers to ocean waves, thereby reducing coastal erosion. In the late 1970's, the elkhorn zone on the east end of Buck Island's barrier reef was described as perhaps the best in the Virgin Islands (Gladfelter et al. 1979). Fifteen to twenty years ago it was possible to find entire stands and impressive, isolated colonies of this species around Buck Island and St. John, but few large, live colonies can be found now. The primary culprit appears to have been white band disease, first observed in the U.S. Virgin Islands in the early 1970's



Courtesy Virgin Islands National Park

Fig. 2. Coral reef in Lameshur Bay, U.S. Virgin Islands.

Courtesy Virgin Islands National Park

Fig. 3. Elkhorn coral at Virgin Islands National Park.

(Robinson 1973; Gladfelter 1982). This disease, which has yet to be correlated with pollution or any other human activity, generally kills the colonies it infects, although occasionally patches of live tissue survive.

At Buck Island, white band disease and physical destruction from Hurricane David and Tropical Storm Frederic (1979) reduced the live coverage of elkhorn coral from 85% to 5% (Rogers et al. 1982; Gladfelter 1991); in 1989 Hurricane Hugo led to even further declines (Gladfelter 1991). Numerous new colonies of elkhorn coral, which had developed from sexually produced larvae and from branch fragments, were seen at Buck Island in the summer of 1995. A few months later, Hurricanes Marilyn and Luis destroyed several of these (Z. Hillis-Starr, National Park Service, Buck Island Reef National Monument, Christiansted, U.S. Virgin Islands, personal observation).

In 1987 a study of 50 individual elkhorn coral colonies in Hawksnest Bay off the north shore of St. John indicated that only 10 remained undamaged 7 months after initial observation (Rogers et al. 1988). Heavy ground seas and damage from snorkelers and boats were probably responsible for the observed decline. The elkhorn coral population in Hawksnest Bay appeared to be recovering when it suffered damage from Hurricanes Luis and Marilyn in September 1995. Though little quantitative information exists, staghorn coral and finger coral also appear to have declined substantially around the U.S. Virgin Islands.

The U.S. Virgin Islands have been hit by 4 hurricanes and numerous tropical storms in the last 15 years. Some of the most severe damage was associated with Hurricane Hugo in 1989 (Edmunds 1991a; Hubbard et al. 1991; Rogers et al. 1991; Bythell et al. 1992). This category 4 storm flattened reefs off the south side of Buck Island, creating widespread areas of rubble. Transport of rubble and coral resulted in movement of the southern reef crest 30 meters toward the island (Hubbard et al. 1991). In contrast, little damage from Hurricane Hugo was noted off the north shore of the island.

At long-term monitoring sites around St. John and Buck Island, coral cover, initially less than 30%, dropped to 8%–18% following Hugo (Edmunds 1991a; Rogers et al. 1991; Bythell and Bythell 1992; Rogers 1992). The dominant coral species, star coral, declined about 35% in Lameshur Bay. Studies have shown that no substantial recovery in total coral cover has occurred, although coral recruitment is occurring. Decreases in the amount of living star coral are of particular concern because it is one of the major reef-building species in the Caribbean.

During Hurricane Hugo, gorgonian corals and sponges were torn apart and ripped off their bases. Many collected in sand channels and other depressions on the reefs, and piles of them washed up on the beaches. Along long-term transects in Lameshur Bay, the number of species and the size of colonies of gorgonians and sponges increased between 1991 and 1992 (Gladfelter 1993). Although there was a slight decrease in the number of sponge colonies during this time, the number of gorgonian colonies increased. These results may indicate ongoing recovery of the sponge and gorgonian communities from Hurricane Hugo.

In September 1995 two hurricanes (Luis and Marilyn) hit the U.S. Virgin Islands within a 10-day period. Reefs off the north side of Buck Island and the south side of St. John suffered severe damage. Although damage was conspicuous at Lameshur Bay, the percentage of live coral cover along the permanent study transects did not decrease, perhaps because of the uneven nature of hurricane damage or because so little coral remained to be damaged (Rogers, unpublished data). In some bays on the north shore of St. John, more physical destruction was caused by boats that had broken loose and dragged across coral colonies than by the storm itself. Large coral colonies, some perhaps more than 100 years old, were split into pieces by boat keels. At the long-term study site in Newfound Bay, little damage from Marilyn was observed; total live coral cover there has remained at about 23% for the last 6 years (Rogers, unpublished data).

Although the physical destruction from hurricanes and white band disease has produced the most drastic changes in U.S. Virgin Islands reefs, other stresses are also taking their toll. Probably the greatest potential threat to the reefs around the U.S. Virgin Islands is sedimentation associated with runoff from coastal development sites. The steepness of the islands exacerbates this problem. A theoretical study of sediment runoff indicated that reef distribution around St. John is a function of watershed size, bay exposure and bathymetry, distance from sources of land-derived sediments, and storms (Hubbard 1987). Cores taken from large coral colonies off St. John give some clues as to the sedimentation regime before, during, and after extensive clearing of vegetation for sugarcane plantations in the eighteenth and nineteenth centuries. Growth data from these cores suggest gradual declines over the last 200 years (Hubbard 1987). Limited data from cores in Hawksnest Bay indicate that upland construction in the early 1980's led to significant decreases in annual growth rates (Hubbard et al. 1987), presumably a response to increased sedimentation. Current developments of private land inside and adjacent to park boundaries, as well as construction of new roads, have increased the sediment flow into nearshore waters (Anderson 1994). U.S. Geological Survey scientists are conducting research on this issue.

Black band disease has also been reported for several species of hard corals, including star corals and brain corals, around St. John (Edmunds 1991b) and at Buck Island Reef National Monument (Bythell et al. 1992). This disease has not been conclusively linked to human activities. Edmunds (1991b) found that less than 1% of the corals in Lameshur Bay were infected. Even though the effects of black band disease are small compared with other stresses, the disease should not be ignored because it infects

primary reef-building species. Like coral bleaching, which was observed in the U.S. Virgin Islands in 1987 and 1990, this disease appears to be correlated with higher seawater temperatures. If algae grow on the bare substrate that becomes available after the infected coral tissue dies, recolonization by hard corals and other reef organisms will be inhibited.

The abundance of algae on the long-term transects in Lameshur Bay has fluctuated between 2% and 32% cover, with the highest amounts occurring in the fall of each year (Rogers, unpublished data). Increases in algal biomass result from nutrient input and reductions in herbivory, but no direct correlations have been documented. In spite of some excellent early studies on herbivorous fishes in Lameshur Bay (Earle 1972), further research is needed to unravel the complex relationship among herbivorous fishes, invertebrates, and the species of algae (primarily *Dictyota*) that predominate on the reefs around St. John. Some fishes and sea urchins graze on algae and open up new space on the reef for colonization by nonalgal reef organisms. It is not clear how the decline in predatory fishes has affected these herbivores (see box on Reef Fishes).

With respect to natural resource protection, national parks are a mixed blessing. Virgin Islands National Park attracts nearly one million visitors a year, most of them arriving on cruise ships or smaller boats. A single anchor drop from a cruise ship in 1988 led to the destruction of almost 300 square meters of reef. Monitoring at this site reveals no significant recovery of hard coral 8 years later (Rogers 1993; Rogers, unpublished data). A survey of 186 boats in 1987 revealed that 32% were anchored in seagrasses and 14% in coral communities. About 40% of the anchors in coral and 58% in seagrass beds caused damage (Rogers et al. 1988). Small boats continue to run aground on reefs within Buck Island Reef National Monument and Virgin Islands National Park. The installation of mooring buoys and limits on the size of vessels allowed in park waters have resulted in less pressure on these reefs, but in some areas there is little coral left to protect.

Coral reefs are highly diverse and complex ecosystems. We have only limited understanding of the ecological processes that occur within and among reefs and associated mangrove and seagrass bed systems. Interactions among these systems include transfer of nutrients and the movements of organisms (primarily fishes). Seagrass beds and prop roots of red mangroves provide critical feeding and nursery areas for reef fishes. The degradation of reefs in the U.S. Virgin Islands is a result of a combination of stresses that sometimes act synergistically. There is no doubt that the reefs have suffered serious declines from hurricanes and white band disease. The hurricanes have scoured out large portions of the seagrass beds around St. John and, in combination with a severe drought in 1994–1995, have killed extensive mangrove areas. The full effects of the changes that have occurred on the associated reefs are impossible to quantify.

Sedimentation, overfishing, and damage from boats continue to degrade U.S. Virgin Islands reefs (see box on Reef Fishes, this chapter). On reefs off the north coast of Jamaica, similar stresses have resulted in a drastic, probably irreversible, decline in the amount of live coral cover to less than 5%, as well as increases in algal biomass of up to 90% (Hughes 1994). Only time will determine if the amount of living coral on the reefs in the U.S. Virgin Islands will drop to these levels, leading to further increases in algae. Future hurricanes, combined with human-related stresses, may tip the balance so that recovery becomes impossible.

See end of chapter for references

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also enhance local reef diversity, provided they disturb the system at an intermediate level (Connell 1978).

Humans also disturb coral reefs. Collection of corals by people and breakage of corals by boat anchoring have considerably damaged these reefs. Anchoring buoys have been installed in some of the best-preserved reef sanctuaries of Puerto Rico, including Caja de Muerto Island. Coral reefs have also been negatively affected by sedimentation caused by poor land-use practices (Loya 1976; Rogers 1977). Of even greater concern are the extensive losses of coral reefs and their dependent species worldwide, including those in Puerto Rico and Mona Island (Williams and Bunkley-Williams 1990). Marine ecologists are concerned that many reefs may not be able to survive as functional ecosystems if bioerosion rates exceed reef accretion rates (± 10 millimeters per year) for extended periods (Smith and Buddenmeier 1992). This poses particular problems for Caribbean reefs, which are more prone to bioerosion than reefs elsewhere (Highsmith 1980).

Seagrass Beds

The tropical Atlantic seagrass beds (that is, beds of species such as turtle grass and manatee grass) may have the highest primary productivity rates of all natural systems in the world. In Puerto Rico, primary production and biomass are extremely high, even under nonoptimal conditions. Under pristine conditions, seagrass primary production may exceed 10,000 grams of organic carbon per square meter per year. Any of the six Caribbean seagrass species may form isolated patches or vast meadows, depending on water quality, nature of the substrate, and geomorphology of the coast (Vicente 1992).

Seagrasses greatly modify the physical, chemical, and geological properties of coastal areas. They provide nutrients, primary energy, and habitats to sustain coastal fishery resources; create foraging grounds for endangered species; and enhance biological diversity and productivity. Seagrass beds have characteristic fish populations and sometimes serve as nurseries for young reef fishes. These meadows are also

Reef Fishes of St. John, U.S. Virgin Islands

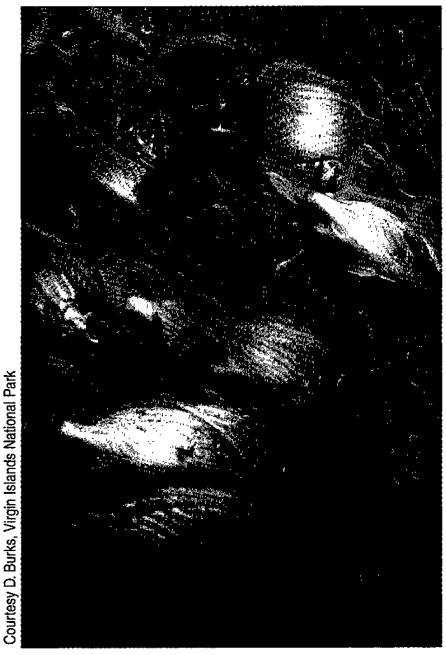
Of the 24,618 known fish species in the world (Nelson 1994), more than 400 reef-associated or inshore-ranging pelagic species (that is, living in open seas) are found in the nearshore waters surrounding St. John, U.S. Virgin Islands (Virgin Islands National Park, unpublished data). Many species, such as the foureye-butterflyfish and the butter hamlet, depend on coral reefs for shelter from predation, as a source of food, or as a place to spawn; juvenile fishes of many species (such as great barracuda and gray snappers) also find shelter amidst red mangrove prop roots. Some species, such as the bucktooth parrotfish and fringed filefish, live their entire lives in seagrass beds, whereas other species use the seagrass beds as nursery areas (such as French grunts; Fig. 1) or for nocturnal feeding (many snappers and grunts). Even habitats dominated by gorgonians (soft corals), sand, or algae and sponges are essential for some fishes, including the scrawled filefish, which feeds on gorgonians; the spotted snake eel, which lives in sand; and the chalk bass, which lives on the algal plain.

Both natural events and human activities can directly kill fish and degrade habitats, adversely affecting the habitat-dependent species. When Hurricane Hugo swept through the Virgin Islands in September 1989, the total abundance of fishes and number of species on two St. John reefs decreased significantly for 2 to 3 months after the storm (Beets and Friedlander 1990). Blue chromis declined sharply in number; surgeonfishes were observed in significantly greater abundance, feeding on the increased amount of algae, and normally secretive squirrelfishes appeared in the open, probably because of extensive reef damage (Beets and Friedlander 1990). It is interesting to note that when Hurricanes Luis (6 September 1995) and Marilyn (15 September 1995) struck St. John, no changes in either the number of fish species or the abundance of fishes were detected (V. H. Garrison, U.S. Geological Survey, Virgin Islands National Park, St. John, unpublished data and personal observation).

In the Virgin Islands today, many human activities are damaging coral reefs (see box on Coral Reefs), seagrass beds, and mangroves. Long-term effects of these activities on the reef fish assemblages are not yet fully understood. Fishing damages habitats when anchors and traps are set on the reef and lines become entangled on the bottom, but, more importantly, fishing can directly affect the abundance, average size, and assemblage of fish species.

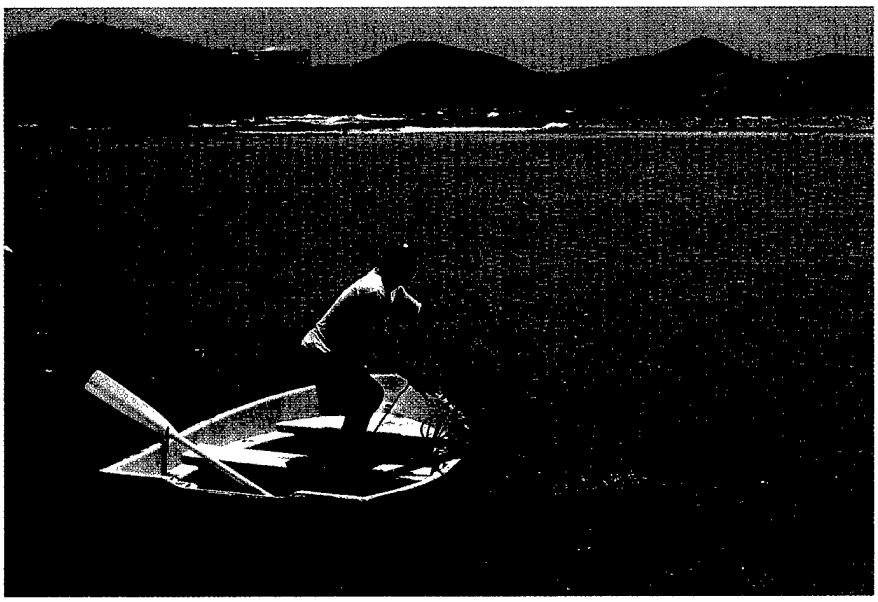
Since about 800 B.P., human inhabitants of the Virgin Islands have harvested a variety of reef fishes for food (Wild 1989). Fishing initially involved gleaning fish by hand in the shallows, then advanced with the development of tools and technology. Today, most fishing in the Virgin Islands is conducted by using traps (or *pots*) made of 3- to 5-centimeter wire mesh reinforced with a wooden or steel frame (Fig. 2). Traps are not selective; they harvest most reef fish species that are too large to escape through the mesh. Some species are trapped frequently whereas others are seldom caught, despite their absolute abundance. Groupers, in particular, tend to be attracted to traps, perhaps by the lure of a meal from the concentration of prey inside. Most types of fishes trapped in the Virgin Islands are eaten (Swingle et al. 1970; Olsen and McCrain 1980), putting pressure on a large number of species. Unfortunately, even the unpalatable species that escape the dinner plate and are discarded (bycatch) do not usually survive (Harper et al. 1994; Garrison, personal observation). Once the larger fish have been removed from an intensely fished area, immature fish make up a greater proportion of subsequent catches. *Recruitment overfishing* can result, which could seriously compromise the future abundance of reef species.

The rapid growth of coastal human populations has fueled the increased demand for marine resources worldwide (Wilkinson and Buddemeier 1994); St. John is no exception. The 1929–1930 Virgin Islands census counted 765 people living on the 52-square kilometer island of St. John, out of a total of 22,012 people living in the U.S. Virgin Islands (Fiedler and Jarvis 1932). As of 1990 the island had 3,500 permanent



Courtesy D. Burks, Virgin Islands National Park

Fig. 1. French grunts off St. John, U.S. Virgin Islands.



Courtesy J. Sneddon, Virgin Islands National Park

Fig. 2. Commercial fisherman using wire traps in the U.S. Virgin Islands.

residents (out of 100,000 total in the U.S. Virgin Islands; U.S. Bureau of the Census 1994) and more than one million visitors per year (Virgin Islands National Park statistics). This 55-fold increase in the number of people has greatly increased the demand for local fish. Consequently, the economic incentive to catch more fish has become so compelling that the local Nassau grouper spawning aggregation has been fished out of existence (Olsen and LaPlace 1979; Beets and Friedlander 1992). Yet fishing pressure continues to increase (Virgin Islands Division of Fish and Wildlife, unpublished statistics). In 1987 the Virgin Islands Division of Fish and Wildlife reported the following trends in the fishery: a continuing decline in the average size of trapped fish; an increase in fishing effort with no significant increase in landings; and prespawning juveniles making up most of the catch (deGraf and Moore 1987). Whereas groupers and snappers made up 33% of the catch in 1967–1968 (Dammann 1969), parrotfishes dominated the fishery in 1987 (deGraf and Moore 1987). Parrotfish populations are now beginning to exhibit signs of overfishing; specifically, the average size of trapped parrotfishes has decreased (Appeldoorn et al. 1992).

In 1992 the Research Division (now part of the U.S. Geological Survey's Biological Resources Division) of Virgin Islands National Park commenced a 3-year study designed to assess the effects of fishing (primarily by trap) on the reef fishes in the waters of St. John and to elucidate trends in species composition, abundance, and sizes of fishes. Park regulations allow fishing in park waters by trap, hook and line, and cast net only; no other fishing methods or types of gear are permitted (Fig. 3). Thus, another objective of the study was to evaluate the effectiveness of park fishing regulations in preserving and protecting the reef fish resource. The research involved several interrelated studies that were carried out and completed through the cooperative efforts of a number of agencies and universities (National Biological Service [now part of the U.S. Geological Survey], National Park Service, the Virgin Islands Department of Planning and Natural Resources Division of Fish and Wildlife, the Florida Marine Research Institute, and the universities of Rhode Island, Richmond, and Hawaii). A comprehensive view of the state of the reef fish and fishery resource of St. John is emerging from analyses of historical data and the results of these projects. The following information summarized from these projects to date is both exciting and disturbing.

- Fish traps have decreased the number of fishes and changed the relative abundance of species on St. John's reefs. Throughout 6 months of experimental trapping on a single reef in the park, the number of groupers, snappers, squirrelfishes, surgeonfishes, and total number of fishes caught in 8 traps declined significantly (Beets 1996). During the same period, visual census data also showed a decrease in the numbers of piscivorous (fish-eating) fishes, squirrelfishes, snappers, grunts, parrotfishes, and surgeonfishes, and in the total number of fishes (Beets 1996).

The results of a study that compared the fishes trapped on a reef in 1982–1983 with those caught on the same reef in 1993–1994 clearly document the decline in numbers and percentage of grunts, porgies, groupers, snappers, goatfishes, and boxfishes (Beets 1996; Table 1). Also, the mean length of most species decreased. Eleven of the species present in 1982–1983 were not observed or trapped during the 1993–1994 study; 4 of the 11 were groupers (rock hind, mutton hamlet, red grouper, and black grouper; Beets 1996).

- There was a decline in the average number of fishes caught per trap and a decrease in the average length of fishes in visually censused fish traps. Over the study period, the average catch was 4.7 fish per trap and the mean length of each fish was 25.0 centimeters.

Table 1. The ten most numerically abundant fish families in one fisherman's trap catches in 1982–1983 and in experimental trap sampling in 1993–1994 at Yawzi Point reef, St. John Island, U.S. Virgin Islands (Beets 1996).

Family common name	Percent	
	1982–1983	1993–1994
Surgeonfishes	25.7	45.2
Grunts	23.1	11.3
Porgies	10.0	3.5
Sea basses (groupers only)	8.8	4.7
Snappers	8.1	5.5
Goatfishes	5.6	3.7
Parrotfishes	5.4	15.4
Boxfishes	2.5	0.6
Squirrelfishes	2.0	5.4
Angelfishes	1.1	2.2

Blue tangs (surgeonfish family) were trapped in greater numbers than any other species; they averaged 15.4% of the catch. Porgies were the second most abundant (11.7%), and gray angelfish the third (9.4%). The highly prized food fish, the Nassau grouper, made up only 0.4% of the catch. The surgeonfishes accounted for 19.5% of the fishes trapped, increasing from 8.6% in 1992 to 34.6% in 1994; the surgeonfishes, butterflyfishes, angelfishes, and boxfishes made up over 50% of the catch. Table 2 summarizes the relative abundance in catches by trophic level. Note the increase in the percentage of herbivorous fishes and the decrease in fish-eating fishes.

- Catch rates (number of fish per trap), species composition, and sizes were similar on reefs inside and outside park waters in the experimental and general trapping studies (Beets 1996) and visual censusing. The results seem to indicate that park regulations and enforcement are not protecting a natural resource the park is mandated to protect.

Courtesy V. Garrison, Virgin Islands National Park

Fig. 3. A fish trap on Yawzi Reef, Virgin Islands National Park.

Table 2. Percentage of number of fish by trophic level in visually censused traps in St. John, U.S. Virgin Islands.

	Percent			
	All years	1992	1993	1994
Herbivores	28.1	23.5	22.8	41.8
Omnivores	16.4	18.7	19.1	9.5
Invertivores (invertebrate-eating)	41.2	41.0	44.1	36.2
Piscivores (fish-eating)	14.3	16.8	14.0	12.5

- Within park waters, 86% of the traps were set on organisms (live corals, soft corals, seagrasses) living on the sea floor. Damage to the live substrate has far-reaching negative effects on the marine ecosystem because the available amount of shelter and food often decreases as damage increases.
- Forty-nine percent of the traps in the park (35% of all traps) did not have a functioning biodegradable panel. Without the required panel, lost traps continue to kill fish for years.

In sum, our analyses have shown that the direct effects thus far from the trap fishing of reef fishes in the waters surrounding St. John include a change in the relative abundance of reef fish species, a change in the species composition, a decrease in the numbers of many species of fishes, and a decrease in the size of fishes.

See end of chapter for references

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important grazing areas for the green sea turtle and the West Indian manatee. In some areas, intensive recreational use has extensively disturbed the shallow seagrass meadows. Other beds have suffered from siltation caused by changing land-use practices or from dredge and fill operations during creation of shipping channels and docking accommodations. High turbidity levels generated by such activities can decrease the depth limit of seagrass beds (Vicente and Rivera 1982) and reduce the depth limit of corals, thereby diminishing the amount of deeper seagrass beds and coral reef habitats.

Mangroves

Only 4 of the 80 mangrove species found worldwide occur in the Caribbean Islands. Like coral reefs and seagrass beds, the functional values of mangrove forests are often critical to fisheries, wildlife resources, and biodiversity. Furthermore, these systems are also highly productive. Mangroves at Joyuda Lagoon, on the southwestern coast of Puerto Rico, produce more than 20 metric tons of organic matter per hectare per year (Levine 1981).

Mangrove forests consist of several salt-tolerant tree species, including black-mangrove, white-mangrove, and red mangrove, and the buttonwood-mangrove. Small islands (*manglares*) formed by clumps of red mangrove trees are important in extending land masses seaward because the trees capture sediments and debris (Fig. 11). The network of manglares, cays, and channels provides inland areas with a buffer from the action of stormy seas.

The extensive prop root systems of fringing mangroves have been reported to contribute to coastal accretion by as much as 25–200 meters per year (Maul 1993). This accretion may play a pivotal role in mitigating the present and projected sea-level rises and coastal erosion problems. Mangroves also play an important role in protecting uplands from storm winds and surge (Dammann and Nellis 1992).

Courtesy J. Colón, U.S. Fish and Wildlife Service

Fig. 11. Mangrove forest at Humacao Wildlife Refuge, Puerto Rico.

Mangrove forests also serve as nurseries for many reef and marine fishes, including commercially important species (Austin 1971). Mangrove ecosystems are also important to birds and other animals that depend on the fishes and invertebrates concentrated there. Manglares serve as relatively safe nesting habitat for some birds, including the white-crowned pigeon (Dammann and Nellis 1992). Two bird species listed as endangered, the brown pelican and the yellow-shouldered blackbird, as well as many species of herons and egrets, roost and nest on the mangrove canopy.

Development by humans has greatly reduced the amount of mangrove forests throughout the islands, although these forests have been protected in both Puerto Rico and the Virgin Islands during the last 20 years. In some cases, such protection has resulted in natural restoration of mangrove forest; for example, in Puerto Rico, 6,426 hectares of mangrove forest remained in 1974, following a period of destruction from 1950 to 1970. At present, there are 8,959 hectares of mangrove forests, an increase of 39.5% (Torres-Rodriguez 1993).

Rocky Coast, Beachrock, and Offshore Rocks

Rocky coast, beachrock, and offshore rock habitats receive heavy wave action and often have algal ridge reefs associated with them. Because of the wave action and salt spray, these areas are typically without vegetation. Only a few species of plants are able to survive in these areas, and the survival of the hardiest of plants is influenced by seasonal and storm-induced wave action. Aside from the importance of coastal rock formations for a wide array of invertebrates, these formations are also routinely used as roosts by shorebirds, gulls, and wading birds (Dammann and Nellis 1992).

Saltwater Ponds

Saltwater ponds are formed as a result of the growth of corals across the mouth of an indented shoreline (Dammann and Nellis 1992). Storm-deposited materials eventually form a berm separating the pond from the sea, and thereafter the pond gradually fills with trapped debris, forming a land mass. These inshore ponds may exchange water and organisms during unusually high tides or through remnant channels. Ponds that are not connected to the sea do not support fish. Water salinity, oxygen content, and temperature are highly variable and influence the fauna of these ponds (Dammann and Nellis 1992). During periods when conditions are favorable, insects and small invertebrates are common and form an important prey base for shorebirds such as plovers and sandpipers. Saline ponds and lagoons are particularly important to migratory waterfowl such as blue-winged teal, as well as the resident white-cheeked pintail and several waders. The usual fringe of mangroves surrounding these saltwater ponds provides habitat for nesting populations of herons, pigeons, and many songbirds.

Spoil Islands

Spoil from dredging a shipping channel in St. Croix was stockpiled offshore, forming spoil islands. Some of these islands have been colonized by terrestrial vegetation and are used by several species of birds (Dammann and Nellis 1992). A major hurricane did not destroy the largest of these islands, and some have been recognized as potential habitat for naturalized plants and animals (Dammann and Nellis 1992).

Freshwater Environments

Problems with freshwater ecosystems are a major environmental issue in Puerto Rico and the Virgin Islands. Water pollution, siltation of reservoirs, and excessive withdrawals of fresh water from rivers are problems associated with the growing human populations of the islands. Also, unauthorized filling of wetlands is a substantial and continuing problem (U.S. Department of the Interior 1994). Detailed descriptions of the freshwater communities in Puerto Rico are available (U.S. Army Corps of Engineers 1978).

Reservoirs

Puerto Rico and the Virgin Islands have no natural inland bodies of fresh water (lakes). In Puerto Rico, 20 reservoirs, varying from 6 to 390 surface hectares, were constructed for the purposes of potable water, irrigation, water power, and flood control. The large native shrimp, gobies, and mountain mullet may come into some of the reservoirs from the rivers, but there are no native fauna adapted to such water bodies. Several game fish, including peacock bass, largemouth bass, and channel catfish, have been introduced into Puerto Rican reservoirs.

Artificial Freshwater Bodies

Ponds are important habitats in Puerto Rico and the Virgin Islands; almost all are artificial and mostly intended for irrigation, livestock, or aesthetic reasons. Most go dry during the year. Fish are stocked in some of the ponds for sport fishing and for mosquito and weed control.

Canals irrigating the sugarcane fields are also important habitats for fishes and aquatic invertebrates. Introduced fishes such as guppies and mosquitofish are often kept in cisterns and water troughs to control mosquitos.

Rivers and Streams

Puerto Rico has about 1,200 rivers, streams, and creeks. Twenty of these rivers have a permanent minimum water flow of at least 0.28 cubic meters per second and are important to the island's fishery. Major river systems are the Rixo Grande de Loíza (64 kilometers), Bayamón (41 kilometers), La Plata (73 kilometers), Arecibo (64 kilometers), Culebrinas (40 kilometers), and Añasco (65 kilometers). The character of the streams changes radically from rapidly flowing in the steep mountains to slower and more winding courses across the narrow Coastal Plain, creating habitats for fishes and other aquatic animals. Many fishes migrate up- or downstream to or from saltwater habitats.

Following heavy rains, many active freshwater streams can be found in St. Croix and the other Virgin Islands. These streams are short-lived now, although previously some did flow permanently. Even the pools left behind dry up during the annual cycle. Near the shoreline, some depressions and beaches retain brackish

pools throughout the year. Despite the ephemeral nature of these streams, fish can usually be found in them during the rainy season (Ogden et al. 1975).

Lagoons

All of the lagoons have shallow water, usually with mud bottoms, are weedy over large stretches, and, if brackish or salty, are surrounded by mangrove forests. Cartagena Lagoon, formerly perhaps the most important wetland in Puerto Rico (Danforth 1926), has been greatly degraded by nearby agricultural practices. The lagoon has recently been acquired as a national wildlife refuge, and restoration is proposed. Other important lagoons include Joyuda, San José, Torrecillas, Tortuguero, and Piñones.

Status and Trends of Animals and Plants

The Fossil Record, Extinctions, and Extirpations

Island ecosystems are, in general, more susceptible to change than are those on continents, and the West Indies are no exception. Deforestation and fire, introduction of grazing animals, cultivation, and the introduction of weedy plants are all important causes of island extinctions (Heywood 1979), but deliberate or accidental species introductions have been singled out as disproportionately critical (Elton 1958). Extinction rates are generally higher on islands because island species typically have small populations, restricted genetic diversity, and narrow geographic ranges (MacArthur and Wilson 1967; Vitousek 1988). In addition, human-caused extinction rates are much higher on islands than on continents (Vitousek 1988).

Large-scale extinctions in the late Ice Age and during more recent prehistory drastically altered the West Indian vertebrate fauna, especially the nonflying terrestrial mammals. Many of these species disappeared from the West Indies about 10,000 years ago as a result of climatic change and the post-Ice Age rise in sea level (Pregill 1981). The species composition of the fossil faunas indicates that the environment of parts of Puerto Rico was a dry, savannalike habitat, quite in contrast to the moist conditions there now. Undoubtedly, the plant community changed with this climatic shift, and probably many rare plants disappeared from the islands or were confined to postglacial ecological refugia (Little and Woodbury 1980). No endemic tree species in Puerto Rico and the Virgin Islands are known to have become extinct, although the fossil flora of Puerto Rico is poorly known. Small, mountainous islands usually lack favorable sites (that is, freshwater lakes) for fossil pollen deposition and preservation.

A second and probably more extensive wave of extinctions took place from about 4,500 years ago to the present, after the arrival of humans on the islands (Morgan and Woods 1986). Many extinctions in the Antilles during the post-Ice Age prehistoric period were probably human-caused, resulting from direct exploitation, habitat destruction, or introduction of nonindigenous species (Olson 1982; Steadman et al. 1984b).

Reptiles and Amphibians

In a review of the world's amphibians and reptiles that are presumed to have become extinct since 1600, Honegger (1981) found that most were island taxa. All of the extinct lizards and snakes had island distributions, and West Indian species made up half of the world's extinctions (Henderson 1992). Pregill (1981) reported 21 fossil reptiles and amphibians from Puerto Rico; these species consisted of 16 genera and 12 families. One of these, *Cyclura portoricensis*, is an extinct form closely allied to the endangered Mona Island ground iguana.

Several reptiles have recently disappeared. In the Virgin Islands, the St. Croix tree snake, once common on St. Croix Island, became extinct about 1950. Similarly, the Puerto Rican racer snake is now extinct on St. Thomas. In Puerto Rico, the Culebra Island giant anole lizard, known only from Culebra Island, seems to have become extinct and thus represents the first of Puerto Rico's reptiles known to have become extinct since Columbus's arrival.

Birds

Although fewer than one-fifth of the world's bird species are restricted to islands, more than 90% of all historical bird extinctions have occurred on islands. The effects of nonindigenous animals introduced on islands by humans are the major cause of such losses. Human activities have precipitated a long history of decline for the approximately 250 native bird species known from Puerto Rico and the Virgin Islands (Raffaele 1989). This number includes ten extinct and two extirpated species. The crested caracara (Olson 1976a), Puerto Rican quail-dove, and Puerto Rican woodcock (Olson 1976b) almost certainly disappeared before Columbus's arrival, although the Puerto Rican barn-owl may have survived into the colonial period (Wetmore 1927). DeBooy's rail, known from Native American middens, probably did not survive long after Columbus's arrival.

Four (1.6%) of Puerto Rico's native birds are known to have become extinct or extirpated since about 1850: Hispaniolan parakeet, white-necked crow, Cuban (lesser Puerto Rican) crow,

and limpkin. Another three species no longer breed on the island but are still occasional visitors: black-bellied whistling-duck, black rail, and greater flamingo. The now-extinct Culebra Island race of the Puerto Rican parrot survived until at least 1899.

In the U.S. Virgin Islands, Raffaele (1989) lists 199 native bird species; 70 breed there. Several species have disappeared since the arrival of the Spanish colonists. Some species now absent from certain islands still survive on others. For example, St. Croix has lost the masked booby, red-footed booby, and the least bittern, and St. Thomas and St. John no longer have populations of the Antillean mango and Antillean nighthawk.

Several species are known from the U.S. Virgin Islands only from bone remains, including a petrel and snow goose from St. Croix; DeBooy's rail from St. Thomas, St. Croix, and St. John; and the purple gallinule, St. Croix macaw, white-necked crow, and Cuban (lesser Puerto Rican) crow from St. Croix (Wetmore 1918, 1937; Olson and Hilgartner 1982). Because the DeBooy's rail is well represented in St. Croix's pre-Columbian refuse heaps, it was probably an important part of the aboriginal diet (Wetmore 1925, 1938). The rail possibly survived up to the twentieth century in the Virgin Islands (Nichols 1943; Ripley 1977).

Mammals

Twenty-two mammal species are known historically from Puerto Rico and neighboring islands; this group includes 1 insectivore, 1 sloth, 4 rodents, and 16 bats (Woods 1990). The number of mammal species in the original mammal fauna was high among the West Indies and was exceeded only by the number of mammal species in the much larger islands of Cuba and Hispaniola in the Greater Antilles. Despite the original high diversity of mammals, all Puerto Rican mammals except bats have been extirpated. Bats have fared much better—only 14% of known West Indian bat species went extinct during the period when terrestrial mammal species dramatically declined.

Likewise, many terrestrial mammal species of the Antilles are also extinct; these losses have a common basis. Taxa evolving in isolation on oceanic islands without competition or predators may not be able to adapt to rapidly changing conditions, such as the extensive climatic fluctuations of the Ice Ages or sudden competition or predation from introduced animals (Woods 1990). The combination of island invasions by aboriginal humans and competition and predation by introduced animals is the most probable reasons for the extinction of several West Indian mammal species (Woods 1989a).

Biodiversity, Endemism, and Endangered Species

Plants

Puerto Rico and the Virgin Islands are rich in plants not found elsewhere. Fortunately, most native trees are protected in natural or near-natural forests on public forestlands and parks. Puerto Rico and the Virgin Islands combined have about 551 species of native trees, of which 539 are found in Puerto Rico. More than one-fourth (142) of these species are known only from these islands. Forty-six plant species are listed as endangered or threatened, including 30 tree or shrub species, 8 fern species, 2 cacti species, 2 orchid species, and 4 herbaceous plant species (Silander 1992; S. Silander, U.S. Fish and Wildlife Service, Caribbean Field Office, personal communication). About 100 other tree species listed as rare are native but are found elsewhere in the West Indies (Little and Woodbury 1980). More than 70 Puerto Rican and Virgin Islands' plant species are candidates for listing or are species of concern (U.S. Fish and Wildlife Service 1993, 1994a; Table 2).

Only 26 (18%) of the region's native endemic trees still grow wild on one or more of the Virgin Islands (Little et al. 1974); this small number of local species is related to lack of isolation. Only five tree species are endemic to the Virgin Islands.

Invertebrates

Invertebrates are important components of the islands' ecosystems, but knowledge of the status of invertebrate wildlife is not nearly as complete as that for the region's vertebrates. Even the functional roles of such fundamental elements as soil microfauna are poorly known in the region (Madge 1965; Coleman 1970). Although the total number of invertebrate species is low in the tropical forests of Puerto Rico and the Virgin Islands—no greater than that of temperate forests—species richness is much higher than in temperate forests (Odum et al. 1970). The richness of insect species has been demonstrated by Drewry (1970a), who reported 1,200 species from the Sierra de Luquillo in Puerto Rico. In the Sierra de Luquillo, the most common herbivores are invertebrates, primarily snails and plant-eating insects, which have a major influence on forest foliage (Martorell 1945; Van der Schalie 1948; Willig and Camilo 1991; Torres 1994). Vélez (1967) listed 36 species of terrestrial and freshwater crustaceans for Puerto Rico.

Researchers have noted invertebrate species in need of special attention. For example, because of the threats to cave ecosystems in

Species	Range in region	Federal status
Birds		
Brown pelican	Puerto Rico	E
Puerto Rican sharp-shinned hawk	Puerto Rico	E
Puerto Rican broad-winged hawk	Puerto Rico	E
American peregrine falcon	Puerto Rico, Virgin Islands	E
Arctic peregrine falcon	Puerto Rico, Virgin Islands	T
Roseate tern	Puerto Rico, Virgin Island	T
Piping plover	Puerto Rico, Virgin Islands	T
Puerto Rican plain pigeon	Puerto Rico	E
Puerto Rican parrot	Puerto Rico	E
Puerto Rican nightjar	Puerto Rico	E
White-necked crow	Puerto Rico	E*
Yellow-shouldered blackbird	Puerto Rico	E
Red siskin (introduced)	Puerto Rico	E
Reptiles		
Culebra Island giant anole	Puerto Rico (Culebra Island)	E
Mona boa	Puerto Rico (Mona)	T
Puerto Rican boa	Puerto Rico	E
Virgin Islands tree boa	Virgin Islands	E
Monito dwarf gecko	Puerto Rico (Monito)	E
Mona ground iguana	Puerto Rico (Mona)	T
St. Croix ground lizard	Virgin Islands	E
Green turtle	Puerto Rico, Virgin Islands	T
Hawksbill	Puerto Rico, Virgin Islands	E
Kemp's ridley	Puerto Rico, Virgin Islands	E
Leatherback	Puerto Rico, Virgin Islands	E
Loggerhead	Puerto Rico, Virgin Islands	T
Amphibians		
Golden coqui	Puerto Rico	T
Puerto Rican ridge-headed toad	Puerto Rico	T
Plants		
Ferns and allies		
Brake family		
Adiantum vivesii	Puerto Rico	E
Shield fern family		
Elaphoglossum serpens	Puerto Rico	E
Polystichum calderonense	Puerto Rico	E
Tectaria estremerana	Puerto Rico	E
Thelypteris family		
Thelypteris inaborensis	Puerto Rico	E
T. verecunda	Puerto Rico	E
T. yaucoensis	Puerto Rico	E
Tree-fern family		
Elfin tree-fern	Puerto Rico	E
Monocot plants		
Grass family		
Aristida chaseae	Puerto Rico	E
Pelos del diablo	Puerto Rico	E
Orchid family		
Cranichis ricartii	Puerto Rico	E
Lepanthes eltoroensis	Puerto Rico	E
Palm family		
Palma de manaca	Puerto Rico	T
Dicot plants		
Bignonia family		
Higuero de sierra	Puerto Rico	E
Boxwood family		
Vahl's boxwood	Puerto Rico, Virgin Islands	E
Buckthorn family		
Auerodendron pauciflorum	Puerto Rico	E
Cacti		
Higo chumbo	Puerto Rico	T
Leptocereus grantianus	Puerto Rico	E
Canella family		
Chupacallos	Puerto Rico	E
Citrus family		
St. Thomas prickly-ash	Virgin Islands	E
Flacourt family		
Palo de Ramón	Puerto Rico	E
Heath family		
Lyonia truncata var. *proctorii*	Puerto Rico	E
Holly family		
Cook's holly	Puerto Rico	E
Ilex sintenisii	Puerto Rico	E
Icacine family		
Palo de rosa	Puerto Rico	E
Madder family		
Mitracarpus maxwelliae	Puerto Rico	E
M. polycladus	Puerto Rico	E
Mahogany family		
Bariaco	Puerto Rico	E
Mezereum family		
Daphnopsis hellerana	Puerto Rico	E
Myrtle family		
Calyptranthes thomasiana	Puerto Rico, Virgin Islands	E
Eugenia woodburyana	Puerto Rico	E
Uvillo	Puerto Rico	E
Myrcia paganii	Puerto Rico	E
Nightshade family		
Erubia	Puerto Rico	E
Matabuey	Puerto Rico	E
Olax family		
Schoepfia arenaria	Puerto Rico	T
Pea family		
Chamaecrista glandulosa var. *mirabilis*	Puerto Rico	E
Cóbana negra	Puerto Rico	T
Pepper family		
Wheeler's peperomia	Puerto Rico	E
Snowbell family		
Palo de jazmín	Puerto Rico	E
Sunflower family		
Vernonia proctorii	Puerto Rico	E
Tea family		
Palo colorado	Puerto Rico	E
Ternstroemia subsessilis	Puerto Rico	E
Verbena family		
Capá rosa	Puerto Rico	E
Palo de nigua	Puerto Rico	E

Table 2. Endangered and threatened wildlife and plants in Puerto Rico and the U.S. Virgin Islands. E = Endangered, T = Threatened, and * = extirpated.

Puerto Rico, the Mona Cave shrimp has been designated as a species of concern (Groombridge 1993), and the Tuna Cave roach has been listed as a candidate for federal listing as endangered or threatened (U.S. Fish and Wildlife Service 1994b).

The Queen conch and the Caribbean spiny lobster, two commercially important invertebrates, are at risk throughout the Caribbean because of heavy commercial demand for their use as human food (Groombridge 1993). Both species have been federally listed, along with the common land crab, as deserving special attention in Puerto Rico (Raffaele et al. 1973).

In Puerto Rico, freshwater shrimp are not only important in the food chains of freshwater streams (Covich et al. 1991); they are also a much sought-after recreational resource in the island and are heavily harvested from some rivers. In Puerto Rico, competition of native snail species with introduced snail species has probably caused the decline of several populations of native snails, including *Physa cubensis* (Erdman 1972). V. Mestey-Villamil (Colegio Universitario de Cayey, Cayey, Puerto Rico, unpublished report) evaluated the status of marine mollusks in Puerto Rico, suggesting that

16 species and one subspecies were of special concern because of possible declining populations (Table 3).

Housing development and pollution in neighboring areas seriously threaten several of Puerto Rico's most spectacular natural areas, including Phosphorescent Bay at La Parguera and Mosquito Bay in Vieques. On dark, moonless nights, tiny marine dinoflagellates (*Gonyaulax* spp.) emit a phosphorescent glow, creating a spectacular light display. At La Parguera, past pollution problems (that is, oil spills) and recent increases in housing and tourism development may jeopardize the future of these phosphorescent dinoflagellates. The lagoons and surrounding mangroves at Mosquito Bay on Vieques Island, managed by the Vieques Conservation Trust, are currently protected, however. The topography of the area around Mosquito Bay and the absence of intense development on Vieques Island help maintain this system as the most pristine and spectacular luminescent lagoon in the region.

Table 3. Status of marine mollusks of concern in Puerto Rico (after V. Mestey-Villamil, Colegio Universitario de Cayey, Cayey, Puerto Rico, unpublished data).[a]

Name	Suggested status
Flame helmet	Undetermined
Cameo helmet	Undetermined
Cameo helmet subspecies	Undetermined
Caribbean helmet	Undetermined
West Indian topsnail	Undetermined
Atlantic trumpet triton	Undetermined
Mangrove oyster	Vulnerable
Angular triton	Undetermined
Angelwing	Undetermined
Clench's nerite	Endangered
Zebra nerite	Vulnerable
Sad nerite	Endangered
Milk conch	Undetermined
Roostertail conch	Undetermined
Queen conch	Undetermined
West Indian fighting conch	Undetermined
Hawkwing conch	Undetermined

[a] Populations of these species have substantially declined and those declines are of concern, but no good quantitative data have been collected.

Fishes

Although Puerto Rico has the fourth-largest insular land mass in the region, it has no native freshwater fishes; it does, however, support 24 established nonindigenous introductions as well as 60 peripheral marine invaders (Erdman 1972, 1974; Burgess and Franz 1989). Similarly, the Virgin Islands have no native freshwater fishes (Ogden et al. 1975), although numerous species have been intentionally or accidentally introduced, and peripheral marine species use freshwater streams during wet seasons.

The Commonwealth of Puerto Rico's Department of Agriculture established a fishery division in 1934 to support the growing interest in sport fishing and to supply a protein source for local residents. Several species were subsequently introduced into Puerto Rico's waters. Rainbow trout eggs were imported and hatched in the Caribbean National Forest in 1934; these trout introductions were unsuccessful because Puerto Rican waters were too warm for trout to breed. A hatchery at Maricao, once managed by the Puerto Rican Department of Agriculture, is now operated by the Fisheries Division of the Puerto Rico Department of Natural and Environmental Resources. In the last 3 to 4 years, the hatchery has been expanded and improved in order to produce various species of game fish, including peacock bass, which are stocked in the island's system of reservoirs.

Considerable habitat loss for freshwater fishes and invertebrates has resulted from water withdrawal from streams for domestic and industrial purposes. This problem will worsen as human populations grow and demands for water resources increase; recent periods of severe water shortage already highlight this problem (Lugo 1994). Inshore marine fisheries have declined as growing human populations have increased pollution levels and the amount of fish harvests. The fisheries have also been harmed because of habitat destruction, especially in the critical mangrove estuaries that serve as nurseries for fishes and their food.

Reptiles and Amphibians

Fifty reptiles and twenty-three amphibians are known from Puerto Rico and adjacent waters. Among the amphibians, 15 species are endemic, and 4 have been introduced. There are 29 endemic reptiles, and 2 introduced species may now be established.

Puerto Rico's 18 indigenous amphibians include the ridge-headed toad, the common mud frog, and 16 species of tiny frogs commonly called coquis. The amphibian fauna of the U.S. Virgin Islands is composed of 4 coquis, the Caribbean white-lipped frog, and 2 introduced species, the marine toad and the Cuban treefrog. All 20 species found in Puerto Rico and the Virgin Islands are unique to the region.

In the Caribbean National Forest of Puerto Rico, leptodactylid frogs (primarily coquis) are the most numerous vertebrates (Drewry 1970b; Rivero 1978). The most common species, the common coqui, existed at high densities (estimated at 20,570 animals per hectare) in the early 1980's (Stewart and Woolbright 1996). Abundant amphibians play important roles as predators on and prey of other species in the island ecosystems. Researchers estimate that in each hectare of forest, common coquis eat 114,000 prey items each night (Stewart and Woolbright 1996). Frogs are also important prey for numerous predators, including birds, snakes, and spiders and their relatives.

Habitat destruction is generally considered the most critical threat to the amphibians and reptiles of Puerto Rico and the Virgin Islands, although the introduction of nonindigenous mammals, such as black rats, has also had a substantial negative effect (Henderson 1992). Puerto Rico's native frogs are experiencing dramatic population declines, even though Puerto Rico's forest cover has recently increased. Many species were still common in their preferred habitats as late as the mid-1970's, but several species and formerly common populations are severely declining.

Several species of Puerto Rican amphibians have experienced drastic population declines in the last 20 years; in fact, almost two-thirds of Puerto Rico's endemic amphibians are declining (R. L. Joglar, University of Puerto Rico, San Juan, personal communication; Table 4). Some species have not been found for several years, including the web-footed coqui (not seen since 1974), the golden coqui (not seen since 1981), and the mottled coqui (not seen since 1990). Furthermore, 3 of 7 populations of amphibians studied in Puerto Rico on a long-term basis were declining (Joglar, personal communication). In the last 8 years, 5 other amphibian populations went extinct in 2 study sites; no recolonization has occurred. At least one Virgin Islands species is also in decline. All declining and disappearing species are highly specialized (morphologically or ecologically) and occur at high elevations. Paradoxically, amphibians in the Caribbean National Forest, the best-conserved forest in Puerto Rico and formerly home to the greatest variety of frog species, seem more negatively affected than amphibians in other localities. The reasons for this decline are unclear but may be related to declines in amphibian populations in many other parts of the world (for example, Barinaga 1990; Wyman 1990; Burrowes and Joglar 1991; Joglar 1992; Carey 1993; Vial and Saylor 1993; Blaustein et al. 1994; Pounds and Crump 1994).

Among the region's amphibians, only the Puerto Rican ridge-headed toad (Fig. 12) and the golden coqui have been listed under provisions of the U.S. Endangered Species Act of 1973 (Table 2). Three species of coquis are also candidates for listing under the Endangered Species Act: the rock coqui, the mottled coqui, and the web-footed coqui (Silander, personal communication). Local and international committees, though, recognize that several other amphibian species need special attention (Moreno 1991; Groombridge 1993; Table 4).

Puerto Rico's 50 reptilian species include 48 indigenous forms: 33 lizards (2 extinct), 8 snakes, 1 freshwater turtle, 1 land tortoise (extinct), and 5 sea turtles. In the Virgin Islands, 26 reptile species are known, including 15 lizards, 5 snakes (1 extinct), 1 tortoise (introduced), and 5 sea turtles. The 60 reptile species that occur in Puerto Rico and the Virgin Islands show a high rate of endemism, with 42 species (70%) found only in these islands. Twelve of the region's species, including all sea turtles, are listed under the U.S. Endangered Species Act of 1973 (Fig. 13; Table 2).

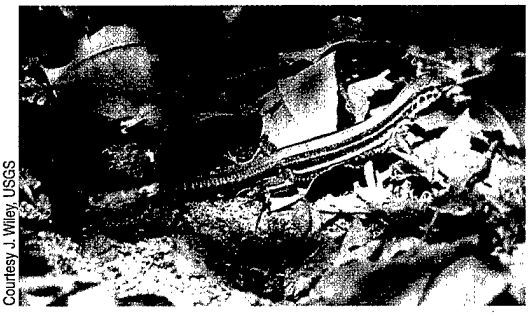
As in other parts of the world, sea turtle populations have greatly declined in the waters surrounding Puerto Rico and the Virgin Islands (see box on Sea Turtles). Once an important resource in regional waters, the green turtle fishery is nearly gone. Coral reefs and turtle grass meadows in the Virgin Islands and the Culebra archipelago are prime habitat for immature green turtles (Carr 1977; Tucker 1988; Collazo et al. 1992). Construction, sediment runoff, pollution, and increased boating and fishing activities in Culebra's coastal zone are threats to the islands' surrounding coral reefs and seagrass beds (Loya 1976; Rogers 1977; Lugo 1978; Goenaga and Canals 1980). The hawksbill, leatherback, and loggerhead sea turtles have also declined, in large part because of killing for food and loss of their habitat. Sea turtles are the subject of intensive research in the Virgin Islands (Eckert et al. 1986; Basford 1988; Groshens 1993; Starbird 1993).

Table 4. Status, including International Union for the Conservation of Nature (IUCN) categories, for 12 species of Puerto Rican and Virgin Island amphibians (as recommended by R. L. Joglar and P. A. Burrowes, University of Puerto Rico, San Juan, personal communication).

Species	Status
Rock coqui	Vulnerable
Mottled coqui	Extinct in the wild
Cricket coqui	Declining
Tree-hole coqui	Declining
Golden coqui	Extinct in the wild
Web-footed coqui	Extinct in the wild
Warty coqui	Vulnerable
Puerto Rican coqui	Declining
Ground coqui	Endangered
Virgin Islands coqui	Declining
Wrinkled coqui	Declining
Ridge-headed toad	Endangered

Courtesy F. J. Vilella, USGS

Fig. 12. A Puerto Rican ridge-headed toad, Guánica Biosphere Reserve.



Courtesy J. Wiley, USGS

Fig. 13. Endangered St. Croix ground lizard, Green Cay National Wildlife Refuge, St. Croix, U.S. Virgin Islands.

Sea Turtles of the Virgin Islands and Puerto Rico

The Virgin Islands and Puerto Rico include a complex of islands and small cays surrounded by coral reefs and seagrass beds adjacent to deep water. These islands provide critical nesting, foraging, and developmental habitat for three species of sea turtles: the leatherback and the hawksbill, both endangered species, and the green turtle, a threatened species. In addition, rare olive ridleys have only been reported in Puerto Rico once (Caldwell 1969); loggerhead turtles are transitory and are only occasionally seen in the area.

Sea turtles have been nesting on these islands since well before recorded history. Leatherback turtles, found in the Virgin Islands only during their nesting season, require for nesting open sand beaches with no nearshore reef; such beaches are found on Culebra Island and the north shore of Puerto Rico; Trunk Bay, St. John; and Sandy Point, St. Croix. Green turtles and hawksbill turtles nest in vegetated dunes, low scrub, and beach forested areas, which are often fringed by shoreline reefs (Hillis and Mackey 1989).

Green turtles and hawksbill turtles forage throughout the coastal areas surrounding the Virgin Islands and Puerto Rico. Juvenile sea turtles live in coral reef and seagrass habitats and remain there until they reach sexual maturity (Limpus 1990; Frazer et al. 1994). Adult female leatherback turtles, which are primarily pelagic (that is, living in open seas), migrate to the tropics every 2 to 3 years to nest (Boulon et al. 1996).

During the nineteenth century, the sea turtle fishery in the Virgin Islands and Puerto Rico was for subsistence only. Leatherback turtles were slaughtered on the nesting beaches for their oil, and their eggs were harvested for food. A substantial green turtle fishery for food and export to Europe existed historically, though the Virgin Islands were not a significant green turtle nesting area but instead were a juvenile foraging ground. Hawksbill turtles are solitary nesters throughout their range. In the Virgin Islands, hawksbills supplied the tortoiseshell industry beginning in the 1920's; the harvest was so great that turtle carcasses were common on the beaches, and hawksbill populations declined dramatically. These animals were killed for their shells only, the keratinized plates of which were exported to be made into curios and jewelry.

In the 1930's, Joe LaPlace, a former Department of Planning and Natural Resources/Division of Fish and Wildlife officer, noted heavy sea turtle nesting in three bays (Wilks, Hard, and Sandy) in St. Thomas, but coastal development boomed in the late 1950's, eliminating many of these sea turtle nesting areas around St. Thomas (Eckert 1992). By the 1950's the sea turtle populations were severely depleted, especially the formerly abundant juvenile populations of green and hawksbill turtles. Subsistence hunting continued, and to meet the demands of a growing human population, sea turtles were imported from other islands. By 1992 only 5 to 10 turtles nested in these bays each year; in some areas where all three species once nested, only an occasional hawksbill turtle now nests (Eckert 1992). In the 1960's, 40 to 50 green turtles were seen nesting on St. Croix's 3-kilometer-long Sandy Point beach during the nesting season (Eckert 1992). Today fewer than 10 females nest there each year, and fewer than 20 females nest on the entire island of St. Croix (Mackay 1994; Mackay and Rebholz 1995; R. Boulon, Jr., Virgin Islands Department of Planning and Natural Resources, St. Thomas, Virgin Islands, personal observation).

In 1972 Virgin Islands' law finally made it illegal to harvest sea turtles on their nesting beaches and allowed harvest in the water only between October and April. In 1973 leatherback and hawksbill turtles were protected under the U.S. Endangered Species Act; in 1978 the green turtle was listed as a threatened species. At present, populations seem stable, and juvenile green turtle populations seem to be increasing in the seagrass beds around the Virgin Islands (Boulon 1989; Boulon, personal observation), but there are no significant signs of recovery despite more than a decade of protection (Eckert 1991).

The greatest threats to sea turtles in the Virgin Islands and Puerto Rico today are coastal and upland development, introduction of domestic and nonindigenous animals, boating (both commercial and recreational), incidental take in fisheries, illegal harvest of adults and eggs, ingestion of and entanglement in marine debris, inadequate local protection and enforcement of laws, and insufficient regional cooperation for turtle protection. Coastal and upland developments that are constructed without concern for their downstream effects cause degradation of nesting beaches, seagrasses, coral reefs, and mangrove areas, which are all critical components of sea turtle habitat. Upland developments also result in increased lighting of nesting beaches, which disorients both hatchlings and adults (Philibosian 1975; Witherington and Bjorndal 1991; Witherington 1992). Such light forces nesting turtles to move away from protected public beaches into adjacent areas, where they are more vulnerable to poaching. Beach landscaping for recreational use causes loss of sand and native vegetation, thereby changing the temperature regime of the nesting beach. Recreational activities also affect nesting beaches. Off-road vehicles (illegal on Virgin Islands beaches) can crush nests and leave deep tire tracks that trap hatchlings on their way to the sea. Introduced domestic and nonindigenous animals (dogs, pigs, goats, horses, and mongooses) harass nesting females and destroy nests and hatchlings. Mongooses destroyed 24% of the nests recorded on St. John in 1980–1981 (Small 1982), and feral hogs destroyed between 44% and 100% of hawksbill nests outside of fenced beaches on Mona Island, Puerto Rico, from 1985 to 1987 (Kontos 1985, 1987, 1988). Before 1981, when mongooses were removed from Buck Island Reef National Monument, St. Croix, they destroyed more than 50% of all hawksbill nests annually (Small 1982).

Local fishing practices, such as trap fishing and gill netting, are hazardous to sea turtles in nearshore waters throughout the Virgin Islands. Offshore, long-line fishermen targeting 1,000 fathoms set trap lines, which are 30 to 65 kilometers in length and which hold more than 400 hooks on each line. Long lines are set to catch swordfish and tuna but have accidentally snagged, or *foul hooked,* leatherback sea turtles. Once snagged by a hook, a turtle becomes entangled and either drowns or is attacked by sharks (W. Tobias, Department of Planning and Natural Resources, St. Croix, Virgin Islands, personal communication). Abandoned fishing gear is especially deadly, entangling and drowning turtles, especially nesting females, which remain near shore between nestings. Young sea turtles also may become entangled in or ingest marine debris. In recent years the number of sea turtles killed by boat collisions has increased, especially along ferry routes where turtles forage (Boulon, personal observation).

The illegal take of sea turtles (eggs, juveniles, and adults) is still a significant threat in the Virgin Islands and in Puerto Rico. Twelve persons were arrested in Puerto Rico in 1994 for selling sea turtle meat in several local restaurants (M. Evans, U.S. Fish and Wildlife Service, St. Croix, Virgin Islands, personal observation). Insufficient

enforcement of protective laws greatly limits the effectiveness of legal protection for nesting sea turtles.

Public education programs have become the most effective weapon against the continued killing of sea turtles. Still, inconsistent regional protection of sea turtles, which use a variety of habitats in different areas during the various phases of their life cycle, offers them little overall protection in their foraging grounds or on their nesting beaches. Despite protective legislation in the U.S. Virgin Islands and Puerto Rico, the subsistence use of sea turtle meat and eggs and the harvest of hawksbills for their shells continue in adjacent island nations, posing a significant threat to the survival of sea turtles in this region.

The period for which data have been collected on sea turtles is extremely short compared with the long life of an individual sea turtle, which may require 20 to 30 years to reach sexual maturity and may be reproductive for 30 or more years (Frazer et al. 1994). Sea turtles are highly mobile and tend to return to particular nesting beaches (Hillis 1992; Melucci et al. 1992); in fact, genetic studies of female nesting populations indicate that female sea turtles may return to their natal beaches to nest (Bass et al. 1996). Once a nesting population is extirpated (removal of all eggs and adults) from a particular beach, it is unlikely that the nesting population will recover in the near future.

Sandy Point National Wildlife Refuge, St. Croix, is the principal nesting beach for leatherbacks in the northern Caribbean (Fig. 1). Tagging studies have shown movement by females among regional nesting beaches in Puerto Rico, Anguilla, and St. Croix (Eckert et al. 1989; Boulon et al. 1994; McDonald et al. 1995). A long-term saturation tagging program now provides essential information on leatherback turtle population trends in U.S. properties. Since 1981, of the 342 leatherback turtles tagged, 18–55 females have nested each year, laying between 82 and 700 nests (McDonald et al. 1995; Boulon et al. 1996). Researchers believe that before protection of leatherbacks, possibly 100% of the nests laid at Sandy Point were either destroyed by poaching or lost to beach erosion (seasonally a 50% to 60% loss). Since 1981 the beach at Sandy Point has been protected, and nests threatened by erosion have been relocated; nest loss is now less than 5% annually. Biologists speculate that the increase in the numbers of females nesting per season (given an average age to maturity for leatherbacks of 10 to 15 years) is a direct result of beach protection and nest relocation (Boulon et al. 1996; Fig. 2).

Observations of green turtle nesting populations have been collected incidentally by both leatherback and hawksbill turtle research programs in the Virgin Islands and Puerto Rico since the 1980's. In 1993 and 1994 daytime beach surveys were conducted for green and hawksbill turtles on St. Croix (Mackay 1994; Mackay and Rebholz 1995). The number of green turtle nests remains low for all the islands, but there appears to have been a gradual increase in the numbers of juveniles observed in the foraging grounds since the mid-1970's (Boulon, personal observation). The only island that still supports any green turtle nesting is St. Croix, which had an average of 100 nests per year between 1980 and 1990 (Eckert 1992). The largest concentration of green turtle nesting occurs on St. Croix's east-end beaches, which average 15 nests per year (Mackay and Rebholz 1995). This pristine area is now threatened by private development plans. In 1992 several green turtle nests were recorded on Isla Caja de Muertos, Puerto Rico, where illegal take of eggs and adults is still a risk (Diaz 1994).

Fig. 1. A leatherback turtle nesting on the beach at the Sandy Point National Wildlife Refuge, St. Croix.

There are very few places in the Caribbean where any large numbers of hawksbill turtles remain today (National Marine Fisheries Service and U.S. Fish and Wildlife Service 1993). In the Virgin Islands and Puerto Rico, hawksbill turtles nest on St. Croix (Buck Island Reef National Monument and east-end beaches), a few isolated beaches on St. John, St. Thomas (primarily on the offshore cays), and on Mona Island, Puerto Rico, as well as some scattered locations on mainland Puerto Rico, Culebra, and Vieques (Fig. 3). In 1993 only 32 hawksbill nesting activities were observed on all of St. John's beaches, even though more than 50% of the island remains an undeveloped national park (Mendelson 1993). In 1994, 100 hawksbill nesting activities were recorded on St. Thomas's offshore cays, 61% of which were on

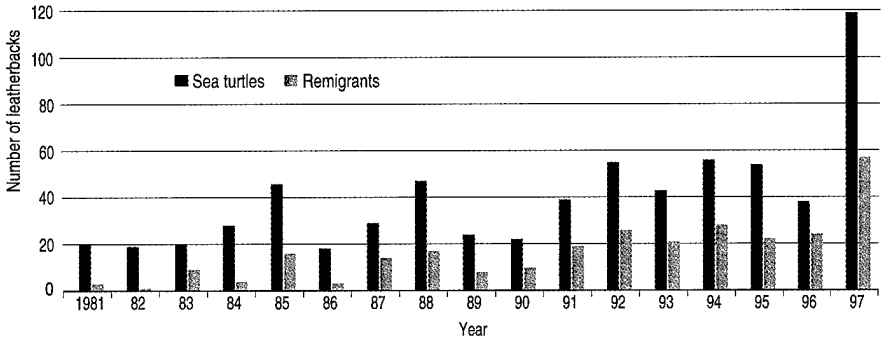


Fig. 2. The number of leatherback turtles and leatherback remigrants (that is, a nesting female who returns to nest at a particular site in subsequent nesting seasons) returning to nesting grounds at Sandy Point, St. Croix, U.S. Virgin Islands, 1981 to 1997 (modified from Boulon et al. 1994).

Courtesy Z. M. Hillis-Starr, National Park Service

Fig. 3. A hawksbill nesting.

Greater Hans Lollick, which is threatened by a proposed major hotel development (Boulon 1994).

The most important concentrations of hawksbill turtles are on Mona Island, Puerto Rico, St. Croix, and on Buck Island Reef National Monument, St. Croix's east-end beaches (Jack's Bay, Isaac's Bay, east-end bays). Mona Island supports more than 160 hawksbill nests annually, laid by about 30 to 40 adults (Kontos 1985, 1987, 1988; van Dam and Sarti 1989; Richardson 1990; van Dam 1990; van Dam and Pares 1991). Hawksbill nesting on Mona Island is still subject to illegal take and feral pig predation, but the Puerto Rico Department of Natural Resources continues conservation and enforcement efforts (Pares-Jordan et al. 1994).

Buck Island and St. Croix's east-end beaches support two remnant populations of between 20 and 30 nesting hawksbill turtles per season (Hillis 1994a; Mackay 1994). Since 1988, 84 individual hawksbill turtles have been tagged while nesting on Buck Island Reef National Monument. Hawksbill turtles return to nest every 2 to 4 years, indicating a high degree of nesting beach fidelity (Hillis 1992). Of these remigrants, between 50% and 80% have returned to nest in subsequent years, which demonstrates the high survivorship of adult sea turtles (Hillis 1994b; Frazer et al. 1996). Although annual survival of adult hawksbill turtles is high (Frazer et al. 1996), unfortunately, annual recruitment to the Buck Island population remains low (10%–15%; Hillis 1994b; Fig. 4). In 1994 a saturation tagging program began on St. Croix's east-end beaches; 14 hawksbill turtles were tagged that season (Mackay 1994), but to date, no Buck Island hawksbill turtles have been observed nesting there. These two populations are possibly distinct from each other (Mackay and Rebholz 1995; Bass et al. 1996). To successfully manage the highly migratory hawksbills, it is essential to resolve the identities of their reproductive populations in the Caribbean (Bass 1994; Bass et al. 1996).

Recent studies of juvenile foraging populations of hawksbill turtles at Mona Island and Buck Island Reef show juvenile hawksbill turtles residing in particular sections of reef over time (van Dam and Diez 1995; Hillis and Phillips 1996). Because juveniles stay in nearshore habitats, coral reefs, and seagrass beds, and because of their slow growth to maturity (15–30 years), their chances increase of being harmed through interactions with humans before they reach sexual maturity. Human actions that harm juvenile sea turtles living in nearshore habitats include boat–turtle collisions, turtle entanglement in abandoned fishing gear, ingestion of marine debris, degradation of habitat and food sources, and illegal capture. If a sea turtle reaches reproductive age, it faces a potential absence of mates and lack of suitable nesting habitat.

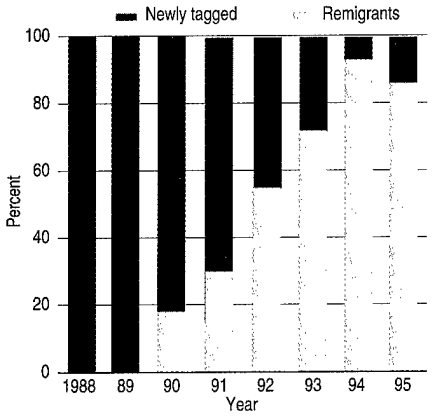


Fig. 4. Results of saturation tagging efforts of remigrant versus newly tagged hawksbills at Buck Island (Z. M. Hillis-Starr, National Park Service, Buck Island Reef National Monument, St. Croix, Virgin Islands, unpublished report).

Any discussion of status and trends of sea turtle populations in the U.S. Virgin Islands and Puerto Rico is incomplete without mention of conflicting regulations in the adjacent British Virgin Islands. About a kilometer east of St. Thomas and St. John, the British Virgin Islands have a 4-month open season (December to March), allowing legal take of sea turtles. In addition, the sale of tortoiseshell items is legal year-round there. This unresolved conflict between two neighboring jurisdictions is the single greatest threat to sea turtle protection in the U.S. Virgin Islands and Puerto Rico.

The British Virgin Islands have historically supported a large turtle fishery. Leatherback turtles were harvested for oil, and all sea turtle eggs were collected for consumption. In the 1920's, during one nesting season, six leatherback females came ashore to nest each night on two beaches in Tortola (Eckert et al. 1992). By 1990 only ten leatherback females came ashore to nest in all of Tortola. By 1991 only four females were observed nesting, and two of those were slaughtered (Eckert et al. 1992). On many beaches, leatherbacks have been completely extirpated. Records of harvest during open season show a similar decline for green turtle and hawksbill populations. In 1981, 700 green turtles were taken, compared with 71 in 1990–1991. In 1981, 400 hawksbill turtles were captured, compared with 32 in 1990–1991 (Eckert 1992). The dramatic decline of sea turtle populations in the British Virgin Islands has prompted the recommendation of stricter regulations to the British Virgin Islands Ministry of Natural Resources, for adoption by the UNEP/Widecast Sea Turtle Recovery Action Plan of 1992. Until such regulations are adopted and enforcement is improved, there is still no protection for sea turtle eggs and no size restriction on turtles harvested during open season in the British Virgin Islands.

Today, illegal trade in tortoiseshell persists and illegal take of turtles for meat continues. Confusion exists among U.S. and British Virgin Island residents about sea turtle products purchased outside the jurisdiction of the United States. Turtle products legally purchased in the British Virgin Islands are frequently brought to the U.S. Virgin Islands with the owner having no

knowledge of the prohibitions on importation of sea turtle products. The items are seized and fines are possibly levied (National Marine Fisheries Service and U.S. Fish and Wildlife Service 1993).

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See end of chapter for references

Birds

A combined total of 247 native bird species live in Puerto Rico (239 species) and the U.S. Virgin Islands (199 species; Raffaele 1989). In addition, many nonindigenous bird species from other areas of the world were introduced to the islands over the last 200 years. The rate of introduction of nonindigenous birds has greatly increased in recent decades; these additions have increased the region's total number of species by 37, with most (36) of these nonindigenous releases known for Puerto Rico. Far fewer species (11) have been introduced to the Virgin Islands (Raffaele 1989). Of Puerto Rico's 239 native bird species, 12 (5%) are endemic to the island. The Virgin Islands have no endemic species, although they share two species that occur only in common with Puerto Rico.

Twelve resident or migrant bird species or populations have been listed under the U.S. Endangered Species Act because of declining populations; the red siskin, an introduced species, is also listed (see Wiley 1985; Table 2). An additional eight species of Puerto Rican and Virgin Islands birds have been proposed as species of concern (S. Silander, personal communication). These include four native waterbird species (the white-cheeked pintail, the West Indian whistling-duck, the West Indian ruddy duck, and the Caribbean coot), as well as two species of forest birds (the elfin woods warbler and the Virgin Islands screech-owl).

Recovery efforts have been made for some of the federally listed species, including the Puerto Rican parrot (Fig. 14), Puerto Rican nightjar (Fig. 15), Puerto Rican plain pigeon, and the yellow-shouldered blackbird (Fig. 16). These efforts have been particularly intense for the pigeon, parrot, and blackbird (Fig. 17) and include population monitoring; nest monitoring; habitat management; predator, competitor, and parasite control; and management of captive populations (parrot and plain pigeon). Recovery efforts for the nightjar have been

Courtesy J. Wiley, USGS

Fig. 14. Endangered Puerto Rican parrot.

Courtesy F. J. Vilella, USGS

Fig. 15. Adult male Puerto Rican nightjar brooding a 3-day-old chick at Guánica Forest, Puerto Rico.

Courtesy J. Wiley, USGS

Fig. 16. Endangered yellow-shouldered blackbird, endemic to Puerto Rico.

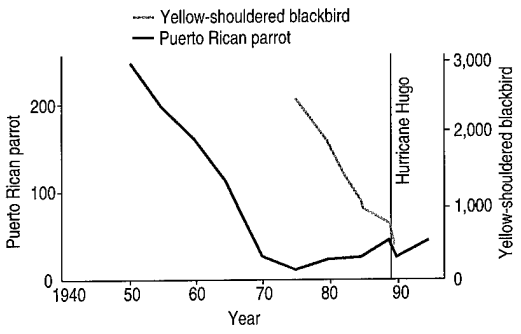

Fig. 17. Population trends of two critically endangered bird species, the Puerto Rican parrot and the yellow-shouldered blackbird.

primarily limited to field research for mapping geographic distribution and abundance and for identifying ecologically limiting factors.

Mammals

Bats are the only native terrestrial mammals left on Puerto Rico and the Virgin Islands. Presumably, bats had adaptations that helped them elude the invading nonindigenous predatory and competitive species. Nevertheless, several of the native bats are threatened by human-caused disturbances and habitat change. Puerto Rico has 13 species of bats, including 7 that are endemic to the Antilles, but none are exclusive to Puerto Rico. The Virgin Islands have 4 bat species, one of which is an endemic of the Greater and Lesser Antilles, but none are endemic to the Virgin Islands (Griffiths and Klingener 1988).

Ten of the thirteen extant bat species in Puerto Rico are cave dwellers. Cave-dwelling bats in Puerto Rico have low reproductive rates and are especially vulnerable to environmental disturbances (A. Rodríguez-Durán, Interamerican University of Puerto Rico, San Juan, personal communication). Bats that inhabit caves are particularly sensitive to direct disturbances, such as the entrance of people into the caves, as well as to indirect disturbances, including the spraying of pesticides or microclimatic changes in caves due to alterations to the cave opening. About 31% of Puerto Rico's caves host bat colonies varying in size from a few to hundreds of thousands of individuals (Rodríguez-Durán 1993). Increasing interest in caves for tourism and the use of chemical agents in insect control pose serious threats to the island's cave bat populations. The red fig-eating bat is a species of concern (U.S. Fish and Wildlife Service 1994b).

Nonindigenous Species

The native ecosystems of Puerto Rico and the Virgin Islands have been seriously disrupted by the introduction of many nonindigenous plant and animal species. At least 118 nonindigenous plant species are reproducing in Puerto Rico (Francis and Liogier 1991). In addition, an undetermined (but likely large) number of invertebrates have become established in Puerto Rico and the Virgin Islands. The nonindigenous vertebrate faunas are better known for the islands, with 24 fishes, 2 reptiles, 4 amphibians, more than 37 birds, and 13 mammals established in breeding populations. Although these introductions may be viewed by some as offsetting the losses of species through extinctions and extirpations, nonindigenous species do not usually fit smoothly into the new ecosystems but instead become aggressive predators on or competitors with native species. Species that have developed on remote oceanic islands in the absence of such predators or competitors are usually at a great disadvantage and may easily fall victim to such invaders.

The history of introductions to Puerto Rico and the Virgin Islands is a long one, perhaps pre-dating the arrival of Europeans in the region. Even so, the rate of introductions, as in other parts of the world, has greatly accelerated as human travel became faster and easier. Rapid and frequent transportation among the islands and mainlands has provided easy access to what were formerly remote regions. Furthermore, our society's increasing interest in stocking gardens with nonindigenous plants and in keeping exotic pets has also aided in the higher rate of nonindigenous species becoming established in the region. These introduced organisms pose a critical problem in the islands, not only because they sometimes threaten food crops but also because they challenge the existence of native species.

Ironically, Puerto Rico may be viewed as an important sanctuary for several nonindigenous species that are experiencing severe population declines or are facing extinction in their native ranges elsewhere in the world. For example, numerous parrot species, including some of those resident in Puerto Rico, are being excessively harvested for the pet trade industry, and continued removal of these birds from their home countries will likely result in more species listed as endangered. The endangered red siskin was probably introduced to Puerto Rico in the nineteenth century and may now occur there in greater numbers than in its native Venezuela and Colombia (Raffaele 1983). In recent years, the Department of Natural and Environmental Resources in Puerto Rico has considered extending protected status to the red siskin, despite its status as an introduced species (J. L. Chabert, Puerto Rico Department of Natural and Environmental Resources, San Juan, personal communication). Such concern stems from the fact that in Puerto Rico, red siskins are being captured by bird collectors

who can legally trap nonindigenous species for export. At present, red siskins are extremely rare in Puerto Rico (F. F. Rivera-Milan, U.S. Fish and Wildlife Service, Washington, D.C., personal communication). Similarly, the Cuban ground iguana is classified as vulnerable in its native range of Grand Cayman and Cuba, but introduced populations in Puerto Rico are thriving. It is conceivable that Puerto Rican populations of such species may someday be valuable as reservoirs for reintroducing species into reserves in their native lands.

Plants

Because of the extensive cutting and modification of natural forests, widespread agriculture, and introduction of many nonindigenous species, little remains of the original vegetation found in Puerto Rico and the U.S. Virgin Islands. Many introduced nonindigenous tree species have become naturalized in the forests of the islands. Common naturalized trees in the humid forests of Puerto Rico include pomarrosa, emajagua, almendra, mountain immortelle, and tulipán Africano. On the dry southwestern coast of Puerto Rico, bayahonda has become naturalized in pastures. In the U.S. Virgin Islands, an outstanding naturalized tree in the forest (particularly in St. Croix) is Dominican mahogany and, in pastures, tibet.

The native vegetation of these islands developed in the absence of large herbivorous mammals and, consequently, may have been quite susceptible to introduced goats and cattle (Fig. 18). Dry forests, which are restricted in Puerto Rico but widespread in Mona, Desecheo, Vieques, and Culebra islands, and also in the Virgin Islands, have been damaged by grazing animals. Nonetheless, Desecheo and Mona islands have been free of permanent human occupation for many years because of the absence of abundant sources of fresh water, the islands' small sizes, and their rough topography. Thus, these islands include some of the best examples of dry forest left in the region. The naturalization of introduced grasses usually occurs as dry forest areas are subjected to selective cutting and high grazing pressures. Periodic fires during the height of the dry season can become a recurring problem at disturbed sites and prevent native trees from becoming established.

Animals

The introduction of animals has had enormous effects on island ecosystems throughout the world (Vitousek 1988). The most disruptive species include vertebrate and invertebrate predators and herbivorous mammals. Most extinctions of birds (King 1985) and mammals (Morgan and Woods 1986) in the West Indies have been attributed to habitat loss and the introduction of rats, cats, dogs, and mongooses. Puerto Rico and the Virgin Islands are now home to all of these nonindigenous species.

Courtesy J. Wiley, USGS

Fig. 18. Seabird nesting habitat damaged by feral livestock, Culebra National Wildlife Refuge.

Invertebrates

Native populations of freshwater snails, including *Physa cubensis*, have been affected by several introduced snails (Erdman 1972). An African species, the quilted melania, is now the most abundant snail in Puerto Rico. At least one introduced snail species has had a more direct effect on humans; for example, the snail *Australorbis glabratus*, a possible introduction from South America, is an intermediate host for the debilitating human parasite *Schistosoma mansoni* (Erdman 1972).

European honey bees, now established throughout the islands, were introduced by the earliest colonists. Honey bees have proven to be fierce competitors for natural cavities used as nests and roost sites for several native species, including the endangered Puerto Rican parrot. Africanized honey bees recently became established in Puerto Rico (Vilella 1995). These aggressive bees pose an even more serious threat to native cavity nesters and to wildlife managers maintaining nesting sites for some species.

Freshwater Fishes

Numerous established nonindigenous species have been intentionally or accidentally released into native waters from aquarium stocks. Several other species have been established as game species. About 24 species are

established in Puerto Rico and 9 in the Virgin Islands (Erdman 1972; Ogden et al. 1975; Burgess and Franz 1989).

Reptiles and Amphibians

Three nonindigenous reptile species and four nonindigenous amphibian species have become established in Puerto Rico and the Virgin Islands. Common caimans, probably escaped or released pets, have become established in some swamps on Puerto Rico. The green iguana was apparently introduced on the island of Icacos in the Cordillera de Fajardo around 1970; others have been sighted on Culebra Island. Breeding populations of the common iguana are found in eastern Puerto Rico. In Fajardo, groups of nesting iguanas are commonly seen near the beach in the coastal forest reserve of Las Cabezas de San Juan, which is owned and managed by the Puerto Rico Conservation Trust. The red-footed tortoise has also been introduced to the Virgin Islands.

The marine toad, which is native to tropical America, was introduced to Puerto Rico around 1919 to control insect pests of sugarcane. The species proliferated and helped reduce cane pests, but it also competes with the endangered ridge-headed toad for food, habitat, and spawning sites. The bullfrog was introduced from North America in 1935–1936 with the intent of supplying an additional source of nutrition for poor people who lived directly off the land (Erdman 1972). Although the bullfrog became established in moderate numbers in many of the swamps and ponds of the Coastal Plain, it has never been accepted as a potential human food source.

Birds

At least 32 species of nonindigenous birds have become established in breeding populations in Puerto Rico and the Virgin Islands (Raffaele 1989); an additional 5 species are suspected of breeding in the region. Most nonindigenous bird introductions are probably the result of accidental releases, but some species were purposely released. Populations of northern bobwhite, introduced as game to Puerto Rico and the Virgin Islands, may survive in small populations, probably because of a lack of suitable habitat and because of predation by introduced mammals. The well-established troupial and turkey vulture were also intentionally introduced to Puerto Rico (V. Barnés [deceased], Puerto Rico Division of Fisheries and Wildlife, personal communication). Many species of cage birds have become established in Puerto Rico. Whereas certain nonindigenous species (for example, some estrildid finches inhabiting grasslands) have had no apparent effect on native wildlife or plants, others are a current or potential threat to native wildlife or crops. House sparrows and European starlings have become entrenched in metropolitan areas within the last 20 years, although the European starling remains uncommon, if not rare (Rivera-Milan, personal communication). Nonindigenous hill mynas and white-vented mynas compete with native cavity-nesting species, such as the Puerto Rico screech-owl, and with introduced psittacines (J. Wiley, U.S. Geological Survey, Grambling, Louisiana, personal observation) for the limited nest sites available. More than 14 species of nonindigenous parrots breed in Puerto Rico (Raffaele 1989) and may pose a threat to the endangered Puerto Rican parrot as competitors for nest sites and food resources, and perhaps through interbreeding and diseases they may carry. Fortunately, none of the nonindigenous parrots have yet entered the virgin forest of Luquillo. However, several nonindigenous species of parakeets, such as the monk parakeet and the orange-fronted parakeet, have become locally abundant and nest in areas of secondary forest surrounding the Luquillo Forest Reserve.

Another nonindigenous species, the shiny cowbird, was indirectly aided by human land-use changes in its invasion of the Virgin Islands and Puerto Rico. The cowbird "island hopped" north from its native South America through the West Indies as original forests were cut to make way for agriculture and pasturelands (Post and Wiley 1977). It arrived in Puerto Rico sometime in the 1940's or early 1950's. The cowbird is a brood parasite (that is, it lays its eggs in other birds' nests), and its parasitic habits have caused some populations of native species to decline (Cruz et al. 1989). Of particular concern is the dramatic decline of Puerto Rico's endemic yellow-shouldered blackbird.

Introduced Mammals

Possibly the earliest human-aided introduction of mammals to the Puerto Rican Bank was the Puerto Rico hutia, a large edible rodent (Steadman et al. 1984a,b), which was brought to Puerto Rico from Hispaniola by native people. The arrival of European colonists accelerated the decline of hutias through increased demand for meat, clearing of forests, and introduction of predators (Allen 1942).

Perhaps the hutia had little effect on native faunas and floras of Puerto Rico and the Virgin Islands, but many subsequent introductions made in colonial times and more recently have had devastating effects on native ecosystems. The combination of competition and predation by introduced forms is the most likely reason for the extinction of several West Indian mammals (Woods 1989b).

Introduced Rodents

The house mouse and black and Norway rats probably arrived when Columbus landed on the western Puerto Rican beaches. Rats are now distributed throughout all natural habitats in the West Indies and occur in large numbers (Woods et al. 1985). Rodents have been implicated in the declines of several native mammal, bird, and reptile populations.

Mongoose

The small Indian mongoose was introduced in various islands of the West Indies from 1872 to 1925 to help control rats and snakes (Wadsworth 1949; Wolcott 1953; Nellis and Everard 1983; Hoagland et al. 1989). Today, mongooses occur in a wide variety of habitats in the West Indies, from sea level to more than 2,000 meters, and have been accused of considerable damage to the natural faunas in those regions (Allen 1911; Seaman 1952; Seaman and Randall 1962; Raffaele 1989). Mongoose populations established on small cays and islands can be highly destructive to native fauna, particularly to reptiles and colonial seabirds (Philibosian and Ruibal 1971). On larger islands like Puerto Rico, though, the effect of mongooses as a primary limiting factor for terrestrial vertebrates is harder to elucidate (Vilella and Zwank 1993).

Cats and Dogs

Cats and dogs are particularly destructive to native wildlife on small islands. Although cats and dogs were introduced into the West Indies hundreds of years before the mongoose (Crosby 1991), it is only relatively recently that they have been implicated for any damage inflicted on native animal populations (for example, Mittermeier 1972; Wiewandt 1977; Iverson 1979; Tolson 1988; Woods 1989a).

Monkeys

A group of 57 rhesus macaques was released on Desecheo Island in 1966 so that researchers could study the process of adaptation in free-ranging monkeys (Morrison and Menzel 1972). The project was subsequently abandoned, and Desecheo was designated a national wildlife refuge in 1976. Meanwhile, the once-important brown booby and red-footed booby colonies there underwent dramatic declines, which some biologists have attributed to the predation of booby eggs by these nonindigenous monkeys (Evans 1989; Meier and Crider *in* Evans 1989). Efforts to trap the monkeys began in 1977 and continued through 1987 (summarized in Evans 1989). Some monkeys, however, remain on the island, and seabird colonies have not begun to recover (Evans 1989; J. González-Martínez, Caribbean Primate Research Center—University of Puerto Rico, Sabana Seca, personal communication).

Macaques were also established on islands off the coast of Puerto Rico, but escapees from those colonies have reached Puerto Rico, where they range widely through the southwest (J. González-Martínez, personal communication). The degree of threat posed by these nonindigenous animals is unknown. Aside from the inappropriateness of the species in the ecosystem, there is a threat to native animals such as the endangered Puerto Rican nightjar (a ground-nesting species) and the yellow-shouldered blackbird.

Several acts of vandalism from 1976 to 1978 resulted in the escape of 107 common squirrel monkeys at Sabana Seca, Puerto Rico (González-Martínez, personal communication). That population is now free-ranging and in 1984 consisted of about 155 individuals. By 1994 the population consisted of about 35 individuals; the decline is possibly related to damage by Hurricane Hugo in 1989. Escaped squirrel monkeys have also been found in the Luquillo Forest and at Lago de Cidra—both areas harbor endangered native species.

Game Mammals

Several attempts have been made to establish various game species in Puerto Rico and the Virgin Islands. White-tailed deer were released on Culebra Island in 1966 and have become established in small numbers. White-tailed deer were introduced to the Virgin Islands before 1800. The deer survive on St. Thomas and St. Croix islands (Seaman 1966).

Feral Livestock

Habitat stripping by grazing livestock (domestic and feral) is commonplace in the West Indies, where stock was introduced by the early colonists (Rudman 1990). As previously discussed, competition among feral and native animals does occur, as does predation of birds and lizards by feral pigs. Feral animals have also been implicated in the decline of certain endangered plants; including Wheeler's peperomia and higo chumbo (Lowe et al. 1990). Hunting of feral pigs and goats is allowed on Mona Island.

Knowledge Gaps and Ecological Outlook

The islands in the Puerto Rican Bank have been practically denuded of native vegetation, have extremely dense human populations, and face an associated array of environmental problems. Not surprisingly, the number of species heading toward extinction, or recently extinct, is

rapidly increasing. Still, with continued aggressive conservation efforts, Puerto Rico and the U.S. Virgin Islands may retain the best-preserved examples of certain natural ecosystems in the West Indies. Unfortunately, most other islands of the West Indies are undergoing accelerating habitat destruction for agriculture, leaving little reason for optimism regarding the future of their natural resources. Changing trends in the economics of Puerto Rico and the Virgin Islands have created an environment favorable for conservation of natural resources. Showcases of natural ecosystems as part of the image of these tropical islands are vital to the tourist industries, which are important to the economies of Puerto Rico and the Virgin Islands. Moreover, there is an increased awareness and concern about environmental and conservation issues among local residents, especially young people.

Most forested lands of the islands are second-growth. The role of plantations and second-growth forests in the rehabilitation of degraded ecosystems should be a priority for research investigations (Parrotta 1992) because a clear understanding of the ecology of plantations and recovering habitats is essential for managing the flora and fauna (Cruz 1988).

Human population growth in Puerto Rico and the Virgin Islands is of concern because human populations will continue to increase in the islands. Although human populations are concentrated in cities, there is a trend toward dispersion of tourist facilities and residential country homes. Many examples of relict ecosystems have been set aside in various state and federal reserves, although lack of money and other resources hampers the management of these areas. Because of the extensive fragmentation of habitats, many populations of plants and animals remain at extremely low levels, which puts them at great risk of local or rangewide extinctions. Forest cover is increasing with the shift away from an agricultural economy, but the resulting second-growth forests are often a mixture of native and non-indigenous species, or are replaced with monocultures of timber-producing trees. Such environments may not provide native species with appropriate habitats. In addition, saline flats, freshwater marshes, and freshwater swamp forests all face developmental pressures in Puerto Rico and the Virgin Islands. Mangrove forests and freshwater wetlands face the greatest risks; these highly productive ecosystems need greater protection. Also, if predictions for global warming prove correct, the frequency of hurricanes in the Caribbean is expected to increase (O'Brien et al. 1992). Consequently, ecosystems can be expected to change in response to the warming trend and to the increase in the frequency of tropical storms.

Scientific knowledge about several groups of organisms is lacking; the frog species undergoing precipitous population declines in the last two decades are cases in point. Likewise, little is known about the status of many invertebrate groups.

The West Indies are critical wintering habitat for certain migratory animals, especially birds. We need to determine the ecology of resident and migrant populations, particularly as related to remnant tracts of natural habitat and areas of recovering vegetation.

With proper maintenance of these reserves, most species of plants and animals will survive as remnant populations. Still, it is vital to ensure that populations are distributed among several parts of the islands as insurance against such natural disasters as hurricanes or the possibility of exotic diseases.

It is likely that Puerto Rico and the Virgin Islands will be able to maintain showcase ecosystems into the future. Because their economies are largely based on tourism, the establishment and maintenance of such examples of original ecosystems are beneficial to these countries. Beyond maintaining the biotic remnants of what now survives in the islands, an exciting opportunity is available to islanders: restoration of some original ecosystems (Wiley 1985). Even though extinctions have caused the disappearance of certain components of recently pristine ecosystems, other species, although extirpated from Puerto Rico or the Virgin Islands, still survive in other islands. Some of those surviving populations are rapidly declining, however, and may become extinct within decades.

Citizens of Puerto Rico have developed a strong conservation ethic. Such an ethic, along with well-enforced regulations to safeguard plants and animals, provides an excellent environment for restructuring some of the original ecosystems. Examples of the wet limestone forest of northwestern Puerto Rico, in large part within the state forest system, could be rehabilitated and, through introductions of native species, critical elements of the original ecosystem could be restored to the area. To do this, the current network of state limestone forest reserves must be expanded and, whenever possible, connected by conservation corridors. At present the area encompassed by limestone forest reserves totals approximately 4,586 hectares, with two of these, the Cambalache and the Vega, existing as small sets of forest fragments isolated from each other. Together, all these forest reserves are less than half the area of the Luquillo Forest Reserve (10,920

hectares; Fig. 19). Additionally, all but one of these limestone forest reserves (Guajataca) are being further degraded and fragmented by a major highway project.

Puerto Rican parrots and plain pigeons, now surviving as small populations in other parts of the island, are scheduled for release in the limestone forest. White-necked crows, limpkins, and rock iguanas, all surviving on other islands, could be reintroduced to these forests. Such restoration attempts should not be delayed too long, though, because the numbers of some surviving species from the original ecosystems are severely declining.

Ironically, Puerto Rico may become a sanctuary for several species facing extinction in their natural ranges. Through innovative reintroductions, entire ecosystems may be reestablished in these islands.

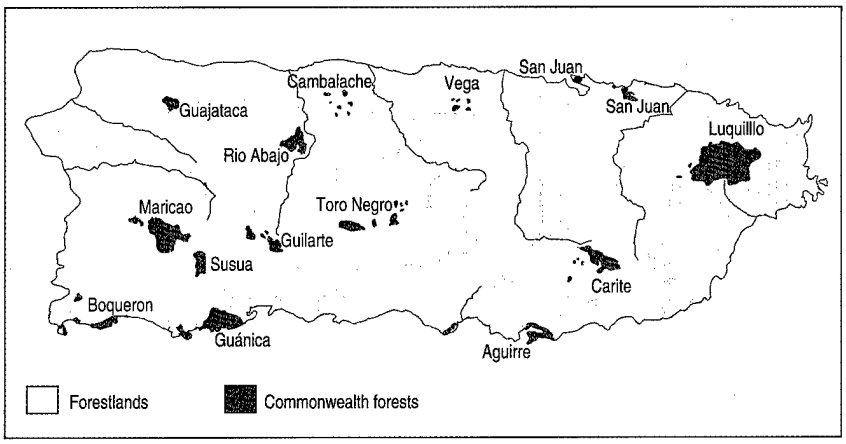

Fig. 19. Public forestlands of Puerto Rico. Green areas represent the Commonwealth Forests (Bosques Estatales) and the Caribbean National Forest, including the Luquillo Experimental Forest. Forestlands are represented by yellow areas (after Little et al. 1974).

Acknowledgments

We are indebted to several people for supplying or verifying the information that appears in this report. At the Puerto Rico Department of Natural and Environmental Resources, we are indebted to J. L. Chabert, D. Ramos, and C. Ruiz. At the U.S. Fish and Wildlife Service's Caribbean Field Office, thanks are due to F. López, M. Rivera, J. Saliva, S. Silander, and B. Yoshioka. We also thank F. F. Rivera Milán (U.S. Fish and Wildlife Service, Washington, D.C.), A. Rodríguez-Durán (Interamerican University of Puerto Rico, San Juan), and Janis González-Martínez (Caribbean Primate Research Center—University of Puerto Rico, Sabana Seca) for their help. We are grateful to R. Joglar of the University of Puerto Rico, San Juan, for information about the status of amphibian communities in Puerto Rico. The useful comments of Herbert A. Raffaele (U.S. Fish and Wildlife Service, Washington, D.C.) and three anonymous reviewers improved the chapter.

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Mississippi River

The Mississippi River is one of the world's major river systems in size, habitat diversity, and biological productivity. It is the longest and largest river in North America, flowing 3,705 kilometers from its source at Lake Itasca in the Minnesota North Woods, through the midcontinental United States, the Gulf of Mexico Coastal Plain, and its subtropical Louisiana Delta. "Mississippi" is an Ojibwa (Chippewa) Indian word meaning *great river* or *gathering of waters*—an appropriate name because the river basin, or watershed, extends from the Allegheny Mountains in the eastern United States to the Rocky Mountains, including all or parts of 31 states (Fig. 1) and 2 Canadian provinces. The river basin measures 4.76 million square kilometers, covering about 40% of the United States and about one-eighth of North America. Of the world's rivers, the Mississippi ranks third in length, third in watershed area, and seventh in average discharge.

The Mississippi River and its adjacent forests and wetlands provide important habitat for fish and wildlife and include the largest continuous system of wetlands in North America. The river supports a diverse array of wetland, open-water, and floodplain habitats, including extensive habitats on national wildlife refuges. Yet human activities have greatly altered this river ecosystem. Most of the river and its floodplain (defined as the adjacent, generally flat surface that is periodically inundated by floodwaters overflowing the river's natural banks) have been extensively modified for commercial navigation and other human developments. Much of the watershed is intensively cultivated, and many tributaries deliver substantial amounts of sediment, nutrients, and pesticides into the river. Pollutants also enter the river from metropolitan and industrial areas.

We examine the recent status and temporal trends in the abundance of several key groups of organisms in the Mississippi River. Our analysis shows that certain native flora and fauna, across many trophic levels, have declined along substantial portions of the river. These declines may signal a deterioration in the health of this ecosystem.

Definitions and General Information on River Reaches

The Mississippi River is divided into three segments: the Headwaters, the Upper Mississippi River, and the Lower Mississippi River. The Headwaters is the reach from the source (Lake Itasca) downstream to St. Anthony Falls in Minneapolis, Minnesota, whereas the Upper Mississippi River extends from St. Anthony Falls downstream to the mouth of the Ohio River at Cairo, Illinois. The Lower Mississippi River flows from Cairo to Head-of-Passes in the Gulf of Mexico. The 314-kilometer segment of the Upper Mississippi River extending from the mouth of the Missouri River (near St. Louis, Missouri) to the mouth of the Ohio is often termed the Middle Mississippi River.

Location along the main channel of the river is denoted by *river miles*, starting with mile 0.0 at Head-of-Passes and proceeding 953.8 river miles upstream to the mouth of the Ohio River. Numbering of river miles starts at 0.0 again at the mouth of the Ohio and continues up the Mississippi to Lake Itasca (Fremling et al. 1989).

Commercially, the Mississippi is one of the world's most important and intensively regulated rivers; the term *regulated* applies to rivers that

Courtesy B.L. Johnson, USGS

are dammed and constrained. The river is navigable by ocean vessels upstream as far as Baton Rouge, Louisiana, and by commercial craft with a 9-foot (2.7-meters) draft as far as Minneapolis. The Headwaters segment is not used for commercial navigation. The U.S. Army Corps of Engineers maintains the commercial navigation channel, federal locks and dams, and federal levees, and the U.S. Coast Guard maintains navigation markers.

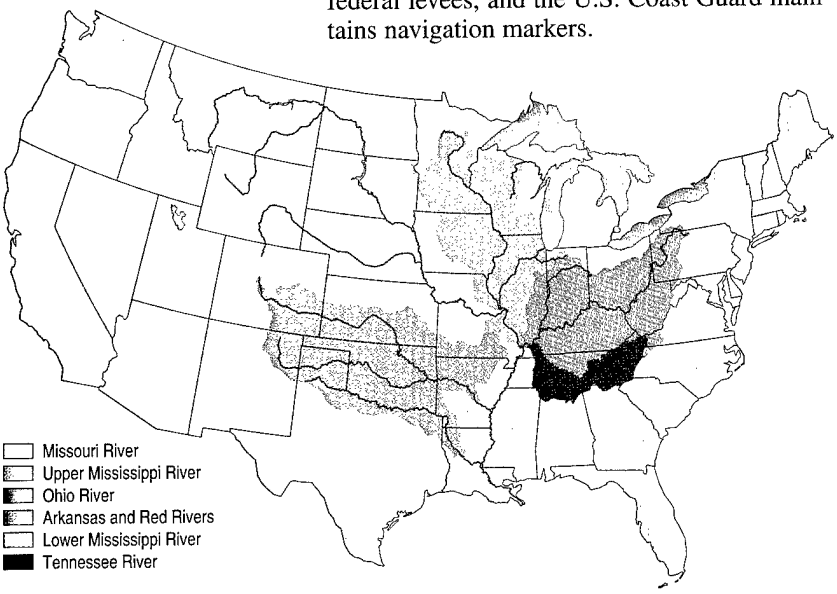


Fig. 1. Drainage basin of the Mississippi River and its major tributaries. The basins for the Headwaters (in Minnesota) and the Upper Mississippi River reaches are combined on the map.

The coastal zone of Louisiana contains about 25% of our nation's wetlands and 41% of our coastal wetlands (see chapter on Coastal Louisiana). These coastal wetlands form one of the world's largest and richest estuaries, essential to the reproduction of marine fishes, oysters, crabs, and shrimp. The coastal wetlands are also critical wintering areas for migratory birds, especially waterfowl. Unfortunately, each year about 100–120 square kilometers of Louisiana's coastal wetlands are lost to open-water or nonwetland habitats because of natural and human causes (Johnston et al. 1995). Especially critical is the erosion of the barrier islands that serve as the first line of defense against hurricanes and storms and which help prevent destruction of freshwater wetlands by saltwater intrusion.

Geography, Geologic History, and Human Development

Headwaters

The Headwaters' reach, located entirely within Minnesota (Fig. 2), has the steepest gradient, exiting Lake Itasca at 440 meters above mean sea level and dropping 204 meters along its 794-kilometer path to St. Anthony Falls, Minnesota (Fremling et al. 1989). This reach passes through spruce swamps, wildrice beds, natural lakes, beds of extinct glacial lakes, artificial impoundments, rapids, and dams (Waters 1977; MacGregor 1995). Beginning as a small, clear stream, the Headwaters gradually are stained a reddish-brown by natural organic acids leached from bog vegetation in the basin. The Mississippi River is a remote stream from Lake Itasca to Bemidji, meandering through corridors flanked by high, pine-topped sand banks, swampy lowlands, alder thickets, wildrice beds, and cattail marshes.

Approaching Bemidji, the wilderness character of the river is gradually lost because of human development. At Bemidji, the river flows through Lakes Irving and Bemidji and then through Stump, Big Wolf, Andrusia, Cass, Winnibigoshish, and Pokegama lakes (Fremling et al. 1989). The outlets of Lakes Winnibigoshish and Pokegama were dammed in 1891 and 1884 as part of a U.S. Army Corps of Engineers navigation and flood-control system that included four other dammed reservoir lakes on Mississippi River tributaries. The Headwaters' dams are now used mainly for flood control, recreation, conservation, and related uses. None of the 11 dams between Lake Itasca and St. Anthony Falls have navigation locks.

In Aitkin County, Minnesota, the river channel meanders for 200 kilometers over a straight-line distance of 64 kilometers. Many meander loops have been cut off, forming crescent-shaped oxbow lakes that are reconnected with the river during high water. Between the cities of Aitkin and Brainerd, the river passes through the Cayuna Iron Range, winding through hilly, heavily forested moraine systems, as well as glacial outwash plains, sand dunes, and swamps. Coniferous forests once covered most of the area, but logging, burning, and farming have produced a mixture of coniferous and hardwood forests. From Brainerd to St. Anthony Falls the landscape is dominated by an extensive system of glacial outwash and alluvial deposits that have been entrenched by the Mississippi River from St. Cloud to Minneapolis. The Headwaters' reach has been described in detail by Waters (1977), Fremling et al. (1989), and MacGregor (1995).

Upper Mississippi River

The Upper Mississippi River flows 1,462 kilometers from St. Anthony Falls in Minneapolis, Minnesota, to the mouth of the Ohio River at Cairo, Illinois (Fig. 2). The major period of valley scouring began about 15,000 years ago when the Wisconsin Glacier began to melt, increasing river flow (Schwartz and Thiel 1963; Wright 1972, 1989; Matsch 1976; Ojakangas and Matsch 1982). About 12,700 years ago, the retreating Wisconsin Glacier blocked the northward drainage routes of its

meltwaters toward Hudson Bay, forming glacial Lake Agassiz. This huge lake spilled over its southern rim for about 2,700 years, forming the glacial River Warren and carving the large valley now occupied by the Minnesota River. The River Warren was much larger than the present Minnesota River but carried little sediment. The glacial St. Croix River provided additional sediment-free overflow from Lake Duluth (glacial Lake Superior). The combined flow of the two rivers greatly increased the erosive capacity of the Upper Mississippi River, enabling the river to remove sediments from its bed and to deepen its channel by as much as 90 meters. The Upper Mississippi River must have been spectacular at that time—a massive, torrential river in a gorge that was eventually scoured more than 250 meters deep. As the Wisconsin Glacier retreated into Canada about 9,200 years ago, however, inflows of meltwater to the Upper Mississippi River ceased. The Upper Mississippi River valley then began filling with glacial outwash, mainly sand and gravel, a process that is still under way.

The Mississippi River valley widens considerably where it joins the Minnesota River, 13 kilometers downstream from St. Anthony Falls. Below its junction with the Minnesota River, the Upper Mississippi River flows through a deep valley carved into the surrounding sedimentary rocks. Steep tributary streams have dissected the plateau, creating a complex dendritic drainage pattern and a rugged landscape with high bluffs bordering the river valley. This reach flows through a driftless area (not glaciated during the most recent glacial advance) that includes parts of southeastern Minnesota, west-central Wisconsin, northeastern Iowa, and northwestern Illinois (Hallberg et al. 1984).

Lake Pepin was formed about 9,500 years ago when a delta of sand from the tributary Chippewa River partially blocked the Mississippi River valley, creating a natural impoundment. The Chippewa River, with its steep gradient, is the primary sand source for the reach of the Upper Mississippi River downstream from Lake Pepin (Nielsen et al. 1984). The constant influx of sand from the Chippewa River where it joins the Mississippi River necessitates intensive dredging in order to maintain sufficient channel depth for commercial navigation.

Modern Lake Pepin in Pool 4 begins about 75 kilometers downstream from Minneapolis–St. Paul and extends 35 kilometers downstream. Ranging from 1.5 to 4 kilometers wide, Lake Pepin has a mean depth of about 5 meters and a mean water-retention time of 19 days (Minnesota Pollution Control Agency 1993). The hydrological effect of Lake Pepin has greatly enhanced the quality of the reach of river farther downstream. The lake traps sediment and associated contaminants (Rada et al. 1990; Maurer et al. 1995), greatly reducing the transport of pollutants from the Minneapolis–St. Paul metropolitan area, the Minnesota River basin, and other sources to the riverine ecosystem downstream. Recent sedimentation rates in Lake Pepin range from 3 centimeters per year or greater in upstream reaches to about 0.5 centimeters per year in downstream reaches (McHenry et al. 1980); 21% of the

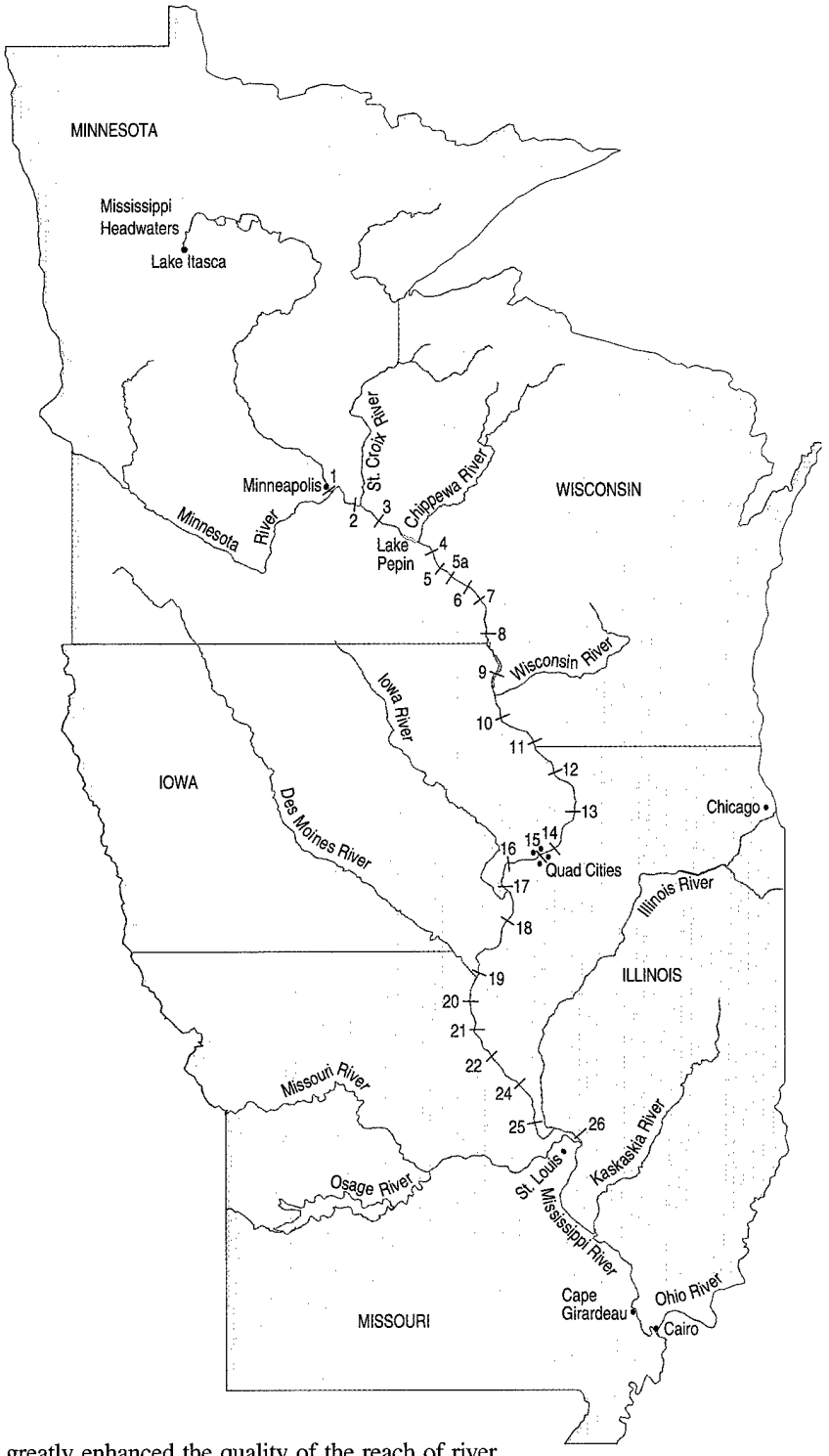


Fig. 2. Map of the Upper Mississippi River and Headwaters, showing locks and dams, selected cities, and other features. The numbers 1–26 represent the navigation pools in this section of the river. (Note: there is no pool 23.)

lake's volume was lost between 1897 and 1986 (Maurer et al. 1995). The sediment-trapping ability of Lake Pepin substantially reduces contamination of hexagenia mayflies and sediment downstream from toxic substances, such as polychlorinated biphenyls (PCB's; Steingraeber et al. 1994) and cadmium (Beauvais et al. 1995). The lake's sediment-trapping ability, however, will diminish as it fills with sediment and its volume declines.

The reach of river below Lake Pepin is part of the Upper Mississippi River National Wildlife and Fish Refuge, which extends from Wabasha, Minnesota, to near Rock Island, Illinois, a channel distance of almost 500 kilometers (U.S. Fish and Wildlife Service 1987). The refuge is an important wildlife and outdoor recreation area, covering about 80,000 hectares of the river floodplain in Minnesota, Wisconsin, Iowa, and Illinois. The refuge includes a diverse array of habitats, including marshes, backwater sloughs and lakes, myriad flowing channels, floodplain forest, sand beaches, and bluffs.

Just upstream from St. Louis, Missouri, the Missouri River joins the Upper Mississippi River from the west. Most tributaries to the Missouri River flow through highly erodible soils, which means that the Missouri River has always been the principal supplier of sediment to the Mississippi. Construction of a series of large dams in the Missouri River basin in the 1950's and 1960's created deep, cold-water reservoirs that trap sediment, reducing the Missouri River's total contribution of sediment to the Mississippi by about 70% (Keown et al. 1986; Meade et al. 1990).

About 160 kilometers downstream from St. Louis, the Mississippi River flows through Thebes Gap, which resembles the stem of an inverted funnel. Where it exits the gap, the constricted river widens as it enters an ancient sediment-filled lobe of the Gulf of Mexico called the *Mississippi Embayment*. The Mississippi River valley expands to a width of about 80 kilometers where it meets the mouth of the Ohio River.

Human development has greatly altered the Upper Mississippi River and its floodplain. The natural river and its tributaries flowed and meandered freely across the floodplain. Flooding, erosion, and sedimentation were powerful natural processes that shaped and maintained the floodplain and its biotic communities (Sparks 1992). Humans have changed the hydrological regime of the river, altering these processes (Fremling and Claflin 1984; Grubaugh and Anderson 1988; Sparks 1992).

Intensive channelization for navigation began in 1878 (Fremling and Claflin 1984). A series of 29 navigation dams with locks (Fig. 2) was constructed, mostly during the 1930's, to create a 2.7-meters-deep navigation channel between St. Louis and Minneapolis (Fremling et al. 1989). The upstream portions of many navigation pools (the reaches between two consecutive dams; see Fig. 2 for pool locations) are similar to the river before impoundment, whereas the downstream portions resemble shallow reservoirs.

The river floodplain has also been extensively modified with levees to accommodate agriculture and to protect human developments from flooding (Grubaugh and Anderson 1988; Interagency Floodplain Management Review Committee 1994). Agriculture has displaced much of the prairie wetlands and floodplain forests that dominated the presettlement floodplain.

Erosion caused by human activities in the watershed, such as agriculture and construction, has increased the rate of sediment delivery to receiving waters. Runoff has also increased because water storage in the watershed has been reduced by drainage of wetlands, urbanization, and other factors (Interagency Floodplain Management Review Committee 1994). Impoundment of the river for navigation has increased the retention of sediment; the valley floor is now blanketed by sediments from the post-settlement era. More detailed descriptions of the Upper Mississippi River are given by Waters (1977), Jackson et al. (1981), Nielsen et al. (1984), and Fremling et al. (1989).

Lower Mississippi River

Below Cairo, Illinois, the Lower Mississippi River and its tributaries follow the broad gulfward-sloping lowlands of the Lower Mississippi Alluvial Valley, which extends to the Gulf of Mexico. The Lower Mississippi River valley's present surface, the Mississippi Alluvial Plain, is characterized by the meandering, silt-laden Mississippi River and its southerly flowing tributaries, including the Black, Tensas, Yazoo, Big Sunflower, White, and Saint Francis rivers. It is an area of broad, nearly level to gently sloping floodplains and low terraces on unconsolidated alluvial material. Relief is generally less than 15 meters, although terraces and natural levees may rise several meters above the adjacent bottomlands. Swamps and bottomland hardwood forests cover large areas, even though much of the floodplain has been cleared for agriculture. There are many sloughs and oxbow lakes, and streams meander widely. The area also contains Yazoo River-type tributaries, which flow along the base of a natural Mississippi River levee, paralleling the Mississippi River for a considerable distance before joining it. The Tensas, White, Arkansas, and Saint Francis rivers all display Yazoo-type characteristics in their lower reaches (Beccasio et al. 1983).

The Lower Mississippi River channel is wide and generally shallow in the northern part of its alluvial valley, where coarse bed materials delivered by tributaries allow the river

to meander. In the southern part of the valley, the sediment delivered to the Mississippi River delta is mainly silt and clay (Autin et al. 1991). This thick upper stratum of fine sediment prevents meandering of the channel, which deepens to a maximum of about 60 meters just upstream from New Orleans, where the channel is less than 1 kilometer wide. At Head-of-Passes, the river splits like the toes of a bird's foot into several outlet channels, called *passes*, that empty into the Gulf of Mexico.

The lower end of the alluvial valley includes the modern Mississippi River delta, a low-lying triangular tract of land formed by sediments deposited at the river mouth (Fig. 3). The modern Mississippi River delta lies within southern Louisiana, extending from the head of the Atchafalaya River south to the Gulf of Mexico. The delta is spatially limited by the Mississippi's outermost distributaries, streams that conduct water away from the river. Through historical time, the Mississippi River has had several distributaries or flood outlets within the delta region. The modern delta is composed of smaller delta complexes formed during the past 8,000 years by a delta-switching process, whereby the river successively abandoned one delta for another as it found shorter, steeper paths to the Gulf of Mexico.

The upper surface of the delta, called the Mississippi Deltaic Plain, includes the coastal wetlands of Louisiana and covers 28,568 square kilometers (Coleman 1988). The deltaic plain is dominated by a complex network of distributary channels and natural levees that radiate outward from the Mississippi River main-stem near Baton Rouge and extend southward into the Gulf of Mexico (Frazier 1967; Penland and Boyd 1985). The deltaic plain includes natural levee ridges rising slightly above surrounding land levels, forested swamps, and coastal marshes vegetated chiefly by sedges and grasses.

Six delta lobes or delta complexes have been identified in coastal Louisiana: the Maringouin, Teche, St. Bernard, Lafourche, Plaquemines (or Balize), and Atchafalaya (Fisk 1944; Frazier 1967; Penland and Boyd 1985; Autin et al. 1991). During the past 5,000–6,000 years, formation of a new delta lobe has begun roughly once every 1,000 years in response to major changes in the Mississippi River's course to the Gulf of Mexico. The formation and aging of delta lobes are accompanied by changes in habitat types and plant communities (Neill and Deegan 1986).

Although the modern Lower Mississippi River has not been dammed, it has been greatly modified (Baker et al. 1991) by being channelized and shortened by 230 kilometers. In addition, its natural floodplain has been reduced about 90% in area by levee construction, which began in 1727. The Lower Mississippi River valley contains about 2,700 kilometers of levees along both sides of the river. Below Baton Rouge, where the levees are most susceptible to damage by river currents and waves, the levee faces are paved with concrete. Throughout Louisiana, the flood levees that normally protect the valley and its cities are augmented by a complex series of diversion projects that divert Mississippi River floodwaters into the Gulf of Mexico via the Atchafalaya River or Lake Pontchartrain, thereby diverting as much as two-thirds of flood flows around Baton Rouge and New Orleans.

Such navigation and flood-control activities have changed the Lower Mississippi River from its natural state (Beckett and Pennington 1986; Baker et al. 1991). Levees have reduced the area of seasonally flooded wetlands along the river,

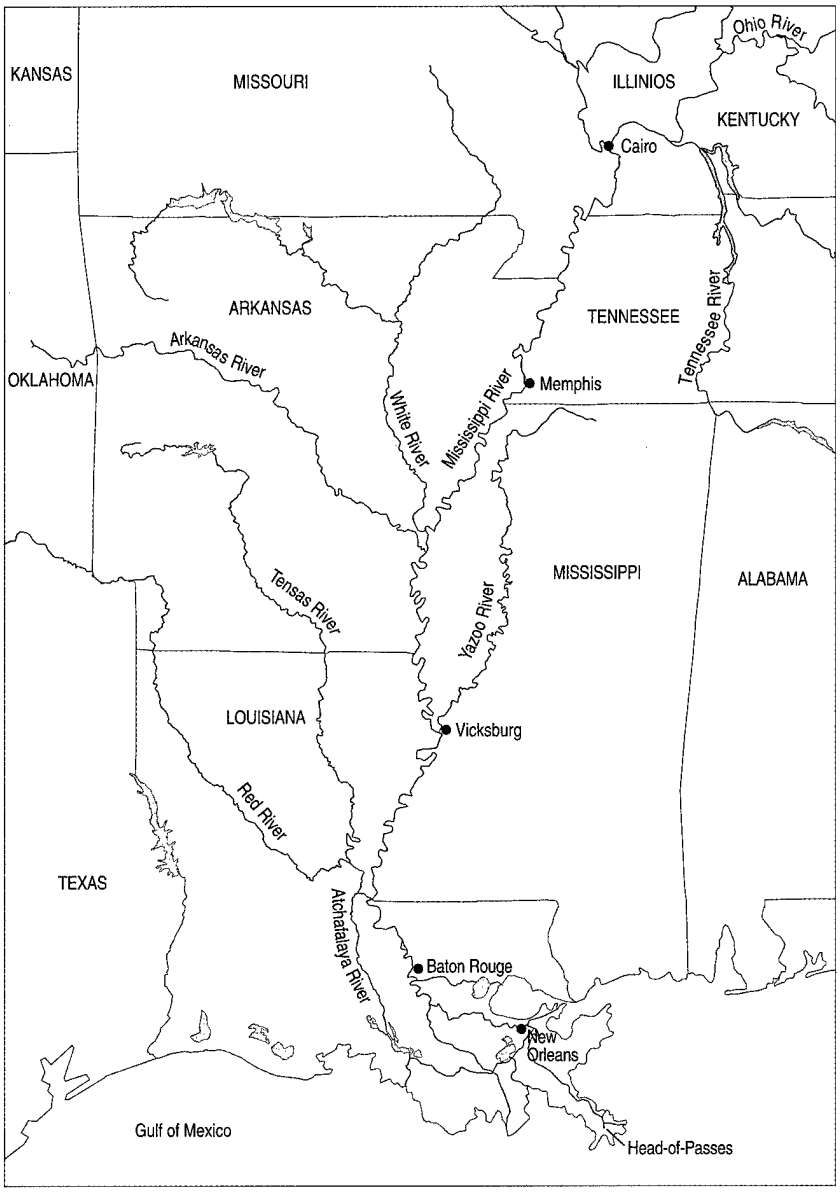


Fig. 3. Map of the Lower Mississippi River and its major tributaries, showing selected cities and other features.

and dikes and revetments used to entrain the channel prevent the river from creating new habitats. The failure to form new habitats, which historically occurred as the river meandered, is undesirable because floodplain lakes on the Lower Mississippi River (oxbow lakes and former channels) are rapidly filling with sediment (Gagliano and Howard 1984; Cooper and McHenry 1989).

Because of seasonal variations in discharge, aquatic habitats of the Lower Mississippi River are characterized by pronounced temporal variations in surface area, volume, depth, and current velocity (Baker et al. 1991). On an areal basis, the main channel is the primary habitat type during low flow, whereas at medium flow both the main channel and sandbars predominate. During overbank flow conditions, sandbars and inundated floodplains predominate. Few such backwater habitats remain on the Lower Mississippi River, though. Aquatic macrohabitats of the channel environment include the main river channel, secondary channels, sandbars, gyres below bars, tributary mouths, natural banks, and areas associated with dike systems and revetted banks (Cobb and Clark 1981).

Degradation of the Delta and Coastal Wetlands

Louisiana's coastal zone contains 41% of U.S. coastal wetlands and 25% of all U.S. wetlands, making it one of the Earth's largest and richest estuarine areas. Natural and human-induced forces, though, have been converting the state's coastal wetlands to open-water or nonwetland habitats at a rate of over 100–120 square kilometers per year during the past four decades (Johnston et al. 1995).

Recent Physical Changes in the Mississippi River Delta

The loss of coastal wetlands has been accelerated by human causes, including inland movement of saltwater via the intracoastal waterway, interception of alongshore sediment transport by jetties and sea walls, weakening of the barrier island profile by oil and gas and access canals, and pollution. The erosion of Louisiana's barrier islands is of critical concern because these islands help ameliorate the effects of hurricanes and tropical storms and prevent saltwater intrusion from destroying freshwater swamps and marshes (Fremling et al. 1989).

Hydrological Regime

Under natural conditions, the Mississippi River would probably have switched its course to the Gulf of Mexico via the Atchafalaya distributary between 1965 and 1975. The river has been prevented from doing so by artificial levees and control structures. The Atchafalaya previously captured the Red River, and in the past 20 years the Atchafalaya delta complex has emerged and is rapidly filling Atchafalaya Bay (Autin et al. 1991). Natural diversion of Mississippi River flow to the Atchafalaya has been imminent because the Atchafalaya is both steeper than the Mississippi (3:1 ratio in bed slope) and shorter (225 kilometers to the Gulf of Mexico from the Red River entrance versus 480 kilometers for the Mississippi). The Atchafalaya now drains about 30% of the combined flows of the Mississippi and Red rivers to the Gulf of Mexico (Fig. 3).

If the Mississippi's flow switched to the Atchafalaya, the supply of fresh water to the cities of Baton Rouge and New Orleans could be reduced, and river transportation would be curtailed during periods of low flow. Moreover, flood-control and navigation structures could be lost (Lower Mississippi Region Comprehensive Study Coordinating Committee 1974; Keown et al. 1981; Fremling et al. 1989). In addition, increased flows in the Atchafalaya River could be detrimental to the Atchafalaya basin, North America's largest bottomland hardwood swamp.

Delivery and Deposition of Sediment

Human influences on sediment transport in the Mississippi River system have significantly affected the process of delta formation. The sediment load of the Mississippi River has decreased markedly in the last half-century because of sediment storage in reservoirs constructed on the Missouri River in the 1950's and 1960's and because of other human modifications and influences (Keown et al. 1981, 1986; Fremling 1987; Kesel 1989; Meade et al. 1990). About one-fourth of the suspended sediment load of the Mississippi River is diverted to the Atchafalaya River (Keown et al. 1986). In addition, the input of sediment to shallow-water deltas has been curtailed by the closing of distributary channels; for example, the La Fourche River in 1904. Only the delta of the Atchafalaya River is now growing; all other deltas are degrading because of insufficient sediment input (Penland and Boyd 1985). Additional sediment has been lost to the depths of the Gulf of Mexico by directing flow beyond the Continental Shelf via the Lower Mississippi River passes.

Glacial Eustatic Changes and Subsidence

Mean sea levels are rising as much as 1.2 to 4.3 centimeters per year along the Mississippi

Deltaic Plain, apparently increasing the rate of landward migration of the shoreline into the delta complexes (Penland and Boyd 1985). About 20% of the rise in sea level may be attributed to eustatic processes, such as melting of polar ice. The remaining 80% of the sea-level change could be caused by subsidence (localized sinking of the Earth's crust), partly due to extraction of water, oil, and natural gas.

The entire Louisiana delta, with the possible exception of some natural levees, has subsided since it was formed (Autin et al. 1991). Estimated annual rates of subsidence in the deltaic plain range from about 1 millimeter to more than 15 millimeters (Trahan 1986). The average elevation of the Mississippi Deltaic Plain is less than 10 meters at its northern limit and is near sea level in much of the southern part.

Biological Responses

The Lower Mississippi River and Atchafalaya River estuarine environments have been important production areas for marine fishes and invertebrates. Commercial landings in Louisiana, produced largely in these estuaries, recently accounted for 30% of the U.S. harvest (U.S. Department of Commerce 1986).

Many saltwater fishes and crustaceans harvested in Louisiana's commercial and sport fisheries depend on coastal wetlands during part or all of their life cycle (Herke and Rogers 1989). Adults of many such species spawn in the Gulf of Mexico, and their young migrate to the coastal wetlands, which provide nursery habitat for their early life stages. After a few weeks or months, the juveniles or subadults migrate back to the gulf, where the survivors eventually spawn. Examples of important species that annually complete this cycle are brown shrimp, white shrimp, gulf menhaden, and Atlantic croaker. Other species, such as the red drum and spotted seatrout, make similar migrations but may take longer to complete the cycle.

Decreased sedimentation in the delta area is causing the loss of nursery habitats and preventing the creation of new ones. In addition, the recent use of levees and water-control structures in attempts to slow the loss of coastal wetlands, to improve habitat, and to reduce saltwater intrusion has also created migration barriers for many fishes and crustaceans (Herke et al. 1992; Rogers et al. 1994).

Riverine and coastal wetlands in the Mississippi River delta also support large numbers of wintering waterfowl (Chabreck et al. 1989). More than two-thirds of the entire Mississippi Flyway waterfowl population winter in the coastal wetlands of Louisiana (Bellrose 1980). These wetlands support more than half of the continental mottled duck populations and 38% of wintering canvasback populations. The Delacroix marshes east of the Mississippi River and south of the Mississippi River gulf outlet were once considered to be southeastern Louisiana's most productive waterfowl marsh habitats. Their productivity has declined, however, because of land subsidence, hurricane damage, and increased salinity and associated vegetational changes following construction of the Mississippi River gulf outlet (Chabreck et al. 1989).

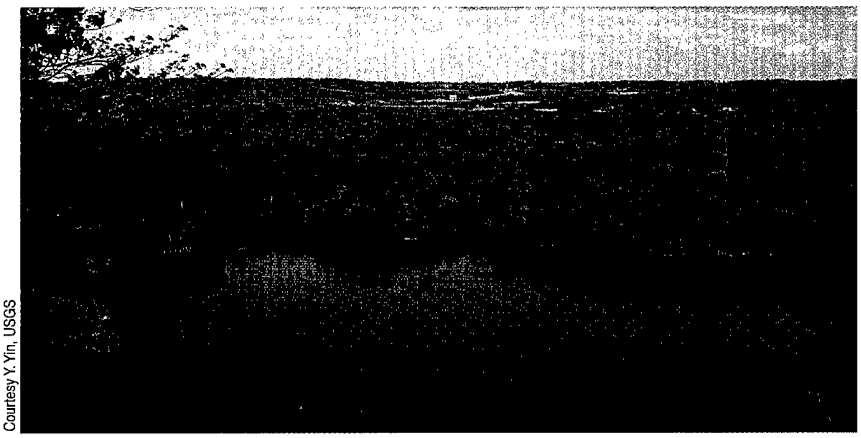
Status and Trends of Plants and Animals

We examined the recent status and temporal trends in the abundances of several key groups of organisms in the Mississippi River. Our analysis included an ecologically diverse array of organisms representative of many trophic levels in the ecosystem, but it was neither spatially nor taxonomically comprehensive. The extent or abundance of many key native biotic communities and organisms has decreased along substantial reaches of the river in recent years or decades; these communities include floodplain forests, submersed plants, pearlymussels, fingernailclams and other bottom-dwelling invertebrates, certain fishes, migratory waterfowl, colonial waterbirds, songbirds, and mink. Abundances of certain nonindigenous plants and animals have increased recently.

Floodplain Forest

Historical Decline

Floodplain forests in the Upper Mississippi River valley (Fig. 4) are now confined to a riparian zone a few kilometers wide at most. By 1989 the proportion of the Upper Mississippi River valley covered by forest had decreased spatially from upstream to downstream as follows: 18.9% between Minneapolis, Minnesota,



Courtesy Y. Yin, USGS

Fig. 4. Floodplain forest in Navigation Pool 13 (near Bellevue, Iowa) on the Upper Mississippi River.

and Bellevue, Iowa; 13.5% between Bellevue and Alton, Illinois; and 7.3% downstream from Alton. In many reaches, especially downstream from Bettendorf, Iowa, most of the remaining floodplain forest occurs on islands.

Agricultural and urban developments have been leading causes of floodplain forest loss along the Upper Mississippi River (Fig. 5). By 1929 farmland and urban areas covered 22% of the floodplain, and forest had declined to 29% of its former extent (Peck and Smart 1986). In 1989 forests covered 1,233 square kilometers (14.3%) of the Upper Mississippi River valley (Laustrup and Lowenberg 1994). The loss of floodplain forests in the Upper Mississippi River valley, although considerable, has been less than that in many other large North American floodplain rivers, such as the Missouri, the Illinois, the Ohio, and the Lower Mississippi. This lower level of loss is attributed to acquisitions of land for navigation pools and national wildlife and fish refuges, which placed more than 800 square kilometers of the Upper Mississippi River valley into public trust.

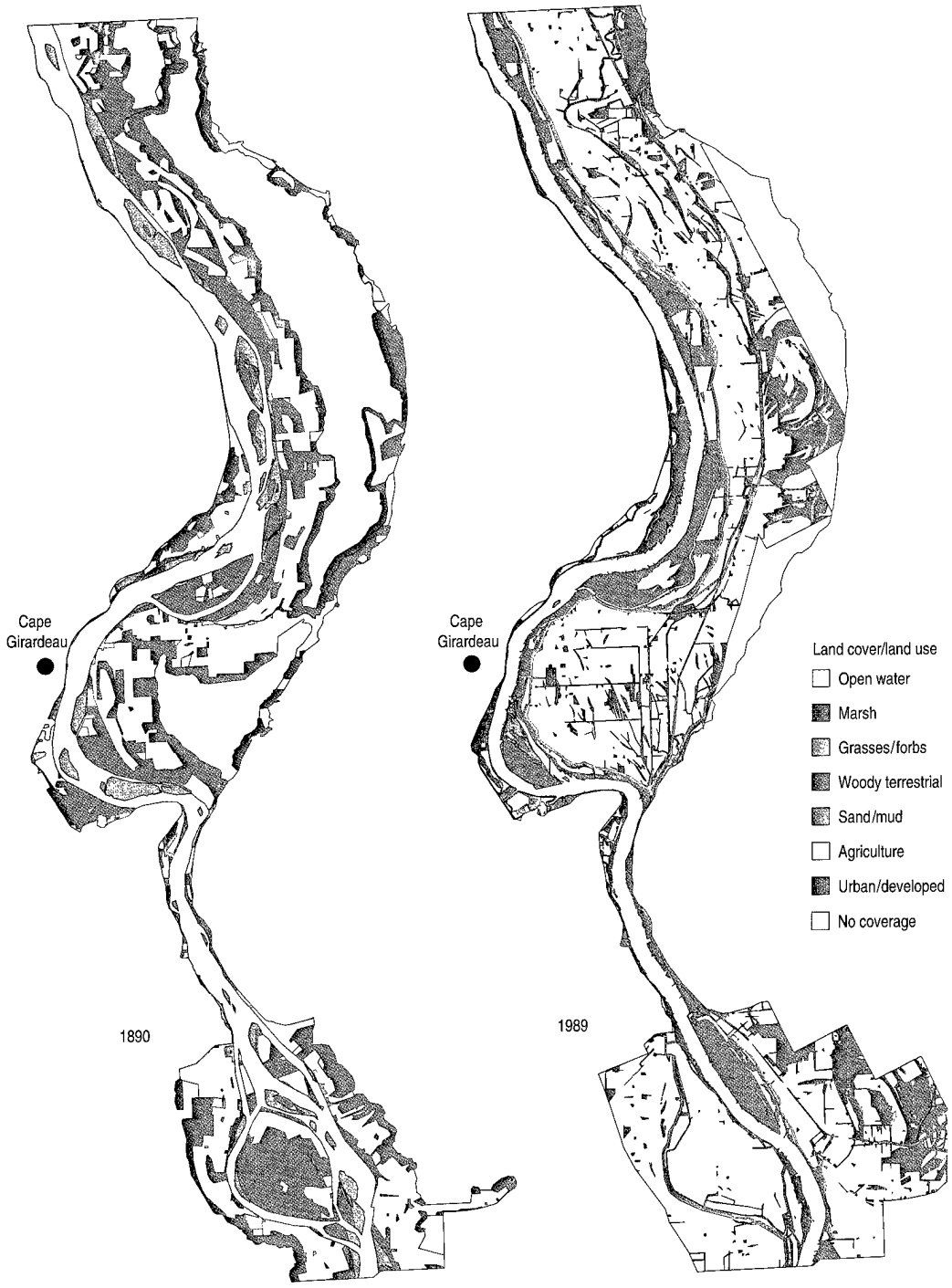


Fig. 5. Comparison of floodplain landscapes in 1890 with 1989 in an 80-kilometer reach of the Mississippi River near Cape Girardeau, Missouri.

Dominant Tree Species

Flooding, erosion, and sedimentation are powerful natural processes that shape floodplain landscapes and affect succession and species composition of floodplain forests (Shelford 1954; Wistendahl 1958; Bedinger 1978; Hupp and Osterkamp 1985). However, these hydrological and geomorphic processes have been constrained for several decades by navigation and flood-protection structures in the Upper Mississippi River.

Individual forest stands in the Upper Mississippi River floodplain can be dominated by any or a few of several species, including (but not limited to) black willow, eastern cottonwood, sycamore, boxelder, silver maple, river birch, green ash, American elm, hackberry, pin oak, bur oak, and swamp white oak. Silver maple is the predominant species in all reaches. In 1993 silver maple was the dominant species in 23% to 49% of the forest stands surveyed at Pools 4, 8, 13, 17, 22, 26, and in an 80-kilometer unimpounded reach about 50 kilometers upstream from the mouth of the Ohio River (Table 1); the mean diameter of trees ranged from 28 to 32 centimeters at breast height, and their mean density varied from 301 to 512 stems per hectare.

The composition of dominant tree species in floodplain forests of the Upper Mississippi River has changed considerably in the last 200 years. American elm declined markedly during the 1900's because of Dutch elm disease. Eastern cottonwood, green ash, and oaks (mainly pin, swamp white, and bur oaks) have become less abundant, compared with silver maple. In the floodplain forest between Minneapolis and St. Paul, for example, George (1924) outlined a successional sequence involving a pioneering cottonwood–willow community, a transitional cottonwood–silver maple community, and a mature community of silver maple, elm, and ash. During early European settlement, the floodplain forests at the tri-state border of Iowa, Minnesota, and Wisconsin were codominated by green ash and silver maple (Moore 1988). Floodplain forests at the confluence of the Mississippi and Illinois rivers, codominated by hackberry, elm, pecan, willows, and eastern cottonwood during early European settlement, are now dominated by silver maple (Nelson et al. 1994). Similarly, floodplain forests along an 80-kilometer unimpounded reach of the Upper Mississippi (starting 21 kilometers upstream from the mouth of the Ohio River) were dominated by eastern cottonwood and sycamore during early settlement times but are now dominated by silver maple and willow (Yin and Nelson 1995). The amount of floodplain forest in pioneering and transitional successional stages has decreased greatly, and much of the present floodplain forest in the Upper Mississippi River valley is mature.

Table 1. Dominant tree species in floodplain forests in the Upper Mississippi River valley at seven river reaches, 1993. Trees were defined as woody stems 10 centimeters or greater in diameter (Y. Yin, U.S. Geological Survey, Environmental Management Technical Center, Onalaska, Wisconsin; and C. E. Korschgen, U.S Geological Survey, Upper Mississippi Science Center, La Crosse, Wisconsin, unpublished data).

	No. 1 dominant		No. 2 dominant				
River reach	Species	Stands dominated (%)	Species	Stands dominated (%)	Mean diameter (centimeters)	Mean density (stems/hectare)	Mean basal area (square meters/hectare)
Pool 4	Silver maple	49	Green ash	16	30	485	41
Pool 8	Silver maple	36	Green ash	15	32	470	45
Pool 13	Silver maple	38	American elm	23	29	483	38
Pool 17	Silver maple	36	American elm	18	28	376	29
Pool 22	Silver maple	35	American elm	19	30	427	39
Pool 26	Silver maple	23	American elm	16	28	512	36
Unimpounded (river miles 30 – 80)	Silver maple	26	Black willow	22	30	301	27

Floods and Forests

Extreme flooding during a single growing season can severely disturb floodplain forests. Such disturbance through flooding is illustrated by the effects of the Flood of 1993, a year when unusually heavy, persistent rainfall caused extreme flooding that lasted from early spring through much of the growing season along a significant portion of the Upper Mississippi River (Parrett et al. 1993; Wahl et al. 1993).

The Flood of 1993 caused substantial tree mortality in the floodplain forests, particularly in the lower reaches of the Upper Mississippi River (Yin et al. 1994), where the flood persisted the longest (Fig. 6). Mortality was positively correlated with flood amplitude and duration, and negatively correlated with tree size. More trees were killed in areas where the flood was most intense and lasted the longest. Smaller

Courtesy Y. Yin, USGS

Fig. 6. A floodplain forest community near St. Louis, Missouri, showing the effects of high tree mortality caused by the Flood of 1993.

trees were most likely to have been killed by flooding. Overall tree death rates ranged from 1% to 4% in Pools 4, 8, and 13, and from 18% to 37% in Pools 17, 22, 26, and in the open river. For saplings, overall mortality rates were higher, ranging from 2% to 9% in Pools 4, 8, and 13 and from 48% to 80% in Pools 17, 22, 26, and in the open river reach between St. Louis, Missouri, and Cairo, Illinois (Yin et al. 1994).

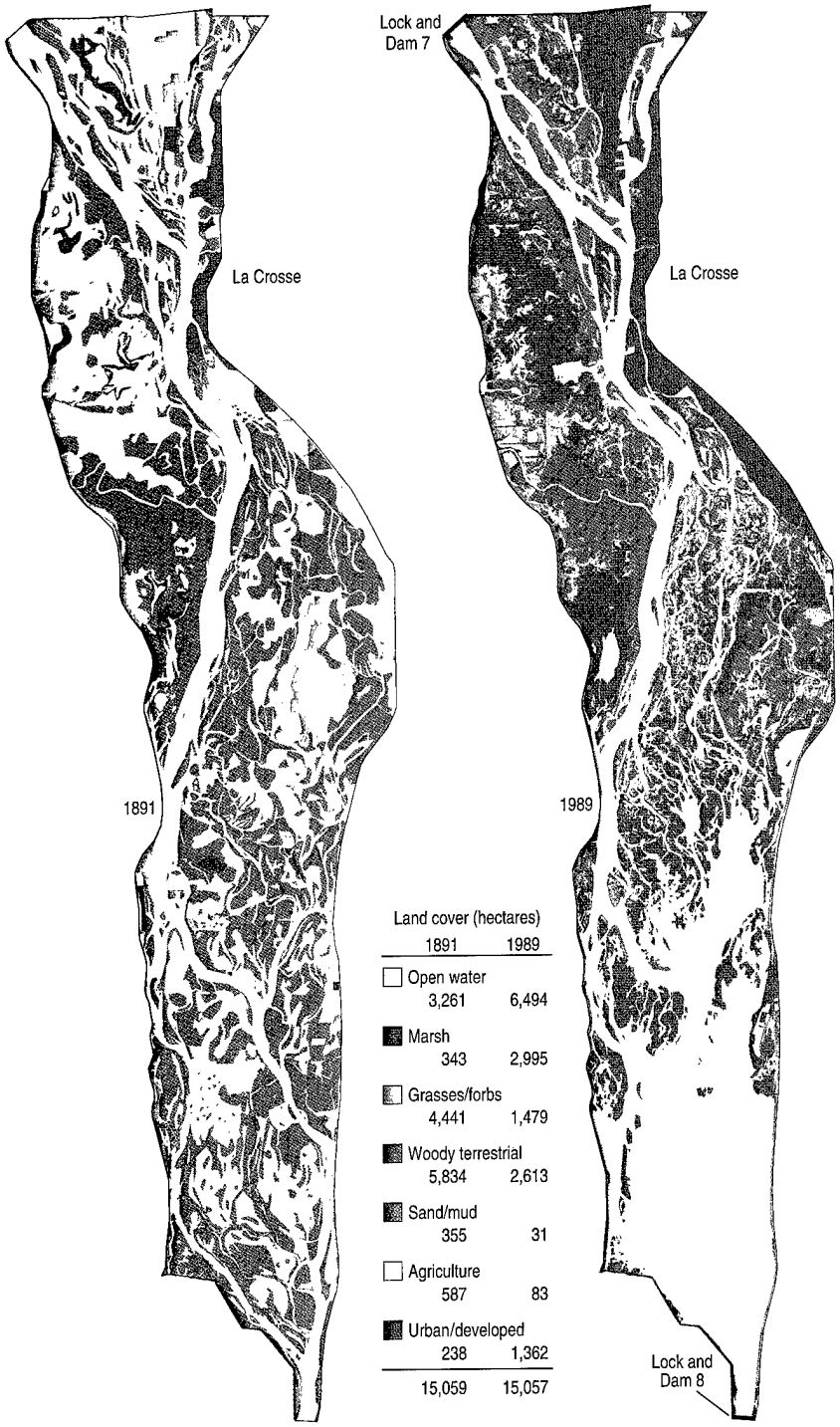


Fig. 7. Changes in land cover over a 98-year period in Pool 8 of the Upper Mississippi River (near La Crosse, Wisconsin). Numbers in the two columns are not equal because of rounding.

The mortality of trees and saplings also varied greatly among species (Yin et al. 1994). The least flood-tolerant trees were hackberry, Kentucky coffeetree, sugarberry, river birch, and white mulberry. Pin oak, silver maple, American elm, and slippery elm were moderately tolerant, and sycamore, hawthorne, green ash, black willow, swamp white oak, and eastern cottonwood were most tolerant. The effects of the Flood of 1993 on floodplain forests along the Upper Mississippi River are expected to persist for decades (Yin et al. 1994).

Aquatic Vegetation

Effects of Impoundment

Emergent and submersed aquatic plants were present but not abundant in the Upper Mississippi River before the locks and dams contructed during the 1930's flooded thousands of hectares of former agricultural areas, lowland hardwood forests, and shallow marshes (Fig. 7). The creation of navigation pools abruptly altered the hydrology of the river; similarly, the diversity, abundance, and distribution of aquatic plant species changed markedly in the decades after impoundment (Peck and Smart 1986). The downstream reaches of the newly created pools provided stable habitat for aquatic plant species. In midpool regions, conditions after impoundment were also favorable to marsh vegetation (Olson and Meyer 1976). Upstream reaches, in contrast, remained similar to their preimpoundment conditions.

Extensive, dense beds of water smartweed developed in the year after impoundment and remained productive for about 5 years (Green 1947). Thereafter, remnant water smartweed was sterile and reproduced only vegetatively. Eventually, water smartweed was replaced by various species of pondweeds, mostly long-leaf pondweed and sago pondweed.

The abundance of submersed plants changed notably after drawdowns of water in several pools during the winters of the early 1940's. Pool 8, for example, was drained from 1 January to 15 February 1944, and from 10 January to 15 March 1945 (U.S. Army Corps of Engineers, St. Paul District, St. Paul, Minnesota, unpublished records). Although Congress ended this practice by the passage of an Anti-Drawdown Law in 1948, the lower water levels apparently stimulated the germination of seeds (Green et al. 1964). The most common submersed plants to become established during this period were long-leaf pondweed, sago pondweed, narrow-leaf pondweed, flatstem pondweed, curly leaf pondweed, coontail, elodea, water star-grass, and wildcelery. Of these, long-leaf pondweed was most

abundant and most widely distributed, occurring in habitats ranging from shallow water to deep, flowing channels (Green 1947).

Wildcelery, which produces a vegetative tuber important as food for certain migratory waterfowl, became the dominant submersed plant around 1960 in much of the 675-kilometer reach of the river between Pools 4 and 19. Minor et al. (1977), who delineated vegetative cover types for Pools 1–12 in the 1970's, found that the aquatic cover class containing wildcelery occupied the greatest area. No stands of water smartweed were identified by Minor et al. (1977), indicating a marked change in species composition since the 1940's. In lower Pool 8, wildcelery contributed nearly 50% of the relative biomass of submersed plant species in 1975 (Sefton 1976); most of the remaining 50% of biomass was collectively contributed by coontail, long-leaf pondweed, water star-grass, sago pondweed, and elodea.

Until the late 1980's, a submersed plant community dominated by wildcelery covered half of Lake Onalaska in Pool 7. Wildcelery covered more than 650 hectares of lower Pool 8 by 1975, and more than 1,275 hectares of Lake Onalaska (Pool 7) by 1982 (Fig. 8). The wildcelery beds were maintained by production of overwintering buds that emerged each spring. By early summer, wildcelery beds were well established and so dense that they significantly affected the hydrology and water quality of the lake. The perimeters of the beds functioned as a sediment screen, making the water inside the beds normally quite clear. Submersed plants grew in all areas of the lake where water was less than 2 meters deep (C. E. Korschgen, U.S. Geological Survey, Upper Mississippi Science Center, La Crosse, Wisconsin, unpublished data). Several other submersed plants were common in these beds, including water star-grass, sago pondweed, Richardson pondweed, narrow-leaf pondweed, flat-stem pondweed, curly pondweed, and Eurasian watermilfoil.

Recent Declines and Status

The abundance of many submersed plants, including wildcelery, declined markedly in much of the Upper Mississippi River in the late 1980's. Information from surveys supported by LandSat photography of Pools 5, 7, 8, 9, 11, and 19 shows that the abundance of wildcelery and other submersed aquatic plants declined greatly between 1987 and 1989 (Fig. 9) and continued to decline through 1994 (Fig. 10) (R. V. Anderson, Western Illinois University, Macomb, Illinois, personal communication; Korschgen, unpublished data; J. Lyons, U.S. Fish and Wildlife Service, McGregor, Iowa, personal communication; E. Nelson, U.S. Fish and Wildlife Service, Winona, Minnesota, unpublished data; W. Thrune, U.S. Fish and Wildlife Service, La Crosse, Wisconsin, personal communication). This decline coincided with the severe midwestern drought of 1987–1989, which affected water quality in the Upper Mississippi River.

In Lake Onalaska (Pool 7), the abundance of wildcelery changed little during 1980–1984 but declined greatly after the extremely dry, hot summer of 1988 (Fig. 10). More than 1,200 hectares of submersed vegetation, mainly wildcelery, disappeared in Lake Onalaska during 1988 and 1989 after the plants failed to produce winter buds during the late summer and fall of 1988 (Korschgen, unpublished data).

Nearly 500 hectares of submersed vegetation disappeared in the lower half of Pool 19, where plant beds dominated by wildcelery, water star-grass, sago pondweed, and coontail had generally been expanding since the 1960's (Anderson, personal communication). In early September 1990, small patches of Eurasian watermilfoil were the only submersed vegetation found in the lower half of Pool 19 (S. Rogers, U.S. Geological Survey, Onalaska, Wisconsin, unpublished data).

Fischer and Claflin (1995) compared the biomass and occurrence of aquatic plants in Pool 8 in 1975 with 1991. Overall biomass and frequency of occurrence of aquatic plants were lower in 1991 than in 1975. According to their study, declines in both frequency of occurrence and biomass were greater for submersed plants than for emergent plants. They discovered declines within several habitats and species, notably wildcelery, in the shallow open-water areas. Many other submersed aquatic plants also declined.

Much of the area formerly occupied by wildcelery remains unvegetated, although Eurasian watermilfoil, a nuisance nonindigenous species, now occupies some of the shallower sites. The abundance of Eurasian watermilfoil has seemingly increased since the mid 1980's. In Pools 8 and 13, monotypic beds of Eurasian watermilfoil have been found near areas where wildcelery had occurred. In Pools 4–8, 13, and 26, Eurasian watermilfoil is occasionally found near or with other submersed plants, including sago pondweed, wildcelery, and coontail (U.S. Geological Survey, Long Term Resource Monitoring Program, Onalaska, Wisconsin, unpublished data; Rogers, personal observation).

The Flood of 1993 also affected the river's submersed aquatic plant communities. During the 1993 growing season, most species of submersed plants decreased in frequency of occurrence at monitoring sites in Pools 4, 8, 13, and 26 (Spink and Rogers 1997). The decreases

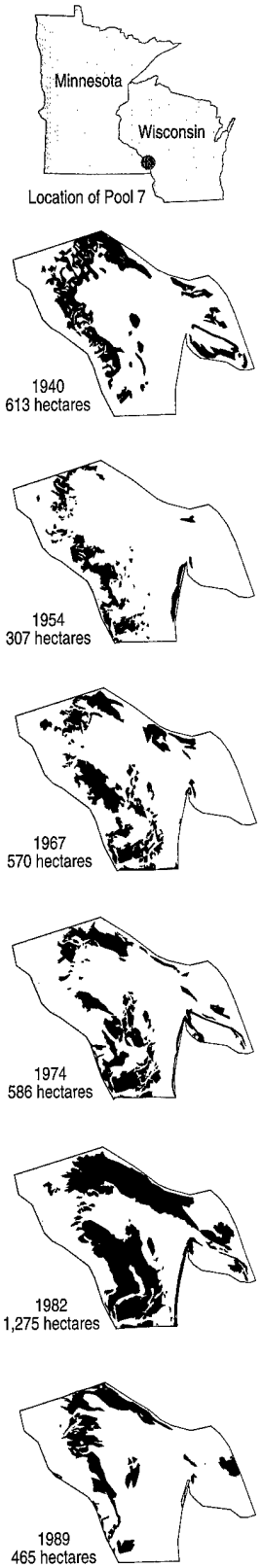


Fig. 8. Spatial distribution of submersed aquatic vegetation (dominated by wildcelery) in Pool 7 (Lake Onalaska) of the Upper Mississippi River in 1940, 1954, 1967, 1974, 1982, and 1989.

were greatest in Pools 13 and 26, which had more severe flooding than Pools 4 and 8. In 1994 submersed aquatic plants had recovered to preflood frequencies in Pools 8 and 13, but not in Pool 26, where the duration and magnitude of the flood were greatest. Interestingly, the distribution and abundance of wildcelery in Pools 8 and 13 were greater after the flood year than before the flood (U.S. Geological Survey, Long Term Resource Monitoring Program, unpublished data).

Fig. 9. LandSat image of Pool 7 (Lake Onalaska) of the Upper Mississippi River, showing abundant and widely distributed aquatic plant beds in a) 1987, and greatly reduced abundance and distribution of plant beds in b) 1989. Beds of submersed vegetation appear as dark green areas within the lake.

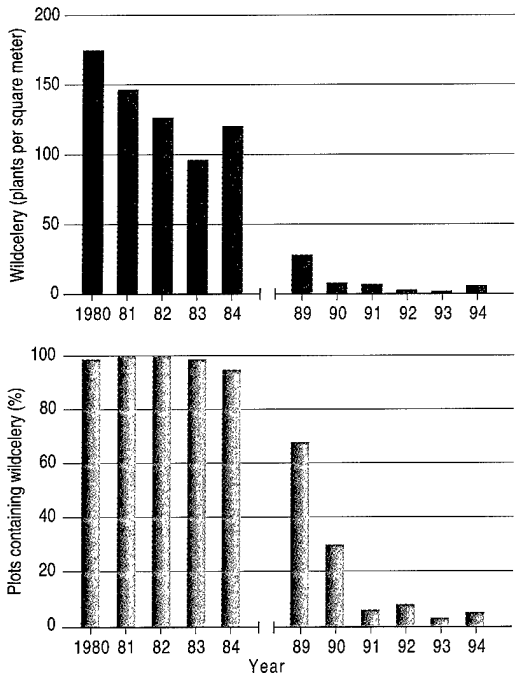


Fig. 10. Abundance of wildcelery, a submersed aquatic plant, in Lake Onalaska (Pool 7) of the Upper Mississippi River, 1980–1994.

Potential Causes of Declines in Aquatic Vegetation

As stated previously, the recent decline in submersed plants in the Upper Mississippi River coincided with the severe drought of 1987–1989. Although information on drought-related conditions in the river is limited, a number of potential causes have been identified.

Blooms of planktonic or attached algae during the drought, particularly in the summer of 1988, may have severely limited the depth to which sufficient light—the source of energy for photosynthesis—penetrated the water column to support the growth of rooted aquatic plants. High concentrations of nutrients in water (retained in backwaters because of extremely low flows) and abnormally high solar radiation during the drought may have stimulated the production of epiphytes or planktonic algae, thereby reducing light penetration in the water column (J. Lennartson, U.S. Fish and Wildlife Service, Winona, Minnesota, and J. Wetzel, Wisconsin Department of Natural Resources, La Crosse; Korschgen, memorandum dated 3 October 1989). Concentrations of orthophosphorus at several main-channel sites were high during the summer of 1988, possibly contributing to the prolific bloom of the blue-green alga *Aphanizomenon*; the bloom extended from Lake Pepin (Pool 4) to Pool 11 (J. Sullivan, Wisconsin Department of Natural Resources, La Crosse, personal communication; see Fig. 2 for location).

This potential mechanism of submersed plant decline is similar to the model devised by Phillips et al. (1978), which illustrates the relationship between nutrient loading, increasing algal growth, and declines of rooted aquatic plants. In some systems, biologically produced turbidity caused by nutrient enrichment has led to the disappearance of rooted plants (Phillips et al. 1978; Hough et al. 1989). Clearly, the reestablishment and recovery of aquatic vegetation have been hindered by limited light availability in the turbid backwaters (Kimber et al. 1995; Owens and Crumpton 1995).

Conversely, there is evidence that submersed aquatic plants may benefit from conditions caused by moderate drought. During summer 1985, for example, water clarity markedly increased in Pool 8 in apparent response to reduced runoff caused by a summer drought, and the mean depth of the light zone during that growing season increased to 1.3 meters. That

summer, the distribution of submersed plants, including wildcelery and Eurasian watermilfoil, increased in Pool 8 in apparent response to the increased availability of light (Korschgen, unpublished data). Similar increases in submersed aquatic plants occurred in 1977 in Pool 19, coincident with a period of increased water clarity, low flow, and stable water levels during spring and summer (Sparks 1980; Steffeck et al. 1985).

Rogers et al. (1995) hypothesized that the availability of sediment nutrients may have been reduced by low flows during the drought. Input of sediments may provide nutrients important to the maintenance of submersed plant beds (Barko et al. 1991). The possible depletion of sediment nutrients, particularly nitrogen, during the low flows of 1987, 1988, and 1989, in combination with above-normal water temperatures, may have reduced plant growth and reproduction in some areas of the river.

The reestablishment of submersed aquatic plants in the river may be inhibited by grazing fish, particularly common carp, whose abundance has increased significantly in Pools 8 and 13 since 1991 (S. Gutreuter, U.S. Geological Survey, Onalaska, Wisconsin, unpublished data). Common carp often forage in beds of submersed plants (Lubinski et al. 1986), where they resuspend bottom sediments, increase turbidity, and uproot some submersed plants, particularly species with shallow root systems. Peitzmeier-Romano et al. (1992) found that fish grazing on unprotected wildcelery plants reduced leaf growth and affected tuber production in backwaters of the Illinois River. Grazing apparently foiled attempts to grow wildcelery in a backwater lake of the Upper Mississippi River, where much of the wildcelery planted into unprotected, suspended buckets was damaged by grazers (Korschgen, unpublished data).

Purple Loosestrife

Purple loosestrife, a nonindigenous wetland plant introduced to North America from Europe in the early 1800's, was probably introduced into the Upper Mississippi River basin in the early 1900's (Thompson et al. 1987). This perennial plant forms dense monotypic stands in wetlands, replacing many native wetland plants (Thompson et al. 1987; Edsall et al. 1995). Purple loosestrife has no food value for wildlife, and its replacement of native emergent plants such as cattail makes wetlands less suitable as wildlife habitat (Thompson et al. 1987; Malecki 1995).

By 1985 purple loosestrife had become established throughout much of the Upper Mississippi River basin (Thompson et al. 1987). In the early 1980's, this nuisance plant had become notably abundant on the Upper Mississippi River National Wildlife and Fish Refuge, and it had infested wetlands of Pools 4 through 14 by the late 1980's (Nelson, personal communication).

Refuge managers have been combating this nonindigenous plant since the mid 1980's with hand-weeding and herbicide application on localized stands. These traditional control methods have met with little success, probably because the plant's seed reservoir is so extensive (Malecki 1995). Biological-control methods are now being attempted through the release of natural enemies such as root-boring and leaf-eating insects (Skinner et al. 1994). Now that we recognize that eradication of purple loosestrife is no longer feasible, our goal is to achieve modest control of the plant (Malecki 1995).

Bottom-Dwelling Invertebrates

Bottom-dwelling invertebrate organisms, collectively termed *benthic invertebrates*, are ecologically important in riverine ecosystems. The Upper Mississippi River has supported a diversity of benthic invertebrates. In 1977, for example, Trapp (1979) found 54 taxonomic groups of benthic invertebrates in Lake Pepin (Pool 4), where flies and segmented worms made up 96% of the total. Elstad (1986), who studied Pool 7 (Lake Onalaska) and Pool 8 in 1976–1977, found at least 144 taxa of benthic invertebrates; eight major groups (segmented worms, leeches, isopods, amphipods, moths, flies, snails, and bivalve mollusks) accounted for more than 90% of the total number sampled.

In 1992–1994, benthic invertebrates were sampled in Pools 4, 8, 13, and 26, and in an open-river reach near Cape Girardeau, Missouri. Initial data from this sampling are available for hexagenia mayflies and fingernail-clams, both of which inhabit soft sediments and are important in the diet of certain fish and waterfowl (Carlander et al. 1967; Jude 1973; Thompson 1973). The 3-year period encompassed by these monitoring data is too short to assess temporal trends; however, the abundances of fingernailclams and hexagenia mayflies varied considerably among the five reaches sampled (Table 2). Densities of both organisms, but particularly fingernailclams, were consistently highest in Pool 13 and lowest in Pool 26 and in the open reach of river. Densities of both mayflies and fingernailclams also varied among habitat types; areas classified as contiguous backwater, impounded, and tributary delta lake had much higher mean densities than main-channel border and side-channel habitats (Table 3).

In the Lower Mississippi River, the distribution of benthic invertebrates is strongly influenced by current velocity and substrate composition, physical variables that vary spatially and seasonally in many habitat types (Beckett et al. 1983; Beckett and Pennington 1986). The shifting, coarse sand and gravel substrates of main and secondary channel habitats in the Lower Mississippi River support few large invertebrates, which are termed *macroinvertebrates* (Wright 1982; Beckett et al. 1983; Beckett and Pennington 1986). Sand substrate in channel habitat, however, contains a recently discovered, unique assemblage of very small invertebrates consisting of midges, worms, and microturbellarians (Baker et al. 1991). Natural clay banks of the Lower Mississippi River contain abundant numbers of burrowing mayflies (*Tortopus incertus* and *Pentagenia vittigera*) and hydropsychid caddisflies (Beckett et al. 1983; Beckett and Pennington 1986). Abandoned channel habitats, characterized by slack currents and silty substrates, support high densities of invertebrates, including phantom midges, segmented worms, and fingernailclams (Mathis et al. 1981; Beckett et al. 1983; Beckett and Pennington 1986).

Table 2. Mean densities of hexagenia mayflies and fingernailclams, weighted by strata (aquatic area), at reaches being monitored by the U.S. Geological Survey's Long Term Resource Monitoring Program. The open river reach is near Cape Girardeau, Missouri. ND = no data available.

Organism / Year	Density of organism (number/square meter)				
	Pool 4	Pool 8	Pool 13	Pool 26	Open river
Mayfly					
1992	57	85	124	29	21
1993	125	111	154	10	ND
1994	199	86	208	21	20
Fingernailclam					
1992	47	22	90	13	4
1993	75	22	2,463	1	ND
1994	85	13	583	4	0

Hard substrates provided by revetments, stone dikes, and articulated concrete mattresses (interconnected concrete blocks used to control bank erosion) support significant numbers of invertebrates in the Lower Mississippi River (Mathis et al. 1982; Beckett and Pennington 1986; Way et al. 1995). The invertebrate communities inhabiting hard substrates are commonly dominated numerically by a few species that are tolerant of moderate to high current velocity (Mathis et al. 1982; Beckett and Pennington 1986; Way et al. 1995). Way et al. (1995), for example, found that three species—a caddisfly, a midge, and an amphipod—represented more than 98% of the invertebrates on articulated concrete mattresses after 3 months of colonization.

Table 3. Densities of hexagenia mayflies and fingernailclams (numbers per square meter) in five habitats on the Upper Mississippi River, sampled as part of the U.S. Geological Survey's Long Term Resource Monitoring Program in Pools 4, 8, 13, and 26, and in the open river near Cape Girardeau, Missouri.

Habitat	Mayfly		Fingernailclam	
	Mean density	Standard error	Mean density	Standard error
Contiguous backwater	105	9	42	5
Impounded	127	11	975	181
Tributary delta lake	158	27	93	9
Main-channel border	16	3	18	5
Side channel	46	6	28	5

Rocky substrates associated with dike structures on the Lower Mississippi River support higher total densities of aquatic invertebrates than abandoned channels, natural river banks, dike fields, temporary secondary channels, sandbars, revetted banks, main channel, and permanent secondary channels (habitats listed in order of decreasing invertebrate density; Mathis et al. 1981, 1982; Wright 1982). Aquatic insects were the most abundant invertebrates in rocky substrates of dikes, accounting for more than 97% of the organisms sampled; the net-spinning caddisfly represented 60% of the total number of invertebrates sampled, two species of tube-building midges represented 24%, another species of net-spinning caddisfly 8.4%, and an isopod 2% (Mathis et al. 1982). Dike fields also contain soft mud substrates that support significant densities of burrowing hexagenia mayflies (Beckett and Pennington 1986).

Recovery from Pollution Caused by Sewage

For decades, benthic invertebrates were absent or scarce in reaches where water quality was degraded by pollution caused by sewage. The 100-kilometer reach of river downstream from the Minneapolis–St. Paul metropolitan area, for example, suffered severe oxygen depletion caused by sewage discharged into the river (Wiebe 1927; Fremling 1964, 1989), and pollution-sensitive organisms, such as burrowing hexagenia mayflies, were absent or scarce in Pools 2, 3, and 4. Burrowing mayflies began recolonizing riverine reaches downstream from the metropolitan area in the early 1980's, when dissolved-oxygen concentrations increased in response to improved wastewater treatment (Johnson and Aasen 1989; Fremling and Johnson 1990).

Recent Declines

Populations of fingernailclams have declined in certain reaches during recent decades. Wilson et al. (1995) examined trends in densities of the fingernailclam from 1973 to 1992 by compiling existing data and by sampling. Significant declines of fingernailclams were evident in five of eight pools examined (declines in Pools 2, 5, 7, 9, and 19) along a 700-kilometer reach of river from Hastings, Minnesota, to Keokuk, Iowa. Densities in Pool 19, which had the longest historical record on fingernailclams, averaged 30,000 per square meter in 1985 and decreased to zero in 1990 (Fig. 11). The declines of fingernailclams occurred chiefly during low-flow periods associated with drought (Sparks 1980; Wilson et al. 1995).

Fingernailclam population declines do not seem to be directly linked to the periodic depletion of dissolved oxygen that occurs in backwater areas. Although fingernailclams are much

more tolerant of low dissolved oxygen concentrations than are burrowing hexagenia mayflies, they have not readily recolonized the reaches recolonized by hexagenia mayflies (Wilson et al. 1995). The observed declines of fingernailclams, as well as their subsequent slow rate of recolonization, were seemingly caused by the uninhabitability of bottom sediments—perhaps due to the presence of one or more toxic substances. Fingernailclams are sensitive to many toxicants, including un-ionized ammonia (Sparks 1984; Arthur et al. 1987).

Recent studies by the U.S. Geological Survey have shown that surficial sediments add considerable amounts of nitrogen to the reach of the Upper Mississippi where populations of fingernailclams have declined. The production of ammonia by microbial decomposition in the sediments would presumably be increased by the conditions of high temperature and nutrient enrichment associated with low-flow, drought periods. High microbial activity (decomposition), stimulated by high temperature and an abundant supply of organic matter, would greatly increase the concentration of toxic ammonia in the sediments (Frazier et al. 1996), possibly causing episodic toxicity in fine-grained sediments during periods of drought and low flow.

Brewer et al. (1995) compared the abundance, standing crop (biomass per unit area), and community composition of benthic invertebrates in Pool 8 of the Upper Mississippi River near La Crosse, Wisconsin, between midsummer 1975 and midsummer 1990. The taxonomic composition of the communities changed in all four habitats studied; similarity of species composition between 1975 and 1990 was 19% in open-water habitat, 44% in bays, 50% in side channels, and 62% in marshes. Between 1975 and 1990, overall standing crop of the benthos decreased significantly in all four habitat types, and overall abundance decreased in all habitats except bays.

In the Lower Mississippi River, the distribution and abundance of benthic invertebrates have been examined in relation to habitat type and its characteristics. We found no information on temporal trends of invertebrates in the Lower Mississippi River.

Native Pearlymussels

The Upper Mississippi River is one of a few large rivers that still has a substantial pearlymussel fauna. The abundance and species richness of pearlymussels in the Upper Mississippi exceed that of many other midsize to large North American rivers (Miller et al. 1987, 1993), although the species richness of native pearlymussels in the Mississippi River has clearly declined since the early 1900's. Thiel (1992) estimated that the number of pearlymussel species had decreased 30% in Pools 4–6 and 26% in Pools 8–10 since the 1920's. Trend analysis of historical data from several mussel surveys (Wiener et al. 1995) showed that overall, the pearlymussel fauna in the Upper Mississippi River drainage has declined from about 50 to 60 species in the early 1920's to about 30 species in the mid-1980's (Fig. 12).

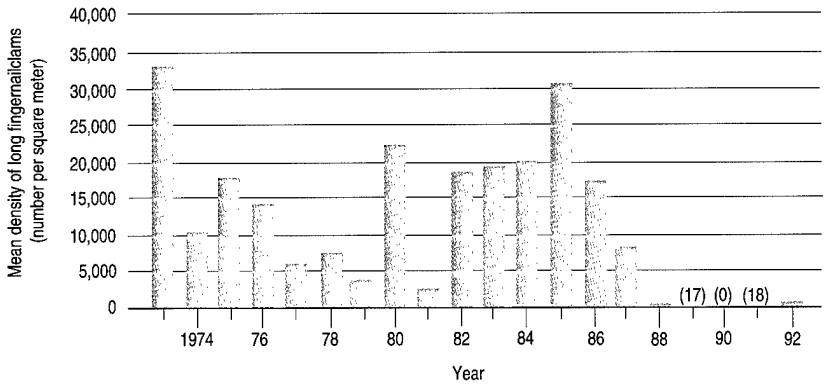


Fig. 11. Mean densities (±1 standard error) of the long fingernailclam in Pool 19 of the Upper Mississippi River during 1973–1992. Mean densities in 1989, 1990, and 1991 were too low to readily appear on the chart and are given in parentheses.

The decline of pearlymussel species richness in the Upper Mississippi River mirrors a broader continental pattern. Almost half of the 292 pearlymussel species in North America are either extinct or at serious risk of extinction (Bogan 1993; Neves 1993; Williams et al. 1993). Several factors are suspected of contributing to declines in North America's native freshwater mussel fauna, including habitat modification and degradation, pollution, overharvest, and commercial and recreational navigation (Williams et al. 1993).

From 1982 to 1986, a notable die-off of pearlymussels occurred in Pools 8 through 25, a 720-kilometer reach of the Upper Mississippi (Blodgett and Sparks 1987; Thiel 1987). Analyses of healthy, moribund, and dead mussels for parasites, disease, and selected contaminants failed to reveal the cause of the die-offs (Thiel 1987). The status of the remaining pearlymussel species varies widely, ranging from abundant to endangered (Wisconsin

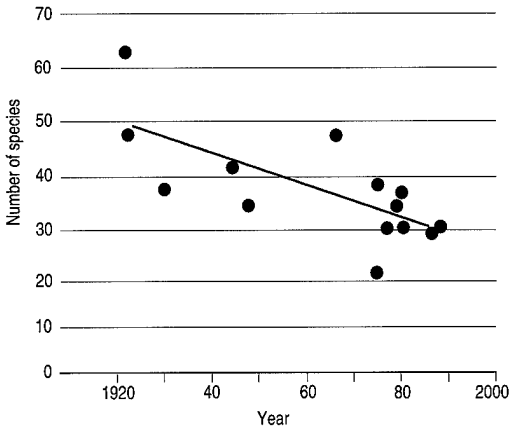


Fig. 12. Species richness of pearlymussels in the Upper Mississippi River drainage has declined substantially. Data compiled from the following sources: Shimek 1921; Grier and Mueller 1922; Ellis 1931a,b; Dawley 1947; Finke 1966; Coon et al. 1977; Fuller 1978, 1979; Mathiak 1979; Perry 1979; Thiel et al. 1979; Ecological Analysts Inc. 1981; Thiel 1981; Duncan and Thiel 1983; Holland-Bartels 1990.

Department of Natural Resources 1985). Three species—the Higgins eye, the fat pocketbook, and the winged mapleleaf—are federally listed as endangered. One of these, the fat pocketbook, may now be locally extirpated in the Upper Mississippi River (Wisconsin Department of Natural Resources 1985). The winged mapleleaf is now restricted to 16 kilometers of the St. Croix River, a tributary of the Upper Mississippi (Mueller 1993).

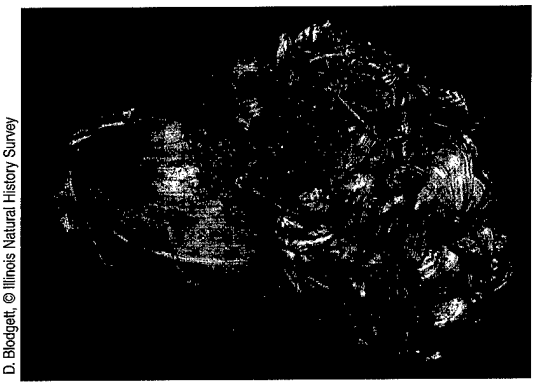
Effects of Zebra Mussels

By 1991 the zebra mussel, a nonindigenous species from eastern Europe, had entered the Upper Mississippi River via the tributary Illinois River (Sparks et al. 1994; Benson and Boydstun 1995). Zebra mussel populations expanded rapidly, and by mid-1993 zebra mussels were found throughout most of the Upper and Lower Mississippi River (Benson and Boydstun 1995). By mid-August 1993, average densities of zebra mussels in the lower Illinois River had increased to more than 50,000 per square meter of river bottom. Subsequent high mortality reduced densities there to about 4,000 per square meter by August 1994.

High densities of zebra mussels can degrade water quality, indirectly harming other organisms. Zebra mussels have caused major depletion of dissolved oxygen in affected reaches of the Seneca River in New York (Effler and Siegfried 1994) and in the Illinois River (Sparks et al. 1994); both rivers had populations exceeding 30,000 mussels per square meter. The concentration of dissolved oxygen in the Illinois River declined to 1.5 milligrams per liter, which is insufficient for the survival of many native aquatic animals.

The zebra mussel can directly harm certain native benthic invertebrates, particularly pearlymussels. Zebra mussels attach to hard surfaces, including the shells of pearlymussels (Fig. 13), by means of a byssal thread. Zebra mussel infestation on pearlymussels may interfere with pearlymussel feeding, reproduction, and movement. In Lakes Erie and St. Clair, pearlymussels suffered as much as a 100% mortality within 1 to 2 years in areas heavily infested with zebra mussels (Nalepa 1994; Schloesser and Nalepa 1994).

Since 1993 most of the native pearlymussels in the Illinois River have been infested with zebra mussels, and mortality of the native mollusks has increased markedly (Whitney et al. 1995). In the Upper Mississippi River, the number of zebra mussels has continued to increase, and the mussels are expected to reach high densities. Artificial substrate samplers deployed in Pool 8 from spring through midautumn, for example, had mean densities of 3.5 zebra mussels per square meter in 1992, 6.1 in 1993, 480 in 1994, and 4,240 in 1995 (W. G. Cope, U.S. Geological Survey, Upper Mississippi Science Center, La Crosse, Wisconsin, unpublished data).



D. Blodgett, © Illinois Natural History Survey

Fig. 13. Pearlymussel encrusted with zebra mussels, a nonindigenous species that recently invaded the Upper Mississippi River via the Illinois River, a tributary.

Pearlymussels in the Upper Mississippi River are being increasingly infested with zebra mussels (Tucker et al. 1993; Tucker 1994). At a site in Pool 26, for example, infestation rates increased from 27% in 1992 to 99.7% in 1993, and the average number of zebra mussels per pearlymussel increased concomitantly from 2 to 37 (Tucker 1994). Ricciardi et al. (1995) estimate that pearlymussel mortality will exceed 90% when the density of zebra mussels reaches 100 attached individuals per pearlymussel or 6,000 zebra mussels per square meter of habitat. Thus, the native pearlymussel fauna in the river could rapidly and severely decline unless methods for protecting pearlymussels from zebra mussels can be developed. Perhaps no other group of freshwater organisms is more seriously threatened with extinction than our native pearlymussels (Neves 1993).

Zebra mussels could also alter the invertebrate communities inhabiting the rock substrates of wing dams on the Mississippi River. Colonization of wing dams by zebra mussels will probably affect certain invertebrate species adversely while benefiting others (Wisenden and Bailey 1995).

Fishes

Distribution of Fishes

The fossil record suggests that the Mississippi River has long provided suitable habitat for many fishes; most present families and many genera of Mississippi River fishes date to the Miocene (5 to 25 million years ago) or earlier (Baker et al. 1991). During the last several million years, the larger rivers of the Mississippi River drainage system have presumably fluctuated between two very different channel patterns (braided and meandering), which provide different types and

abundances of aquatic habitats. Although major changes in climate, including the Pleistocene glaciations, have also occurred, there have been few fish extinctions. Many fishes probably retreated ahead of southward-moving glaciers and repopulated northern reaches of the basin as the glaciers receded (Hynes 1970).

The 195 species of freshwater fishes in the main-stem of the Mississippi and Atchafalaya rivers represent almost one-third of the freshwater fish species in North America (Fremling et al. 1989). An additional 46 or more marine fishes may occur as far upstream as St. Francisville, Louisiana, during low-flow periods when saltwater intrudes into the river. Fremling et al. (1989) estimated that 67 fish species inhabit the Headwaters, 132 species inhabit the Upper Mississippi River, and about 150 species inhabit the Lower Mississippi and Atchafalaya rivers. Baker et al. (1991) estimated that 91 species of freshwater fishes inhabit the Lower Mississippi, with 30 or more other species present intermittently. Reviews have summarized the recent distribution and status of fishes in the Headwaters reach (Fremling et al. 1989), the Upper Mississippi River (Rasmussen 1979; Van Vooren 1983; Fremling et al. 1989; Pitlo et al. 1995), and the Lower Mississippi River (Fremling et al. 1989; Baker et al. 1991).

The fishes in swift-current habitats of the main-stem Lower Mississippi River have not been studied much because of the sampling difficulties posed by the channel's great size, depth, and strong current (Baker et al. 1991). Moreover, the abundance of fishes in swift-current habitats of the main-stem Lower Mississippi has probably been underestimated by traditional sampling methods (Baker et al. 1991).

The distribution of fishes in the Mississippi River has been influenced by natural and human barriers to migration. Until modern times, St. Anthony Falls at Minneapolis prevented the colonization of the Headwaters by 59 species that originally occurred in the Upper Mississippi. In 1963 completion of the locks at St. Anthony Falls provided access for all species previously excluded from the Headwaters above the falls. The dam at Coon Rapids, Minnesota, completed in 1906, is now the principal barrier to fish migration and maintains the distinct assemblage of fishes in the Headwaters upstream. Lock and Dam 19 at Keokuk, Iowa, may have impeded fish migration, particularly of the skipjack herring (Coker 1914, 1930). Work by Holland et al. (1984) supports this view but shows that some species do pass through Lock and Dam 19 and other navigation dams. Heavily polluted zones within the river have also impeded the movement of fishes. In August 1927, for example, organic (sewage) pollution caused about 75 kilometers of river below Minneapolis–St. Paul to lack sufficient oxygen to sustain any fishes. This situation may have persisted seasonally for decades.

Fish Habitats

Most fishes require several different habitats to complete a life cycle. The quantity and quality of certain habitats, however, have diminished in many reaches. In the Upper Mississippi, the navigation pools are aging, and overwintering habitats for fish have declined as sedimentation reduces water depth (McHenry et al. 1984; Bhowmik and Adams 1989; Holland-Bartels 1992; Gent et al. 1995). Recent die-offs of aquatic vegetation have reduced the suitability of many areas as nursery habitats for fishes. In many places, declines of invertebrate prey organisms associated with soft bottom sediments (Brewer et al. 1995; Wilson et al. 1995) and aquatic vegetation (Chilton 1990) have diminished food resources for fishes.

The Upper Mississippi River provides many aquatic habitats, including main channel, tailwater, main-channel border, side channel, navigation pool, floodplain lake or pond, slough, and tributary mouth (Littlejohn et al. 1985; Fremling et al. 1989). These habitats can differ markedly in current velocity, depth, temperature, water quality, bottom substrate, vegetative structure, food resources, and other characteristics.

The main channel has a swift current, coarse-sand or gravel substrate, and deep water. Tailwaters, which extend about 0.8 kilometers below each dam, have well-oxygenated water, rapid currents, and coarse substrates. Walleye, sauger, white bass, freshwater drum, and catfishes concentrate in these tailwaters. Dike fields along the main-channel border provide rocky substrates where walleye, sauger, channel catfish, smallmouth bass, white bass, black crappie, bluegill, redhorse, freshwater drum, and smallmouth buffalo concentrate (Holzer 1980; Pierce 1980; Pitlo 1981). Main-channel borders have multiple substrates, including silt, sand, wing dikes, snags, and riprap. Abundance of fishes in main-channel borders varies with season and river stage. The flow of side channels links them to other habitats during most of the year; these channels are used by many species. Nearshore zones in main-channel borders, side channels, and pools provide important nursery areas for many fish species, especially sunfishes (including bluegill, crappie, and largemouth bass); these same zones are important areas where certain sport-fish species, particularly sunfishes, are caught by anglers.

Pools upstream from dams are lakelike, shallow, and have bottoms composed of fine sediments; structure and hard substrates are limited to stumps, snags, wing dikes, and riprap. Vegetated areas in these navigation pools

provide important spawning and nursery habitats. Many floodplain lakes and ponds are connected to the river only when flow is high. Sloughs, lakelike habitats that receive inflows from the river only when water levels are high, are much warmer than the main channel, may stratify thermally, and provide spawning and rearing habitat for many fishes.

In the northern reaches of the Upper Mississippi River, many fish populations seem limited by a lack of suitable winter habitat. During ice cover, dissolved oxygen is depleted in many shallow backwater lakes, reducing the suitability of these lakes for fishes (Bodensteiner and Lewis 1992; Gent et al. 1995; Knights et al. 1995). Even though flowing areas, such as the main channel and side channels, typically contain sufficient dissolved oxygen in winter for fishes, the high current velocities and cold temperatures (as low as 0°C) of flowing waters are stressful, and often lethal, to many fishes that inhabit the Upper Mississippi River (Sheehan et al. 1990; Bodensteiner and Lewis 1992). Consequently, the distribution of fishes in winter in the northern reaches of the river is strongly influenced by dissolved oxygen, temperature, and current velocity. Knights et al. (1995), in their study of a series of backwater lakes in Pool 5, found that bluegills and black crappies select areas where water temperature exceeds 1°C and the current is undetectable when dissolved oxygen is above 2 milligrams per liter. When dissolved oxygen falls below this level, fish move to areas with higher oxygen concentration and may tolerate water temperatures below 1°C and current velocity of 1 centimeter per second. Fish avoid areas with water temperatures lower than 1°C if the current velocity exceeds 1 centimeter per second (Knights et al. 1995).

In the main-stem Lower Mississippi River, swift-current habitats include the river channel, natural steep banks, revetted banks (covered with protective materials, mostly limestone rock, to prevent erosion), and flowing sandbars (Baker et al. 1991). Channel habitat has deep water, a swift current (1 to 5 meters per second), constantly shifting coarse-sand or gravel substrates, high suspended solids, and low primary productivity. The Lower Mississippi River provides plentiful habitat for fishes that thrive in swiftly flowing water. Few species, however, can tolerate the high current velocities of the upper and middle water column of channel areas for very long (Fremling et al. 1989; Baker et al. 1991). Most fishes probably inhabit areas near the banks (Pennington et al. 1983a) and the channel bottom where the current is slower (Baker et al. 1991).

Dike fields in the Lower Mississippi River often contain many fish species (Pennington et al. 1983b). Constructed of rock and wood pilings, dikes are used to constrain flow to the river's navigation channel. Some dike fields on the Lower Mississippi fill with sand, however, forming terrestrial habitats (Beckett and Pennington 1986).

Several fish species forage in the floodplain of the Lower Mississippi River when it is inundated by high water levels (Baker et al. 1991); these include gars, bowfin, common carp, buffalos, river carpsucker, channel catfish, blue catfish, white bass, crappies, and freshwater drum. Many fishes also use the inundated floodplain for spawning. Densities of larval fishes in the Lower Mississippi River are highest in backwaters, which are important nurseries for fishes and which contain a larval fish assemblage differing from that of the main-stem river (Beckett and Pennington 1986). The Lower Mississippi River floodplain includes many artificial floodplain ponds (borrow pits excavated during the construction of levees), which may also serve as important nursery areas for fishes (Sabo and Kelso 1991; Sabo et al. 1991).

Fish Harvest and Recent Trends

Lakes on the Headwaters reach are readily accessible and fished heavily in summer and winter for walleye, northern pike, muskellunge, basses, and other species (Fremling et al. 1989; MacGregor 1995). In the Upper Mississippi River, the catch of sport fishes has been dominated by bluegill and crappie (Farabee 1979). Other sport fishes, in approximate order of importance, include white bass, freshwater drum, sauger, channel catfish, yellow perch, walleye, and largemouth bass (Farabee 1979).

No commercial fishery exists in the Headwaters. For the Upper Mississippi River, commercial catch data are provided voluntarily and may be underreported. In the Lower Mississippi and Atchafalaya rivers, the commercial harvest of fishes is difficult to assess because of inconsistencies in methods of gathering and reporting data (Fremling et al. 1989).

The commercial harvest in the Upper Mississippi River is dominated by four groups of fishes: common carp, buffalos (bigmouth buffalo and smallmouth buffalo), catfishes (channel catfish and flathead catfish), and freshwater drum (Fremling et al. 1989). Between 1953 and 1977, these fishes made up 95% of the total catch and 99% of the monetary value. The common carp has ranked first among species in commercial catch for decades.

Although the commercial harvest on the Upper Mississippi has not changed greatly in the last century—totaling 6,200 metric tons in 1894, 3,200 tons in 1931, and 5,200 tons in 1987—the abundance of several species in the

catch has changed greatly. The common carp, an introduced nonindigenous species first reported in the Mississippi River in 1883 (Cole 1905), has increased the most in abundance. In 1894, 206 metric tons of common carp (3% of the total harvest) were taken from the river; by 1899, the catch had risen to 1,400 metric tons. During 1953–1977, an average of 2,400 metric tons of common carp (47% of the average total annual harvest) were harvested each year (Kline and Golden 1979).

The grass carp, another nonindigenous species, first appeared in Pool 25 in 1975 and has since expanded upstream to Pool 5A (Rasmussen 1979; Fremling et al. 1989). Commercial harvest of grass carp was 6.1 metric tons in 1983 and 7.7 metric tons in 1991. Grass carps seem to be reproducing successfully in the Lower Mississippi River, in lower reaches of the Upper Mississippi River, and in tributaries as far upstream as the Illinois River (Raibley et al. 1995).

A decline in the harvest of buffalo fishes coincided with the increase in catch of common carp. Buffalo fishes made up 43% of the total catch in 1894 and averaged 22% of the total harvest during 1953–1977 (Kline and Golden 1979). The decline in buffalo fishes may have resulted from competition with common carp and from destruction of their spawning habitat (Coker 1930).

During 1978–1991, the total annual commercial fish harvest varied little, ranging from 3,900 metric tons in 1982 to 5,200 metric tons in 1987 (Duyvejonck 1997). Throughout this period the common carp ranked first in catch, about 30% of the total annual harvest. Buffalo fishes were second in biomass harvested, followed by freshwater drums and catfishes in roughly equal amounts. During this 14-year period, the harvest of American eel declined from 1.2 metric tons in 1978 to 0.3 metric tons in 1991. In the past 30 years, the reported commercial harvest of channel catfish has also declined.

Some fishes that inhabit swift-current habitats have apparently declined in the Upper Mississippi River since the construction of navigation dams but have not declined in the unimpounded Lower Mississippi (Pflieger 1975; Baker et al. 1991). These include the shovelnose sturgeon, blue sucker, and blue catfish (Pennington et al. 1983a; Beckett and Pennington 1986). The reproduction of paddlefish in the Upper Mississippi may be adversely affected by dams, which could impede paddlefish access to suitable spawning habitat. The decline of the federally endangered pallid sturgeon may be attributable to channelization of the open river below St. Louis, Missouri.

In Pool 2 of the Upper Mississippi River, the abundance and diversity of fishes have increased markedly in recent years in response to improved water quality. For decades, Pools 2 through 4 suffered severe oxygen depletion caused by sewage pollution from the Minneapolis–St. Paul metropolitan area (Wiebe 1927; Fremling 1964, 1989). In 1964, Pool 2 was badly polluted, oxygen depletion was common on summer nights, and only three fish species (common carp, gizzard shad, and white bass) were found during electrofishing surveys. Dissolved oxygen levels and overall water quality in this reach subsequently became much more favorable for fishes because of improved treatment of wastewaters, including advanced secondary treatment, nitrification, dechlorination, and a pretreatment program for industrial wastes (Fremling 1989; Johnson and Aasen 1989). In 1980 sampling through electrofishing produced a count of 16 fish species—13 more than in 1964—including walleye, sauger, smallmouth bass, largemouth bass, and channel catfish. In short, the pool has been transformed from a polluted water with few or no game fishes to one supporting a significant walleye and sauger fishery (D. Zappetillo, Minnesota Department of Natural Resources, St. Paul, personal communication). Clearly, a riverine fishery affected by pollution can be rejuvenated if water quality is improved.

Birds

The Mississippi River is a major bird migration corridor within North America. Millions of migratory birds use the Mississippi River corridor each year during fall and spring migration. The river's north-to-south orientation and nearly contiguous habitat make it critical to the life cycle of many migratory birds. Diving ducks, swans, pelicans, and cormorants use the river's large open-water pools, and dabbling ducks, geese, herons, egrets, black terns, bitterns, rails, and numerous resident and Neotropical migrant songbirds use shallow backwater riverine wetlands. Bottomland forests support migrating and nesting populations of songbirds, bald eagles, ospreys, herons, egrets, hooded mergansers, mallards, and wood ducks.

Riverine floodplain habitats are vital to the life cycles of many migratory birds. The modern landscape along the Mississippi River has been altered by an expanding human population for agriculture, industry, and urbanization and therefore contains far fewer wetlands, forests, and prairies than were present before the arrival of European settlers. Concerns regarding the long-term viability of bird populations that require these habitats relate directly to the adverse effects of sedimentation, operation

and maintenance of the 2.7-meter channel navigation project, navigation-induced developments (including the impoundment of water), industrial and sewer effluent, urban and agricultural runoff, recreation, and other human-induced influences.

Colonial Waterbirds

Eight species of colonial waterbirds nest within Mississippi River habitats (Thompson 1977; U.S. Fish and Wildlife Service, Winona, Minnesota, unpublished data). Populations of great blue herons, great egrets, and double-crested cormorants appear to have declined on the Upper Mississippi River (Thompson 1977, 1978; Graber et al. 1978; Kirsch 1995; U.S. Fish and Wildlife Service, Winona, Minnesota, unpublished data). The range of cattle egrets has expanded to include areas in and near the river floodplain as far north as Pool 13 (U.S. Fish and Wildlife Service, Winona, Minnesota, unpublished data). Populations of least terns, which occur on the lower portion of the Mississippi River, appear stable. Information is not sufficient to estimate trends of black terns specific to the river, although the Breeding Bird Survey data (1966–1987) indicate 4% annual declines of black terns in Iowa, Minnesota, and Wisconsin (Hands et al. 1989). Data are not sufficient to examine abundance trends of Forster's terns, black-crowned night-herons, and yellow-crowned night-herons.

The Upper Mississippi River is an important nesting and feeding area for great blue herons and great egrets because its extensive bottomland forests and diverse aquatic areas provide suitable nesting and foraging habitats (Thompson 1978). Possible causes for apparent population declines in great blue herons and great egrets include poor water quality, loss of nesting trees and foraging areas, and toxic contaminants (Thompson 1978). Thompson (1977) reported that in 1977, 31 heron and egret colonies (18 colonies contained both species) occurred within the Upper Mississippi River. Thompson (1977) also reported average nesting success of 3.0 young herons per nest (518 nests examined) and 2.5 young egrets per nest (73 nests). Little reliable data on heron and egret productivity have been obtained since Thompson's study, though by 1978 the number of colonies had decreased to 27, again with 18 colonies containing both species (Thompson 1978). Several state and federal agencies have censused colonies since Thompson's study, but the years, methods, and reaches examined differed among surveys. The Upper Mississippi River National Wildlife and Fish Refuge began standardized surveys of great blue herons and great egrets in the refuge in 1993, but the Flood of 1993 hampered the initial survey. Refuge personnel reported that 6 of 18 colony sites that were active in 1992 were abandoned after nest initiation or were not colonized in 1993.

The Illinois Department of Conservation has aerially surveyed heron and egret rookeries since 1983, and other states along the Upper Mississippi River have conducted intermittent surveys. The Illinois surveys revealed that the number of active heron nests along the Illinois stretch of the Mississippi River substantially increased—from 2,111 nests in 21 colonies in 1987 to 5,045 nests in 20 colonies in 1991. Active egret nests also increased, from 351 nests in 14 colonies in 1987 to 1,099 nests in 18 colonies in 1991.

Double-crested cormorants were common breeders and abundant migrants on the Upper Mississippi River from St. Paul, Minnesota, to St. Louis, Missouri, during the 1940's and 1950's. The effects of contaminants and human disturbance caused their numbers to decline in the 1960's and 1970's; their numbers remained low for several years but slowly increased in the late 1980's (U.S. Fish and Wildlife Service, Winona, Minnesota, unpublished data). Current numbers of breeding and migrating cormorants remain much lower than historical levels (Figs. 14 and 15). A minimum of 418 cormorant pairs nested in 4 colonies in 1992 (Kirsch 1995), and 504 pairs nested in 9 colonies in 1993 (Kirsch 1997). Only 500 to 2,000 cormorants were seen during spring 1992–1993, and 5,000 to 7,000 were seen during the fall migration of 1991–1992, much lower numbers than the counts of 20,000 to 50,000 cormorants in the 1940's (U.S. Fish and Wildlife Service, Winona, Minnesota, unpublished data; Fig. 15).

The least tern, which breeds along the Mississippi River between Cape Girardeau, Missouri, and Vicksburg, Mississippi, has been monitored since 1985 (Rumancik 1985, 1986, 1987, 1988, 1989, 1990, 1991, 1992). A 100% increase occurred in tern numbers along the Lower Mississippi River (2,503 to 5,038) between 1989 and 1990; this increase cannot be explained by increased survey efforts or methods. Since 1990, least tern numbers have decreased slightly (Fig. 16).

Waterfowl

Waterfowl are the most prominent and economically important group of migratory birds on the Mississippi River. Numbers of waterfowl on the river often reflect national population trends and habitat conditions elsewhere. Four major groups of waterfowl use the Mississippi River during migration, and a few species also breed on the river. During fall and spring migrations, ducks tend to occupy areas with submersed and emergent aquatic vegetation or seasonally flooded areas rich in plant foods.

The most numerous diving ducks using the Mississippi River are canvasback, lesser scaup, redhead, and ring-necked duck. Other diving ducks, such as greater scaup, bufflehead, common goldeneye, hooded merganser, common merganser, and ruddy duck, also use the river, but their peak numbers during migration are relatively low. The most important areas for migrating diving ducks are Pools 5, 7, 8, 9, and 19. Together, Pools 5–9 extend for about 150 kilometers and include large open-water areas and shallow marsh zones that have supported luxuriant communities of submersed and emergent aquatic vegetation. Pool 19 extends from Keokuk, Iowa, to Oquawka, Illinois, but the most important area for diving ducks is the 32-kilometer reach from Keokuk to Fort Madison, Iowa. Tundra swan and Canada geese are also

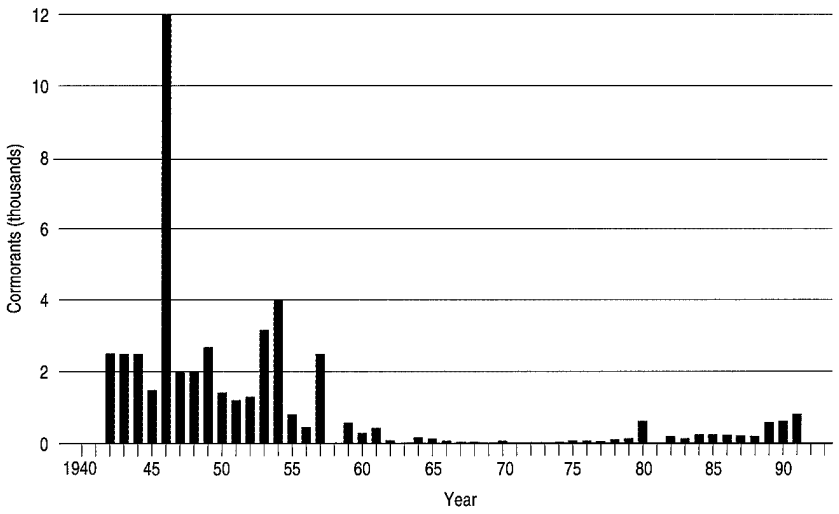


Fig. 14. Abundance of double-crested cormorants during the breeding season on the Upper Mississippi River National Wildlife and Fish Refuge from 1942 to 1992.

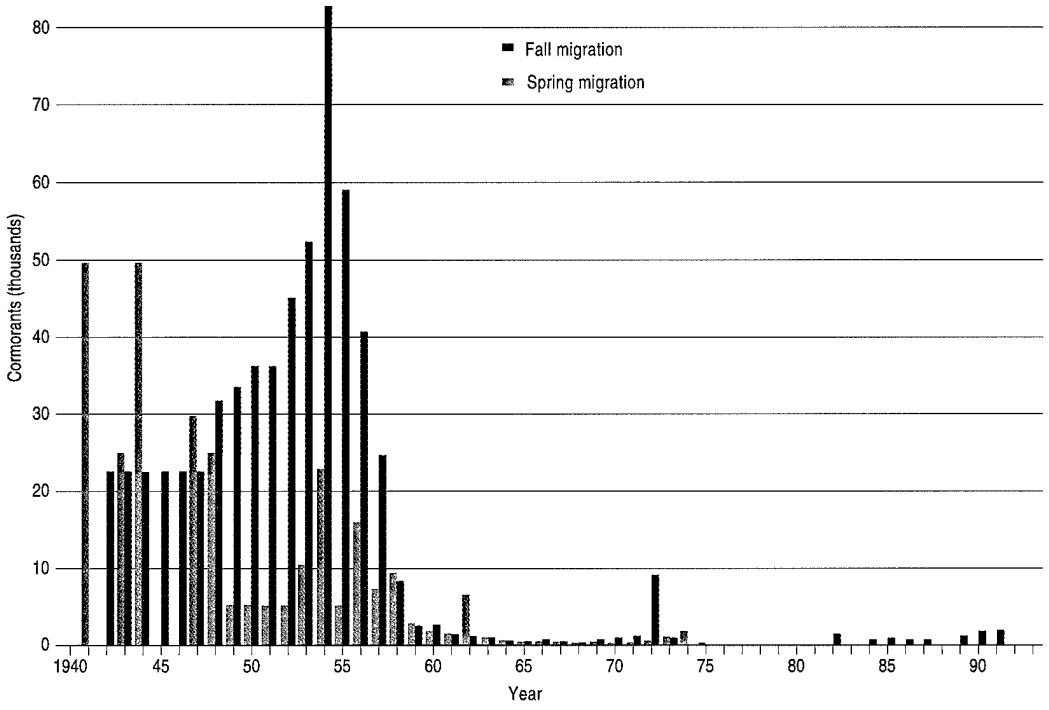


Fig. 15. Abundance of migrating double-crested cormorants on the Upper Mississippi River National Wildlife and Fish Refuge from 1942 to 1992.

common migrants on the river. Most populations of canvasback and tundra swan that migrate in the Atlantic and Mississippi flyways now stage on the Mississippi River. Concentrations of these species are associated with the availability of food resources, particularly wildcelery and arrowhead tubers (Korschgen et al. 1988).

Most continental populations of diving ducks depend upon large lakes and riverine impoundments in the upper portions of the Mississippi Flyway of the United States for feeding and resting areas during fall migration (Korschgen 1989). Historically, wetlands were a dominant feature of the landscape in Minnesota, Wisconsin, Iowa, and Illinois, totaling several million hectares. Wetland losses now total 6.7 million hectares in these states (Tiner 1984). Most of the riverine and deepwater wetlands remain, although few are used by waterfowl because of human-caused and natural changes; still, these wetlands may have future management potential.

Population survey data in the upper Midwest have been collected most consistently by the U.S. Fish and Wildlife Service and the Illinois Natural History Survey. Serie et al. (1983) compiled data from 1961 to 1977 on canvasbacks in Mississippi River Pools 7 and 8 (combined) and Pool 19. A peak of 147,000 canvasbacks was estimated in 1975 in Pools 7 and 8 and 169,000 in 1970 in Pool 19. During 1978–1994, a peak of 195,000 canvasbacks was estimated on Pools 7, 8, and 9 (Korschgen, unpublished data); large numbers of ring-necked ducks and lesser scaups also used these pools during this period

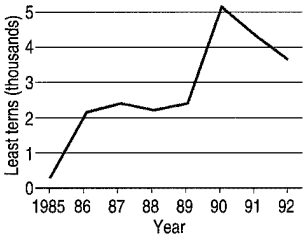


Fig. 16. Numbers of least terns counted during a small boat survey (Rumancik 1985, 1986, 1987, 1988, 1989, 1990, 1991, 1992) on the Mississippi River between Cape Girardeau, Missouri, and Vicksburg, Mississippi, from 1985 to 1992. The low numbers reported for 1985 reflect an incomplete and late survey.

(Fig. 17). In 1969 a peak of 875,000 diving ducks was estimated in Pool 19 in 1969. In Pool 19, fall waterfowl censuses between 1948 and 1984 revealed a mean yearly peak of 345,000 diving ducks (F. Bellrose and R. Crompton, Illinois Natural History Survey, Havana, unpublished data). The percent composition of peak numbers was 71% for lesser scaups, 18% for canvasbacks, 10% for ring-necked ducks, and 1% for redheads. Peak counts of these four species in Pool 19 have been much lower during the past 10 years (S. Havera and M. Georgi, Illinois Natural History Survey, Havana, unpublished data; Fig. 18).

The numbers of migrating waterfowl on the river have fluctuated greatly among years because of variations in waterfowl production on the breeding grounds, in food resources, and in weather. Censuses made by Bellrose in the Pool 19 area in fall 1941 revealed only moderate numbers of diving ducks. By 1946 lesser scaup numbers had greatly increased, whereas canvasback populations were low, peaking at only 5,500. Fall canvasback numbers increased steadily to 168,000 in 1970. Peak counts of canvasbacks, lesser scaups, and ring-necked ducks in Pools 7, 8, and 9 were relatively low during 1989–1991 (Fig. 17), probably because of the effects of drought on both continental reproductive success and on food resources in the Mississippi River. Drought conditions in the late 1980's also may have contributed to the decline in numbers of lesser scaups, ring-necked ducks, and canvasbacks in Pool 19 (Fig. 18). Submersed aquatic vegetation and fingernailclams, the principal food resources of diving ducks in Pool 19, have dwindled as a consequence of stresses incurred during low-flow periods resulting from drought (Wilson et al. 1995). The use of Pool 19 by migrating lesser and greater scaups, which feed heavily on fingernailclams, decreased substantially after the recent decline in this invertebrate food resource (Fig. 19).

Most of the changes in the distribution of migrating diving ducks in the Upper Midwest over the last several decades are directly attributable to habitat alteration caused by changes in land and water use. The Illinois River illustrates the potential severity of human modifications on such habitat (Mills et al. 1966; Havera and Bellrose 1985). Drainage and levee districts drained almost half of the existing bottomland lakes between 1909 and 1922, increasing flood heights and the deposition of sediments on the remaining lakes and floodplain (Bellrose et al. 1983). Erosion from uplands and tributary stream banks has caused high sedimentation rates and rapid filling of bottomland lakes. Loss of the invertebrate and plant-food components of the Illinois River habitat between 1946 and 1964 seriously reduced the numbers and distribution of lesser scaups, ring-necked ducks, and canvasbacks. Factors directly affecting the species composition and abundance of the wetland plants were fluctuating water level, water turbidity, water depth, and competition among plant species. The primary food item for diving ducks at Pool 19 has been fingernailclams (Thompson 1973), which may not have reached high densities until the early 1950's.

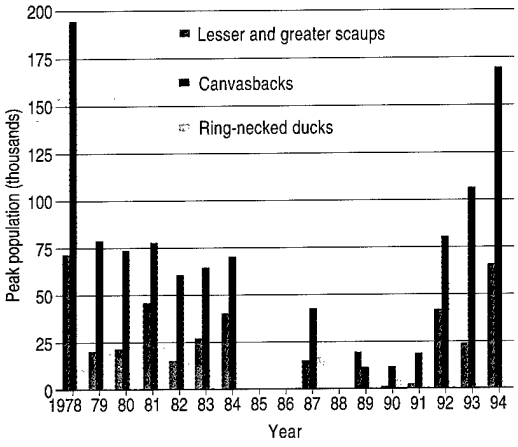


Fig. 17. Peak numbers of migrating lesser and greater scaups, canvasbacks, and ring-necked ducks from 1978 to 1994 in Pools 7, 8, and 9 of the Upper Mississippi River. No data are available for 1985, 1986, and 1988.

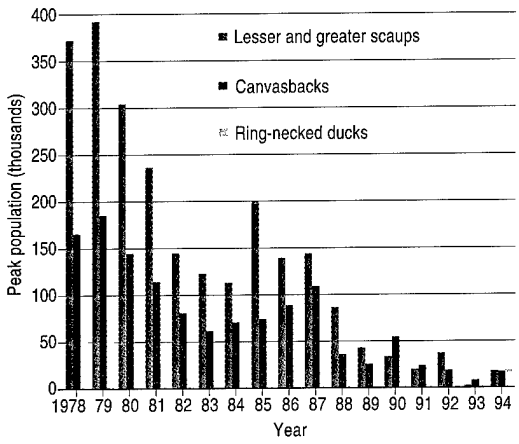


Fig. 18. Peak numbers of migrating lesser and greater scaups, canvasbacks, and ring-necked ducks from 1978 to 1994 in Pool 19 of the Upper Mississippi River.

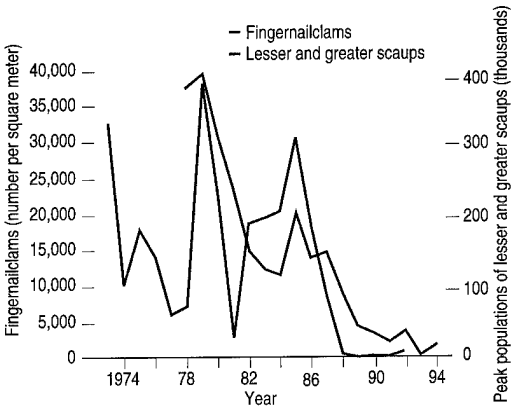


Fig. 19. Peak numbers of migrating lesser and greater scaups on Pool 19 during fall migrations are strongly linked to the abundance of fingernailclams, small mollusks important in the diet of scaup.

Mallards, wood ducks, blue-winged teals, hooded mergansers, and Canada geese nest in the Upper Mississippi River. Islands in Pools 7, 8, 9, and 10 may have high densities of nesting mallards (J. Wetzel, Wisconsin Department of Natural Resources, La Crosse, and R. Dahlgren, U.S. Fish and Wildlife Service, La Crosse, Wisconsin, unpublished data). Canada geese and, on occasion, blue-winged teals nest on islands that lack predators. Wood ducks and hooded mergansers, both cavity nesters, are common in bottomland hardwood forests. Mallard nesting densities as high as 70 nests per hectare, with nest success of 86%, have been recorded on islands managed for ground-nesting birds. From 10% to 40% of mallard ducklings typically survive to fledgings in places where adequate brood habitat is available near nesting islands (Korschgen and Kenow, unpublished data).

The floodplain of the Lower Mississippi River also includes critical wintering habitat for waterfowl (Reid et al. 1989). As much as 40% of the continental populations of mallards and American black ducks, as well as much of the continental wood duck population, overwinters in the Mississippi Alluvial Valley (Reinecke et al. 1989). Winter mallard populations formerly averaged about 1.5 million (Bellrose 1980; Bartonek et al. 1984) but have declined recently because of poor recruitment in prairie and parkland nesting areas in the northern United States and Canada. Habitat-protection efforts in the Mississippi Alluvial Valley now attempt, through acquisition and management of public lands, to offset habitat losses on private lands.

Raptors

The Upper Mississippi River is a major migration route and wintering area for bald eagles. During winter, more than 100 bald eagles roost at several traditional sites depending on ice conditions on the river. Peak numbers of bald eagles seen on informal roadside surveys between Winona and Red Wing, Minnesota, were 677 in the winter of 1990–1991, 540 in the winter of 1991–1992, 302 in the winter of 1992–1993, 363 in the winter of 1993–1994, and 206 in the winter of 1994–1995. Between 1963 and 1967 bald eagles were surveyed annually from Cairo, Illinois, to Minneapolis, Minnesota; the minimum number counted on these surveys was 397 in 1964, and the maximum was 885 in 1965.

Numbers of breeding bald eagles along the Upper Mississippi River have increased from 2 to 5 pairs in the 1970's to 43–44 pairs in 1993 and 1994 (Fig. 20). Productivity of young per occupied nest varied little between 1986 and 1993, with 0.95 to 1.5 young per nest (U.S. Fish and Wildlife Service, Winona, Minnesota, unpublished data).

Red-shouldered hawks are listed as endangered in Iowa and Illinois, threatened in Wisconsin, and of special concern in Minnesota. The Upper Mississippi River floodplain includes most of the forested habitat in Iowa and Illinois. Consequently, the floodplain is important for maintaining red-shouldered hawk populations in these states and for linking the habitats of northern and southern populations. The ecology of red-shouldered hawks has been studied along the Upper Mississippi River since 1983, and surveys have recently been expanded to cover more of the river (Pools 9–11 and 16–19). Thirty-two breeding territories were confirmed in 1992, and 37 territories in 1993 (J. W. Stravers, Midwest Raptor Fund, Pella, Iowa, unpublished data).

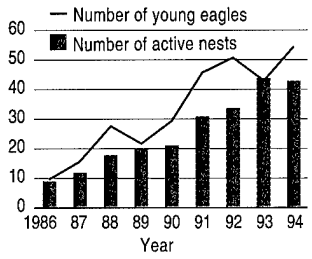


Fig. 20. Numbers of active bald eagle nests and young eagles produced between Pools 4 and 14 of the Upper Mississippi River.

Songbirds

The U.S. Geological Survey Breeding Bird Survey is the only long-term data set for assessing population trends of breeding birds (migratory songbirds, as well as certain other migratory birds, and residents) along the Mississippi River corridor (Peterjohn 1994). Unfortunately, too few survey routes include portions of the Mississippi River floodplain to estimate trends specific to the river. Trends have been estimated, however, from routes within physiographic strata of the United States and Canada. Two of these strata (17 and 5) lie mainly along the Mississippi River but also include large areas removed from the river. Stratum 17 encompasses portions of Minnesota, Wisconsin, Illinois, and Iowa along the Upper Mississippi River from near St. Croix Falls, Wisconsin, to Clinton, Iowa, as well as up the Wisconsin River to Stevens Point, Wisconsin. Stratum 5 lies along the Lower Mississippi River valley and includes eastern Louisiana, eastern Arkansas, southern Missouri, western Tennessee, and western Mississippi. All of the other strata through which the Mississippi River flows primarily encompass upland areas away from the river.

In the Upper Mississippi River (stratum 17), 35 of the 119 species for which trends could be calculated from Breeding Bird Survey data had significant trends during 1966–1994. Twenty, or 59%, of these significant trends were positive, indicating increasing populations, whereas 15 (41%) were negative, indicating decreasing populations (Table 4). The continental trends for 27 of these species (80%) were in the same direction as the regional trends and were also significant. The continental trend for the American redstart was negative, but was positive for stratum 17. These trends may indicate that habitats in this region are not influencing

populations of these bird species differently than elsewhere in North America. There were no significant continental trends for 6 species that had significant trends within the stratum (5 positive, 1 negative). For the 6 species, factors influencing populations may differ between the Upper Mississippi River and the rest of the continent.

In the Lower Mississippi River valley (stratum 5), 47 of the 105 species for which trends could be calculated had significant trends during 1966–1994. Thirteen of these significant trends were positive (population increasing), and 34 were negative (population decreasing) (Table 4). The continental trends for 24 of these species were significant and in the same direction as those for the region, which may indicate habitats in the Lower Mississippi River valley are not influencing populations of these bird species differently than elsewhere in North America. However, for 24 other species, the factors influencing populations may differ between the region and the rest of the continent. Continental trends for 6 species were significant and in the opposite direction of the trends on the Lower Mississippi River valley. Continental trends were not significant for 17 species with significant trends (2 positive, 15 negative) in the Lower Mississippi River.

Habitat-specific data on the occurrence and relative abundance of bird species are not yet available for most areas along the Mississippi River. Furthermore, the breeding success of most species along the Mississippi River is unknown. Finally, there are few site-specific data concerning songbird use of the river corridor during migration. Preliminary species lists and counts are available for a few areas within the refuges managed by the U.S. Fish and Wildlife Service.

Resident Birds

The only other nationwide, long-term survey of birds is the Christmas Bird Count. The methods used in this survey are far less standardized than the methods used in the Breeding Bird Survey, although certain methods of analysis can be used to assess trends in wintering and resident bird species. We used the methods of Morrison and Morrison (1983) to examine population trends for the ruffed grouse, red-bellied woodpecker, pileated woodpecker, downy woodpecker, hairy woodpecker, house finch, northern cardinal, great horned owl, and barred owl from 11 Christmas Bird Count locations centered on the Upper Mississippi River (Table 5). The house finch, which has been expanding its range and numbers throughout the upper Midwest, was the only species exhibiting a significant change in abundance in the Christmas Bird Count data.

Table 4. Bird species with significant trends in one or both of the two physiographic strata that lie primarily along the Mississippi River (data from the U.S. Geological Survey Breeding Bird Survey). Stratum 17 encompasses portions of Minnesota, Wisconsin, Illinois, and Iowa along the Upper Mississippi River (see text). Stratum 5 lies along the Lower Mississippi River valley and includes eastern Louisiana, eastern Arkansas, southern Missouri, western Tennessee, and western Mississippi.

Species	Stratum 17	Stratum 5	Continental
Pied-billed grebe	–	▼	
Anhinga	–	▼	
Mallard	▲	▲	▲
Canada goose		▲	▲
Great blue heron	▲		▲
Little blue heron	–	▼	
Cattle egret	–	▲	▲
Black tern	▼	–	▼
Killdeer	▲		
Northern bobwhite		▼	▼
Wild turkey	▲	▲	▲
Mourning dove		▼	
Turkey vulture	▲		▲
Mississippi kite	–	▼	
Red-tailed hawk	▲		▲
Broad-winged hawk	–	▼	
American kestrel		▲	
Barred owl	▲		▲
Great horned owl	▲		▲
Black-billed cuckoo	▼	–	▼
Yellow-billed cuckoo		▼	▼
Belted kingfisher	▼	▲	▼
Red-headed woodpecker	▼		▼
Red-bellied woodpecker	▲		▲
Yellow-shafted flicker	▼	▼	▼
Common nighthawk		▼	
Ruby-throated hummingbird		▼	▲
Eastern kingbird		▼	
Eastern wood-pewee		▼	▼
American crow	▲		▲
Fish crow	–	▼	
Bobolink	▼		▼
Red-winged blackbird		▲	▼
Orchard oriole		▼	▼
Baltimore oriole		▼	
Western meadowlark	▼	–	▼
Brown-headed cowbird	▼		▼
Common grackle		▼	▼
House finch	▲	–	
Northern cardinal	▲		
Rose-breasted grosbeak	▲	–	
American goldfinch		▼	▼
Grasshopper sparrow	▼	▼	▼
Lark sparrow		▲	▼
Chipping sparrow		▼	
Dickcissel	▼		▼
Field sparrow	▼	▼	▼
Vesper sparrow	▼	–	▼
Indigo bunting		▼	▼
Painted bunting	–	▼	▼
Purple martin		▼	
Barn swallow		▲	▲
Tree swallow	▲	▲	▲
Northern rough-winged swallow		▲	
Cedar waxwing	▲	–	▲
Yellow-throated vireo	▲		▲
White-eyed vireo	–	▼	
Bell's vireo	▼	–	▼
Marsh wren	▼	–	
Prothonotary warbler	–	▼	▼
Prairie warbler	–	▼	▼
Blue-winged warbler	▲	–	
Common yellowthroat		▼	
Yellow-breasted chat	–	▼	▼
American redstart	▲	▲	▼
House sparrow		▼	▼
Northern mockingbird	–	▼	▼
Grey catbird		▼	
Carolina chickadee	–	▼	▼
Blue-gray gnatcatcher	▲	▼	▲
American robin	▲	▲	▲

▲ = Positive trend (increase in abundance).
▼ = Negative trend (decrease in abundance).
= There was no significant change.
– = The trend was not estimated.

Table 5. Locations of Christmas Bird Count (CBC) surveys along the Upper Mississippi River.

Year CBC initiated	City and state	Latitude and longitude
1972	Wabasha, Minnesota	44°16'N 92°02'W
1986	Winona, Minnesota	44°02'N 91°38'W
1972	La Crosse, Wisconsin	43°49'N 91°15'W
1986	Dubuque, Iowa	42°29'N 90°42'W
1957	Clinton, Iowa	41°58'N 90°09'W
1980	Burlington, Iowa	40°52'N 91°06'W
1962	Muscatine, Iowa	41°25'N 91°00'W
1987	Keokuk, Iowa	40°28'N 91°27'W
1972	Quincy, Illinois	39°51'N 91°25'W
1971	Hannibal, Missouri	39°42'N 91°21'W
1985	Pere Marquette, Illinois	39°00'N 90°36'W

Mammals

We are only aware of one comprehensive assessment of the mammalian fauna along the river corridor—the monitoring of annual furbearer harvest on the Upper Mississippi River National Wildlife and Fish Refuge. Dahlgren (1990) recently assessed trends in the abundance of mink and muskrats by examining indices of furbearer harvest per unit of trapping effort (total harvest divided by total number of trappers) on the refuge and in states along the river corridor.

Mink

The abundance of mink on the Upper Mississippi River National Wildlife and Fish Refuge declined precipitously during 1959–1965, remained low until about 1970, and then began to slowly increase to numbers less than half those of the 1950's (Fig. 21). In contrast, mink populations in the adjoining states of Iowa (Fig. 21), Minnesota, and Wisconsin were relatively stable during this same period and did not exhibit the pattern of decline and partial recovery seen in refuge populations. These patterns indicate that some causal factor was operating in the river corridor but not in the mostly agricultural watersheds of the adjoining states.

Contamination of the riverine food web with polychlorinated biphenyls (PCB's) was the most probable cause of the decline in mink populations during 1959–1965; mink are one of the organisms most sensitive to PCB's (Giesy et al. 1994; Leonards et al. 1995), and their survival and reproduction are adversely affected by dietary exposure to small doses of PCB's (Aulerich and Ringer 1977; Wren 1991; Leonards et al. 1995). The PCB's biomagnify in aquatic food webs (Rasmussen et al. 1990), and mink, which feed largely on fish, occupy a position at or near the top of the aquatic food web.

Significant amounts of PCB's have entered the river in Pool 2, which receives treated effluents and urban runoff from the Minneapolis–St. Paul metropolitan area as well as inflow from the Minnesota River (Boyer 1984; Metropolitan Waste Control Commission 1990; Steingraeber et al. 1994). The PCB's entering the Mississippi River at Pool 2 have been transported downstream, contaminating a reach extending at least 200 to 375 kilometers downstream (Steingraeber and Wiener 1995). Navigation Pool 15 is another significant source area of PCB's entering the Upper Mississippi River (Steingraeber et al. 1994; Steingraeber and Wiener 1995); however, PCB contamination of the reach downstream from Pool 15 is not readily apparent, in contrast to the area downstream from Pool 2.

The decline of mink on the refuge coincided with the probable period of most severe PCB contamination of the river. Conversely, the partial recovery of mink populations began in the late 1970's and coincided with a period of declining PCB levels in riverine fishes (Hora 1984; Sullivan 1988). Based on experimental studies (Platonow and Karstad 1973), R. B. Dahlgren and K. L. Ensor (U.S. Fish and Wildlife Service, Bloomington, Minnesota, personal communication) estimated that a diet containing 33% fish that have PCB concentrations similar to those in the early 1970's would contain enough PCB's to prevent reproduction in mink. Several recent studies have confirmed the extreme sensitivity of mink to PCB's (Giesy et al. 1994; Heaton et al. 1995a,b; Leonards et al. 1995). Heaton et al. (1995a) found that female mink fed a diet containing 0.72 parts per million of PCB's for 2 months before breeding produced kits (young) with low body weight and survival rates. In another study (Hornshaw et al. 1983), female mink fed a diet containing 1.5 parts per million of PCB's for 7 months before breeding produced no live kits. Average concentrations of PCB's in common carp from the Upper Mississippi River, for comparison, were 4.0 parts per million during 1975–1976 and 2.1 parts per million during 1979–1980 (Hora 1984).

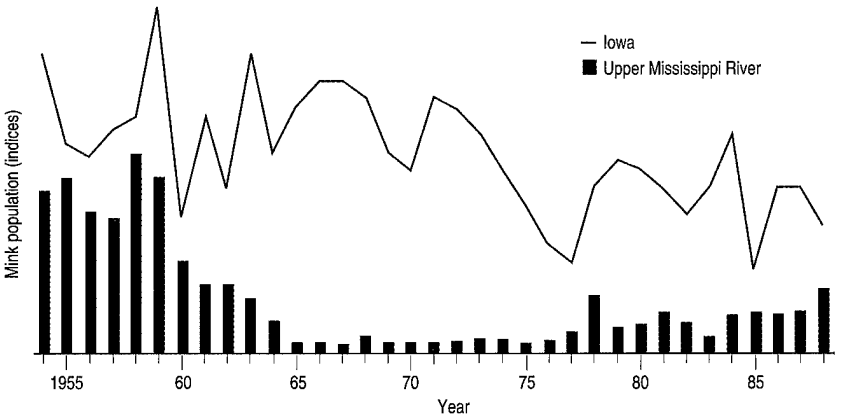


Fig. 21. Trends in the harvest of mink on the Upper Mississippi River National Wildlife and Fish Refuge and in the adjoining state of Iowa during 1954–1988.

In 1989–1991, PCB concentrations in mink carcasses from the Upper Mississippi River in Minnesota averaged 0.26 parts per million, exceeding concentrations in mink from all other areas of the state except Lake Superior (Ensor et al. 1993). Furthermore, recent studies show that PCB's continue to enter or cycle within the riverine ecosystem, suggesting that PCB's are transferred from the sediment to higher trophic levels via the benthic food chain (Steingraeber et al. 1994).

Muskrat

Soon after the lock and dam system was constructed in the 1930's, the abundance of muskrats increased on the Upper Mississippi River, probably because of the increase in water surface area and the development of marsh habitat (Dahlgren 1990). From 1960 to 1988, the harvest of muskrats varied annually but no overall trends in the population were obvious (Fig. 22), particularly given the potential influence of fur prices and the number of trappers on furbearer harvest. In Pool 9, Clay and Clark (1985) found that densities of muskrats were lower in backwater habitats than in open-water habitats, a difference that they attributed to past overharvest and long-term habitat degradation. Muskrat populations on the Upper Mississippi may decline if emergent plant communities continue to decline or change.

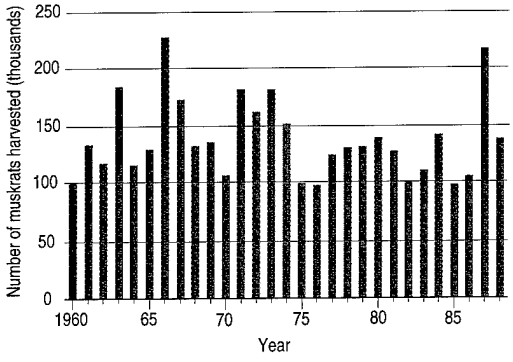


Fig. 22. Harvest of muskrats on the Upper Mississippi River National Wildlife and Fish Refuge during 1960–1988.

Gaps in Knowledge

Information on status and trends is sparse or unavailable for certain species and groups of organisms native to the river. Zooplankton, for example, are clearly important as a food resource during the life cycles of many riverine fishes, yet we are unaware of any systematic studies of the composition, abundance, or production of zooplankton in the river. Similarly, during our review we located only one published report about amphibians and reptiles in the Mississippi River valley (Collins 1991), and we are unaware of any systematic attempts to assess their abundance in the river's floodplain. In Iowa, which borders part of the Upper Mississippi River, most species of amphibians and reptiles declined substantially during the past century (Christiansen 1981).

From the forest manager's perspective, information on the composition and diversity of presettlement and existing floodplain forests is needed for restoration. The relationships among hydrological regimes (including the timing, frequency, intensity, and duration of floods), natural regeneration, and growth of woody species also merit examination. Forest simulation models could be developed to synthesize field data and to predict the effects of different river regulation schemes on forests (Bedinger 1978).

We lack sufficient information to predict long-term trends in aquatic vegetation, a key ecological component of habitat in the Upper Mississippi River ecosystem. Long-term monitoring and research have only recently begun to determine mechanisms of the decline that occurred in native submersed plants in the late 1980's. Elucidation of such cause and effect relationships and of long-term patterns in aquatic vegetation communities could aid in the restoration and maintenance of submersed, native aquatic plants in the pools of the Upper Mississippi.

The assessment of fish abundance in much of the Mississippi River, particularly the Lower Mississippi River, is complicated by swift currents, large fluctuations in river stage and discharge, deep water, wind-driven waves, floating debris, shifting substrates, navigation traffic, and the river's large size. Standardized approaches to fish sampling are hampered by the extreme variations encountered in such environmental conditions, both among habitats and over time within a limited area. There are few precise estimates of standing crops of fishes in the river (Pitlo 1987), and the large uncertainties in what estimates we do have greatly impede the detection of spatial or temporal variation in fish abundance. Gradual changes in riverine fish populations could long remain undetected because of the limited quantitative data available and the spatial and temporal variation in the riverine ecosystem.

Likewise, we encountered many difficulties when we attempted to determine the status and trends of bird populations on the river and its floodplain. In particular, standardized survey procedures are critically needed to assess river-wide trends. Assessment of trends in some colonial waterbirds, for example, was complicated or precluded by methodological differences among surveys and by inadequate spatial coverage of the river corridor in past surveys. To identify the demographic causes of population changes in bird populations, more information

is needed on productivity and survival so that we can effectively develop models and guide management programs for any given group of birds.

Riverine resource managers may soon need information on how to manage an ecosystem in which the flows of energy and nutrients have been substantially altered by rapidly increasing populations of the nonindigenous zebra mussel. Studies of the Great Lakes indicate that the potential for food web modification in the backwater habitats of the Mississippi River is considerable. Zebra mussels will probably compete with some native biota for resources such as food and space, and the mussels will probably serve as prey for other species. Zebra mussels may also significantly modify the riverine habitat and its trophic resources by reducing the quantity of suspended solids and increasing water clarity, thereby affecting the distribution and abundance of native organisms. The ecological consequences of zebra mussels on the riverine ecosystem should be critically examined, with particular regard to their effects on food webs, trophic structure, and energy flow.

The biodiversity of the native pearlymussel fauna in the Mississippi River basin could soon be greatly reduced unless refugia from zebra mussels are provided. Examples of potential temporary refugia for native pearlymussels include hydrologically unconnected lakes, artificial ponds, and decommissioned fish hatcheries. Methods for moving native mussels to refugia with minimal handling stress, while ensuring that the native mussels are free of viable zebra mussels, are also needed.

Integrated resource management, based on science, is clearly needed for the Mississippi and other large rivers (Sheehan and Rasmussen 1993). However, the identification of appropriate management actions is often hampered by a lack of information on the ecological structure and function of this and other ecosystems. Information gaps concerning the causes of observed fluctuations in plant and animal communities also hamper the application of corrective measures. Comprehensive, long-term studies of the Mississippi River are surprisingly few, given the size and importance of this ecosystem. Existing long-term studies have focused on a few small segments of the river. Much of the data concerning the status and trends of riverine biota are unpublished or exist only in agency reports and gray literature. Many complex questions concerning environmental degradation, declining flora and fauna, and human effects require objective analysis to prevent continued deterioration of this natural resource.

Ecosystem Status and Health

The declines in key native species across many trophic levels signal a deterioration in the health of this riverine ecosystem. The Mississippi River ecosystem is often heralded as a multiple-use resource, and human use of the river and its floodplain for various purposes is expected to increase while inputs of sediment, nutrients, and potentially harmful chemicals from the watershed continue. Clearly, the greatest challenge on the Mississippi and other large rivers is to maintain ecological integrity while sustaining multiple human uses of the ecosystem (Sheehan and Rasmussen 1993).

Evidence is mounting that the cumulative effects of human activities have already exceeded the ecosystem's assimilative capacity. The abundances of many key native organisms, including submersed plants, native pearlymussels, fingernailclams, certain fishes, migratory waterfowl, colonial waterbirds, songbirds, and mink, have decreased along substantial reaches of the river in recent years or decades. The degradation of the Mississippi River delta represents a severe, nationally significant loss of wetland resources. Sediment deficiency is aiding in habitat destruction in Louisiana's coastal zone while, ironically, sediment deposition is threatening to destroy aquatic habitats in the impounded Upper Mississippi River.

Abundances of undesirable nonindigenous organisms in the river have increased along with these other problems. The common carp, a nonindigenous species present in the river since the late 1800's, has for decades ranked first among fishes in commercial fish harvest on the Upper Mississippi River. There is evidence, however, that common carp have contributed to declines in native submersed aquatic plants and buffalo fishes. The grass carp, another nonindigenous species, has greatly expanded its range in the river in the past two decades and appears to be reproducing in the Lower Mississippi River and in lower reaches of the Upper Mississippi. Dense stands of nonindigenous purple loosestrife are displacing native plants in many wetland areas within the floodplain. The submersed nonindigenous plant Eurasian watermilfoil has also increased in the past decade, particularly in areas of the Upper Mississippi River where native submersed aquatic plants have declined. Populations of the zebra mussel, which entered the Mississippi via the Illinois River around 1990, are expanding rapidly. At high densities, zebra mussels can adversely affect native organisms by direct attachment, by competing for space and planktonic food resources, and by depleting dissolved oxygen in the water column. The zebra mussel poses a

particularly severe and immediate threat to the river's native pearlymussel fauna.

Recent declines in benthic invertebrates and submersed aquatic plants constitute a partial, yet significant, collapse in the food web supporting certain key fish and wildlife species. The decline in submersed aquatic plants in the late 1980's, unprecedented in the Upper Mississippi River, has greatly affected migratory canvasbacks, which feed on wildcelery tubers. Effects of the decline of submersed plants on the river's fish fauna have not been assessed but are likely, given that more than 80 resident fish species use aquatic vegetation for some habitat function (Janecek 1988).

The fingernailclam made up a substantial proportion of the biomass of the benthic fauna in the Upper Mississippi in the decades before its decline (Sparks 1980; Elstad 1986). Fingernailclams were important in the diets of migrating lesser scaups (Gale 1973; Thompson 1973) and certain bottom-feeding fishes (Starrett 1972; Jude 1973). In 1967, for example, diving ducks in Pool 19 consumed more than 2,000 metric tons of fingernailclams (Gale 1973). The use of Pool 19 by migrating lesser and greater scaups decreased greatly after the decline in fingernailclams. Similarly, in the mid-1950's, use of the Illinois River by migratory lesser scaups diminished rapidly after fingernailclams declined in response to pollution and acutely toxic conditions in bottom sediments (Sparks 1980, 1984; Schubauer-Berigan and Ankley 1991).

The riverine ecosystem of the Mississippi has undergone many changes. Most of the natural changes have occurred gradually over hundreds or thousands of years, whereas human-induced changes have occurred rapidly and recently. Several factors have apparently contributed to the recent declines in the river's flora and fauna, including habitat loss and degradation, point and nonpoint pollution, toxic substances, commercial and recreational navigation, deterioration of water quality during drought periods, reduced availability of key plant and invertebrate food resources, and invasions of nonindigenous species. The continued accumulation of sediment in the navigation pools on the Upper Mississippi River will eventually destroy or degrade much of the aquatic habitat in the pools (McHenry et al. 1984; Bhowmik and Adams 1989).

Some favorable biological trends are occurring on the Mississippi River. The abundance of bald eagles along the river corridor has increased, paralleling the national trend, in apparent response to the ban on eggshell-thinning insecticides. Mink populations have begun to recover, probably because of the declines in PCB contamination in riverine fishes that followed the ban on production of PCB's as well as other efforts to reduce PCB release into the environment. The fish and benthic invertebrate communities in the reach downstream from the Minneapolis–St. Paul metropolitan area have responded favorably to improved water quality resulting from advanced wastewater treatment.

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Acknowledgments

We thank the following persons for sharing their unpublished data, preprints of manuscripts in press, or both: R. Anderson of Western Illinois University; J. Sullivan of Wisconsin Department of Natural Resources; D. Blodgett, M. Georgi, S. Havera, R. Sparks, and S. Whitney of the Illinois Natural History Survey; G. Cope of the U.S. Geological Survey, Upper Mississippi Science Center; P. Joria of Saint Mary's University of Minnesota; R. Dahlgren (retired), J. Duyvejonck, E. Nelson, and P. Thiel of the U.S. Fish and Wildlife Service; D. Dieterman and D. Zappetillo of the Minnesota Department of Natural Resources; and K. Johnson of the Twin Cities Metropolitan Council and Wastewater Services. We also thank M. Bartsch, G. Cope, T. Naimo, J. Sullivan, P. Thiel, and two anonymous reviewers for helpful comments on an earlier draft of the manuscript. We are grateful to L. Hill (U.S. Fish and Wildlife Service) for her excellent assistance with preparation of the figures.

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Coastal Louisiana

Unlike most terrestrial environments, the ecosystems of coastal Louisiana experience rapid changes that are driven by changes in topographic relief, geological processes, and climate. In most terrestrial ecosystems, the underlying geology is stable within the period of ecosystem development and through many human generations: thousands or tens of thousands of years. Ecosystems of coastal deltas, though, are changed by water regimes and geological processes that operate in thousands, hundreds, and even tens of years. Coastal Louisiana, therefore, is an excellent laboratory in which to study ecosystems and their component species that have evolved in a rapidly changing environment. Because significant topographic and water regime change has taken place within the lifetimes of currently active scientists, the research record documenting these changes is unusually complete. The recent geological record for the coast of the Gulf of Mexico has been intensively studied because of the important fossil fuel resources in this region. In light of the knowledge gained, scientists have been able to interpret changes that are occurring in this century in the context of cycles that have been repeated since the last glaciation, some 6,000 years ago.

McNab and Avers (1994) classified coastal Louisiana in the Outer Coastal Plain Mixed Forest Physiographic Province, an extensive and diverse area that includes the Atlantic and Gulf of Mexico coastal plains from Maine to the Texas boundary with Mexico. The province includes the Louisiana coast prairies and marshes, which is an area of weakly dissected alluvial plain with poorly drained soils subject to flooding and high water tables and plant communities dominated by prairie grasses, marshes, and forested wetlands, including baldcypress (Fig. 1) and baldcypress–tupelo swamps.

Rapid Loss of Wetlands in Coastal Louisiana

The annual rate of loss in the area covered by Louisiana's coastal wetlands is currently about 66 square kilometers per year, down from a high of 107 square kilometers per year in the early 1980's (Dunbar et al. 1992; U.S. Geological Survey, National Wetlands Research Center, Lafayette, Louisiana, unpublished manuscript). Most of the change results from loss of vegetated marsh that reverts to open water. No other coastal areas of the United States experience such large-scale wetlands changes. Wetland scientists report additional large areas of coastal Louisiana that now appear to show the same visual pattern of stress that is exhibited by vegetated marsh before it disappears. These wetlands have always been dynamic systems, and the expansion and shrinking of deltas and subdeltas and their associated wetland and barrier systems have been in a fluctuating balance for millennia.

A combination of natural processes modified by humans is responsible for the present high rates of wetland degradation and loss along the Louisiana coast. The sea level relative to the land surface (*relative sea level*) is rising because the rates of coastal land lowering are very high. Large winter storms and hurricanes resculpt the coastline and rapidly change habitats. As the relative sea level rises, wetlands sink beneath the intertidal zone, and barrier island systems move shoreward and become thinner. Some barrier islands have submerged entirely in the last 50 years, and more are on the verge of total submergence.

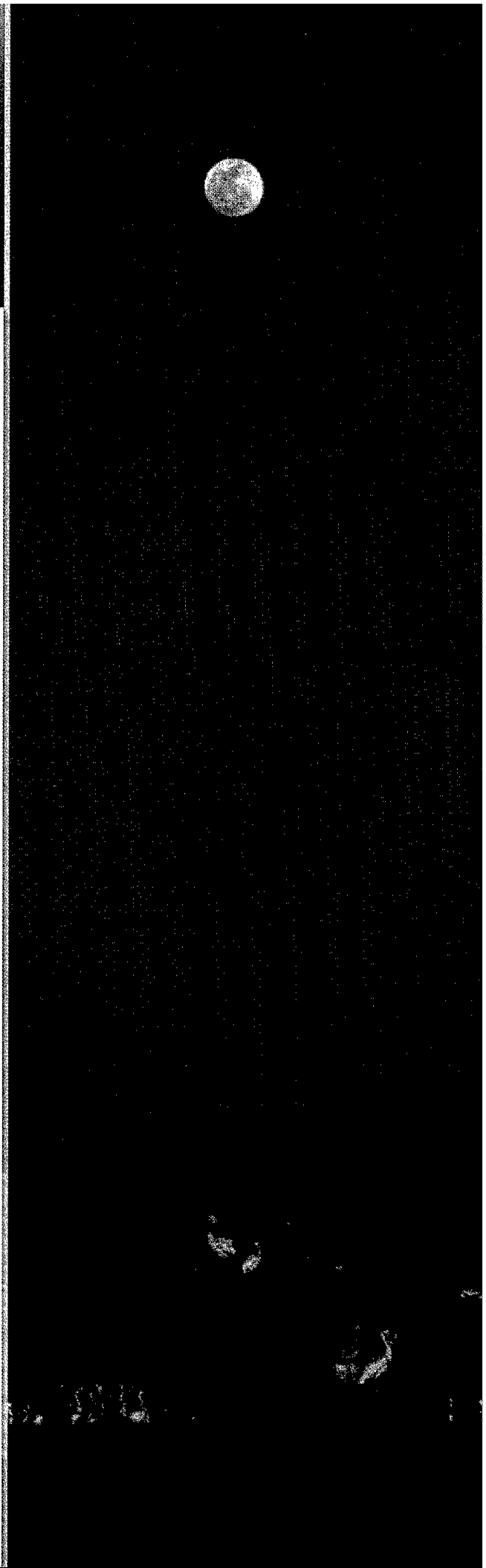

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Fig. 1. Baldcypress in the Red-eye Swamp of the Atchafalaya basin; the cypress stumps are the remains of logging that occurred in the basin from the late 1880's to the late 1920's.

Human influences have helped tip the balance of growth and shrinking of coastal delta ecosystems. In particular, the levees and associated navigational works of the Mississippi River prevent the overflow of fresh water and sediments into the adjacent marshes during spring floods. These structures extend to the river's mouth, where fresh water and heavy, delta-building sediments enter deep water on the edge of the Gulf of Mexico Continental Shelf. The levees have eliminated almost all inflow to the marsh system from the Mississippi River, except in the Atchafalaya basin and at the very mouth of the river at the Balize delta. When levees were built to control flooding and aid navigation, no one anticipated their contribution to wetland loss. Canals built for oil and gas exploration, pipelines, well maintenance, and transportation have also contributed to wetland loss. Artificial canals and their associated spoil deposits are directly responsible for at least 10% to 30% of the loss, and an additional but unknown percentage of loss may be attributed to their indirect effects.

Ecosystems that are threatened by continued losses of coastal Louisiana wetlands provide habitat for internationally significant migratory waterfowl concentrations. The threatened habitats, which cover almost 3,000 square kilometers, also support large nesting concentrations of other birds, including threatened and endangered species such as the eastern brown pelican and the bald eagle. These areas also include 12 national wildlife refuges, Jean Lafitte National Park, and several state wildlife management areas, with land holdings totaling almost 300,000 hectares (National Park Service 1993; U.S. Fish and Wildlife Service 1996).

Cycles of Change in Coastal Ecosystems

Change in natural systems is fundamental and universal (see chapter on Natural Processes). The defining geomorphic processes acting upon the Louisiana coast are nearly all cyclic and thus, to some degree, predictable. These cycles range in length from the alternating marine–delta environments of the Tertiary (especially the Miocene, 20 million years ago, when the oil and gas reserves underlying the coast were formed) through the successive glacial–interglacial intervals of the Pleistocene, to the cycles of delta lobe formation and loss of the past 10,000 years that define the extent and present surface pattern of the Louisiana coast. The geomorphic cycles are linked to the flows of water down the Mississippi River and to long-term climatic events and cycles. Scientists have also described short-term cycles of wet and dry years that modify hydrology and directly affect animal and plant populations.

Although recent 100- to 5,000-year geomorphic cycles control the pattern of ecosystems on the landscape and its consequent change through time, all biotic processes also demonstrate seasonal cycles of growth and dormancy and respond to the seasonal flood cycle. Particularly important in the coastal region is the seasonal cycle of bird, fish, and shellfish migrations, which vary in space as well as time.

Coastal Ecosystems Are Open Systems

Coastal ecosystems in general, and Louisiana coastal ecosystems in particular, are open systems—they both gain and lose matter and organisms to other environments (Watzin and Gosselink 1992). Ecologically, they are defined as a type of *ecotone*, a transitional area that here is between the ocean and terrestrial uplands and is influenced by both. The Louisiana delta receives its enormous supplies of fresh water, sediments, and nutrients (as well as toxins) from the Mississippi River watershed, which covers about 41% of the conterminous United States. The delta's fate is thus controlled by events occurring all over this enormous watershed, including dam building (see chapter on Water Use), forest clearing (see chapter on Land Use), and heavy nutrient runoff from Midwest farmlands. It is also influenced by tides and marine storms that flood the coastal zone and deposit sea salt in coastal soils. Alterations to the Lower Mississippi River, including levees, blockages of former drainage systems, large and small water-control structures, canals, and channelization to

support shipping, have all greatly influenced Louisiana's coastal wetlands. Biologically, the coast is also open and is dominated, at least seasonally, by migratory animals—fishes, shellfishes, and birds that move in and out of the coastal estuaries and wetlands.

Geology and Geomorphology of the Louisiana Coast

The Mississippi River Deltaic Plain

Geologically, the Louisiana coast consists of an eastern deltaic system and associated barrier islands built by the Mississippi River, and a geologically distinct Chenier Plain to the west, which is named for the linear, oak-dominated ridges that parallel this part of the coast (*chenier* is the French word for *oak*).

The Mississippi River, the largest river system in North America, drains an area of 4.76 million square kilometers. The average discharge of the river at the Mississippi River delta apex is approximately 15,400 cubic meters per second, with a maximum of 57,900 cubic meters per second and a minimum of 2,830 cubic meters per second. Sediment discharge is generally about 240 billion kilograms annually. The sediments brought by the river to the delta are 70% clay, mixed with silt and sand.

The river has had a pronounced influence on the development of the northern Gulf of Mexico. In the Tertiary (65–2.5 million years before the present), the large volumes of sediment carried by the Mississippi River created a major sedimentary basin, and many of the subsurface deposits, especially those that formed in localized centers of deposition, have been productive reservoirs of oil and natural gas. Faulting of these Tertiary sediments led to the migration and accumulation of hydrocarbons in fields below the coast, especially along the flanks of salt domes that were forced up through the sediments from the underlying rock strata (Roberts et al. 1989). These are sites of intensive oil and gas extraction, an activity that has strongly influenced the development of coastal ecosystems (Louisiana Coastal Wetlands Conservation and Restoration Task Force 1993).

In more recent geologic times, changing sea levels associated with the advance and retreat of inland glaciers during the Pleistocene ice ages greatly influenced sedimentary patterns off the coast. To understand the development of the present-day coastal wetlands, it is necessary to view the changes in the Mississippi delta and its adjacent coastal plains in relation to several time scales. These time scales range from those geologic periods associated with changing sea levels to recent changes in the past 100 years in the formation of minor subdeltas in the most recent deltaic lobe, the Balize delta. Sediments deposited by the river during the last several million years have caused excessive loading and resulting subsidence throughout the Mississippi River Deltaic Plain. To a large degree this loading has controlled the rate of coastal wetland addition and loss through much of recent geologic history (Gosselink 1984; Fig. 2).

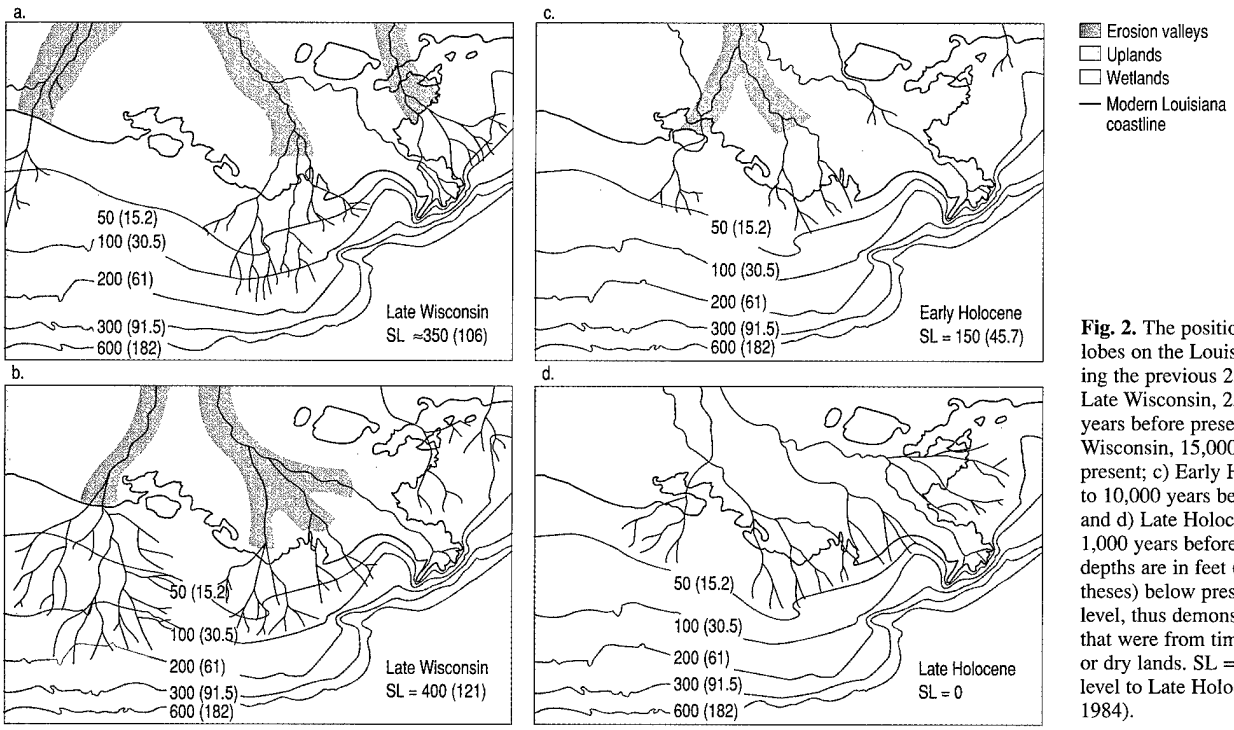


Fig. 2. The position of major delta lobes on the Louisiana coast during the previous 25,000 years: a) Late Wisconsin, 25,000 to 20,000 years before present; b) Late Wisconsin, 15,000 years before present; c) Early Holocene, 12,000 to 10,000 years before present; and d) Late Holocene, 5,000 to 1,000 years before present. Bottom depths are in feet (meters in parentheses) below present-day sea level, thus demonstrating areas that were from time to time marsh or dry lands. SL = relative sea level to Late Holocene (Gosselink 1984).

Recent Geomorphic Delta Cycles

The past 5,000 to 6,000 years have been characterized by relatively stable climates and small changes in sea level along the Louisiana coast. Most authorities agree that there are at least seven delta lobes (Fig. 3), which formed one after another. The result of the building and subsequent abandonment of these delta lobes by the river was the construction of a modern deltaic Coastal Plain with a total area of 28,000 square kilometers (Coleman 1976).

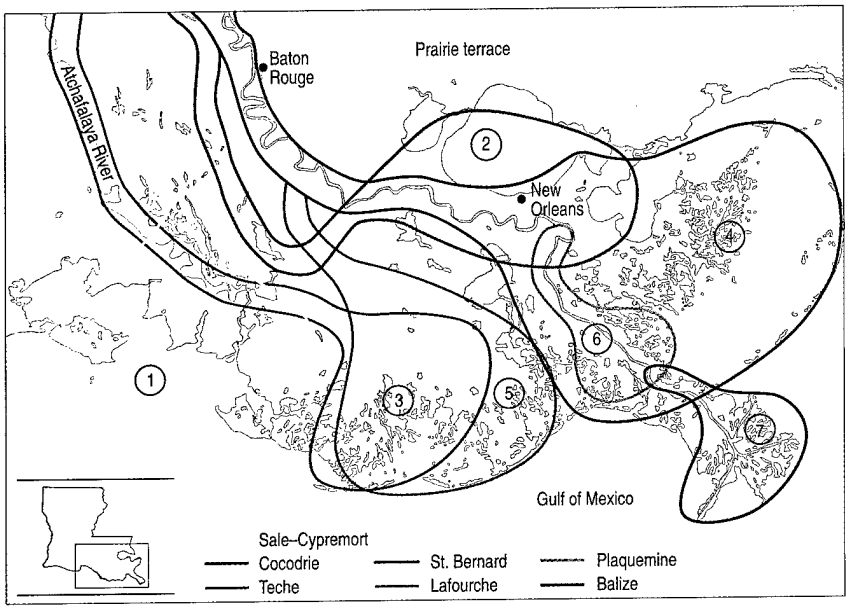
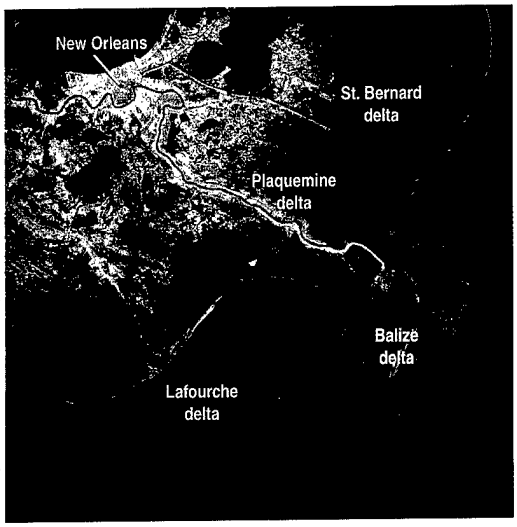


Fig. 3. Lobes of Mississippi River deltas, numbered in chronological order of formation (modified from Kolb and Van Lopik 1958). Light shading shows extent of current coastal marsh and bottomland forest.

One of the earlier deltas, the Sale–Cypremort delta, developed along the western flanks of the present Mississippi River Deltaic Plain (Fig. 3). In approximately 1,200 years, an extensive coastal marshland emerged before the river switched its course and began depositing sediments in another location, the Cocodrie system (Fig. 3). Over time this site of deposition was also abandoned, and a new delta lobe began to form. This process continues, each delta completing a cycle of expansion that lasts about 1,000 to 1,500 years. Over the last 600 years, the most recent delta cycle formed the modern birdfoot or Balize delta (Figs. 3 and 4). The modern Balize delta has nearly completed its expansion cycle, and in this century a new distributary, the Atchafalaya River, began drawing off a portion of the Mississippi River's water and sediment discharge. Thus, the new Atchafalaya delta is beginning its expansion phase (Van Heerden and Roberts 1980; Wells et al. 1982).

Broad coastal marshes form during each expansion phase of the delta cycle. Scruton (1960) referred to this as the *constructional phase*. However, once the river begins to abandon its major deposition site, the unconsolidated mass of rapidly deposited deltaic sediments is immediately subjected to reworking and subsidence, resulting in progressive flooding of the marshes, and within a few thousand years the delta lobe sinks beneath the sea. Scruton (1960) called this stage of the delta cycle the *destructional phase*. Thus, both land gain and land loss take place in the relatively short geologic period of 4,000–5,000 years.

A satellite image of the eastern portion of the Mississippi River Deltaic Plain shows several delta lobes in different stages of construction and destruction (Fig. 4). The oldest lobe shown is the St. Bernard delta, which was actively expanding some 3,000 years before present. This delta lobe remained active for approximately 1,200 years, forming a coastal marshland along the eastern Mississippi River Deltaic Plain (Gosselink 1984). Approximately 1,800 years ago, the Lafourche channel began its expansion. The St. Bernard delta, deprived of its sediment load, began to subside. The Lafourche distributary gradually increased its sediment yield, and within 1,000 years had built a major delta lobe west of the modern Balize delta. The sea began to intrude into the formerly freshwater marshes of the St. Bernard delta, and the marshland deteriorated rapidly. Coastal headlands and barrier islands formed at the mouths of the former distributaries. Eventually the Lafourche delta system reached its maximum development, while the modern delta lobes (Plaquemine and Balize) began their expansions. The Lafourche delta, abandoned by the river, was then subjected to marine reworking and compaction. During the past 800 years, this delta has lost land, mainly through saltwater intrusion and flooding of the marshland behind a coastal barrier still attached to the former distributaries.



Courtesy National Aeronautics and Space Administration (NASA)

Fig. 4. Satellite image of the Mississippi River delta region showing delta lobes of different ages (Gosselink 1984).

The Mississippi River has constructed a major delta lobe in the modern Balize delta. However, changes in river gradient and flow resistance now favor diversion of this flow to a more efficient path to the Gulf of Mexico. If artificial river-control structures did not limit diversion to about one-third of the Mississippi River's discharge, the river would soon abandon this lobe in favor of the Atchafalaya River course, diverging from the Mississippi River 480 kilometers upstream from the river's present mouth.

The Modern Mississippi River Delta

The modern Balize delta (Fig. 5) was constructed during the past 500 years. Because it is relatively young, it offers researchers an opportunity to evaluate the short-term processes responsible for delta building and inundation which mimic, on a smaller scale of time and space, the construction and destruction of the major delta lobes. When a break (or *crevasse*) occurs in the natural levee of one of the river distributaries, water rushing through the break deposits sediment into the adjacent bay (Fig. 6). After an initial break in the levee of a major distributary during flood stage, flow through the crevasse gradually increases through successive floods, reaches a peak of maximum deposition, then decreases and is cut off (Coleman 1976). As a result of compaction, the crevasse system is flooded by marine waters and reverts to a bay environment, completing its sedimentary cycle. Of the six recent crevasses (Fig. 5), four have bay fill sequences that have been dated from historical records, and much of their development during the past few hundred years can be traced by reviewing historical maps. Historical maps of Cubits Gap, for example, illustrate a cycle of delta building and abandonment (Fig. 7). The area shown on the 1838 map was surveyed before the break and shows a narrow, natural levee separating the Mississippi River from the shallow Bay Rondo. In 1862 the daughters of an oyster fisherman named Cubit excavated a ditch to allow passage by shallow draft boats. Although the original ditch was only about 120 meters wide, the flood of 1862 enlarged the opening, and by 1868 the break was 740 meters wide. By 1884 the initial development of a complex series of distributary channels had deposited relatively coarse sediment near the break, with shoaling in the bay caused by underwater deposition of the finer-grained deposits. A 1905 map shows that many of the major distributaries had developed and that rapid expansion had taken place since 1884. A major portion of the subdelta had been constructed by 1922; some small bays were already beginning to open up, indicating that some parts

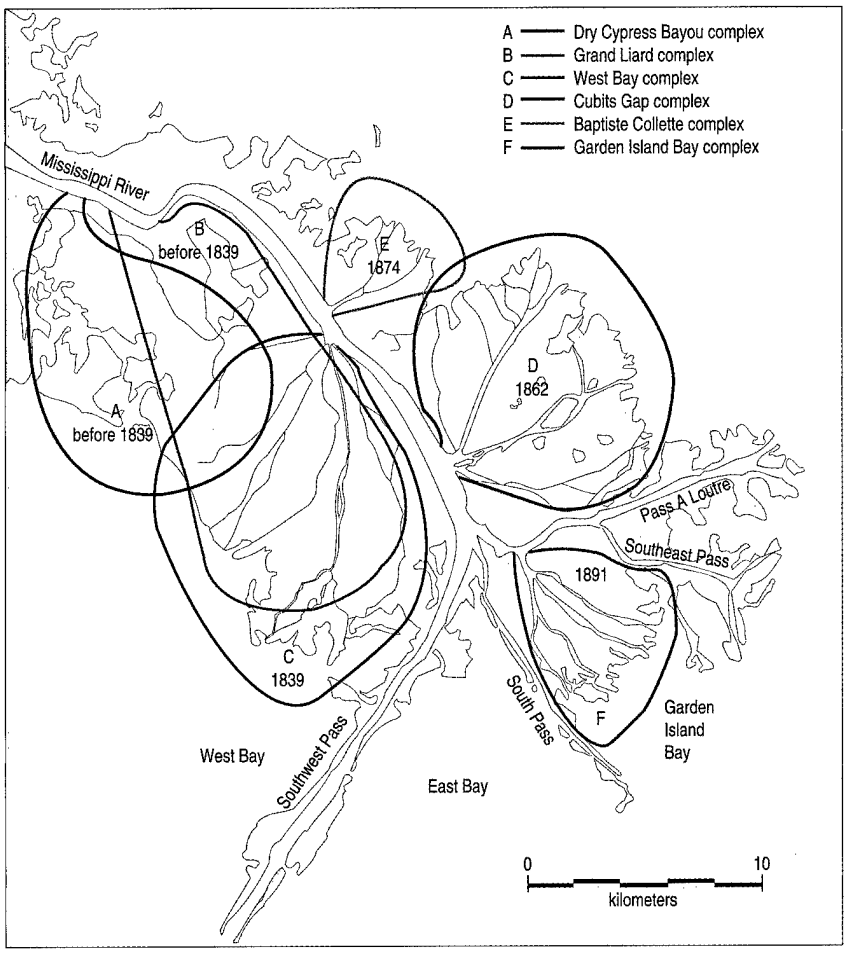


Fig. 5. Six subdeltas of the modern Mississippi Balize delta recognized from maps and sediment analysis. Dates indicate years of crevasse openings (Wells et al. 1982).

Courtesy D. White, Loyola University, New Orleans; modified from an original image from NASA

Fig. 6. The bird's foot formation in the center of this photo shows the early stage of formation of a subdelta lobe after a break (crevasse) occurred in the natural levee of the adjacent channel. Another delta lobe can be seen in the top center of the photo.

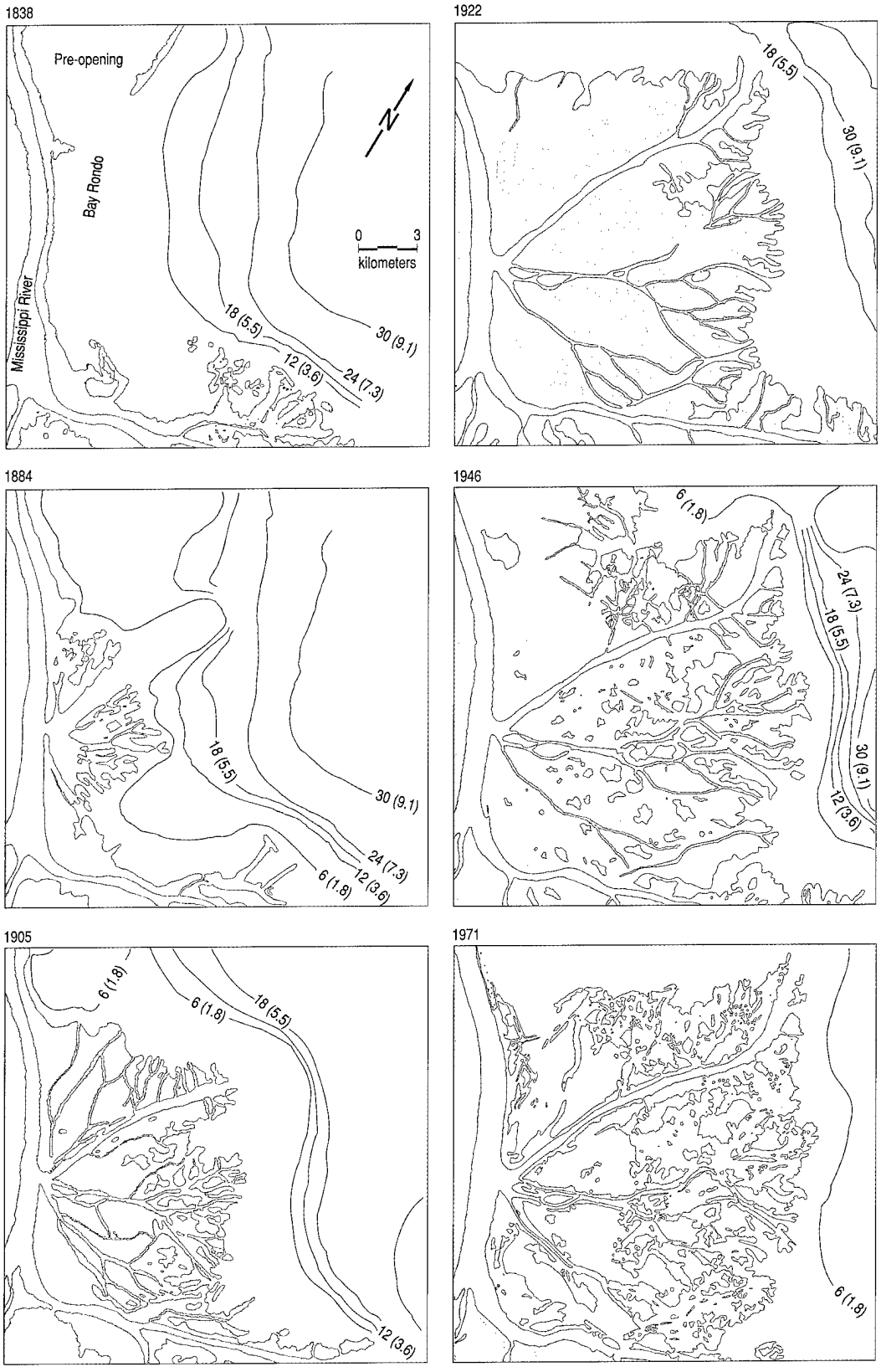


Fig. 7. Sequential development of Cubits Gap subdelta. Bottom depths are in feet (meters in parentheses) below sea level (Wells et al. 1982).

of the crevasse (subdelta) system were being deprived of sediments. The 1946 map shows sedimentation primarily at the seaward ends of selected distributaries; it also reveals that marshland loss was beginning. By 1971 a large part of the crevasse system was inundated by seawater, and marsh loss was becoming significant. The only sediment deposition occurring was at the seaward ends of some of the distributaries and underwater in the bay fill front. Note

that land loss begins first near the crevasse break where sedimentation is extremely slow, depending only on overbank flooding, whereas higher sedimentation rates still prevail near the most remote parts of the crevasse system.

The growth and deterioration cycle of bay fills over a relatively short period of 50 to 100 years parallels the cycle of major delta lobes described previously. The growth period in a delta cycle approaches 800 to 1,000 years, and the deterioration period can be as long as 2,000 years. Bay fills provide an excellent model for evaluating the future growth of the newly formed Atchafalaya delta (Wells et al. 1982) and the deterioration of the former Mississippi River delta lobes.

Barrier Island Formation

The inactive delta lobes of the Mississippi River are fronted by a series of headlands and barrier islands. The sediments are derived from the reworking of formerly active distributary mouths, and they form erosional headlands with flanking barrier deposits after the distributary is abandoned (Penland et al. 1988). Sand deposits in the abandoned headland are reworked and dispersed along the shore into flanking barriers, thereby enclosing bays between major delta lobes (Fig. 8). Gradual submergence of the delta lobe separates the headland from the shoreline, creating a lagoon behind a barrier island. The island migrates landward but does not keep pace with the retreating mainland shoreline. Eventually, the island is left far from the mainland and deteriorates into a shoal (Reed 1995; Fig. 8).

Geomorphology of the Chenier Plain

West of the Mississippi River delta, the Louisiana coastal zone was created by forces related to the sediment supply of the river but not by direct sediment deposition, as in the delta. Pleistocene deposits, which form the geologic substrate of the Chenier Plain region, are found at the surface a few kilometers inland from the coast and dip gently seaward to include the slope of the Continental Shelf. When the last continental glaciers lowered sea level to 135 meters below its present level (Fisk and McFarlan 1955; Gould and McFarlan 1959) and the shoreline was about 200 kilometers seaward of its present position (Russell and Howe 1935), coastal streams cut valleys into the exposed Pleistocene deposits. As the level of the Gulf of Mexico rose during the subsequent glacial melt, layers of sediments were deposited on the eroded Pleistocene surface (Saucier 1974), including in the open gulf, bays, lakes, marshes, and swamps. In contrast to the deep Holocene sediments of the Mississippi River Deltaic Plain, on the Chenier Plain Holocene sediments form a thin veneer, except in the eroded river valleys. Today, the Chenier Plain supports an extensive marshland interspersed with large inland lakes formed in river valleys that were drowned after the last glaciation.

When the sea reached its present level, the shoreline was landward of its present location. During periods when the course of the Mississippi River was at the western edge of the Deltaic Plain, sediments from the river were carried westward by currents along the shore, forming mudflats along the Chenier Plain

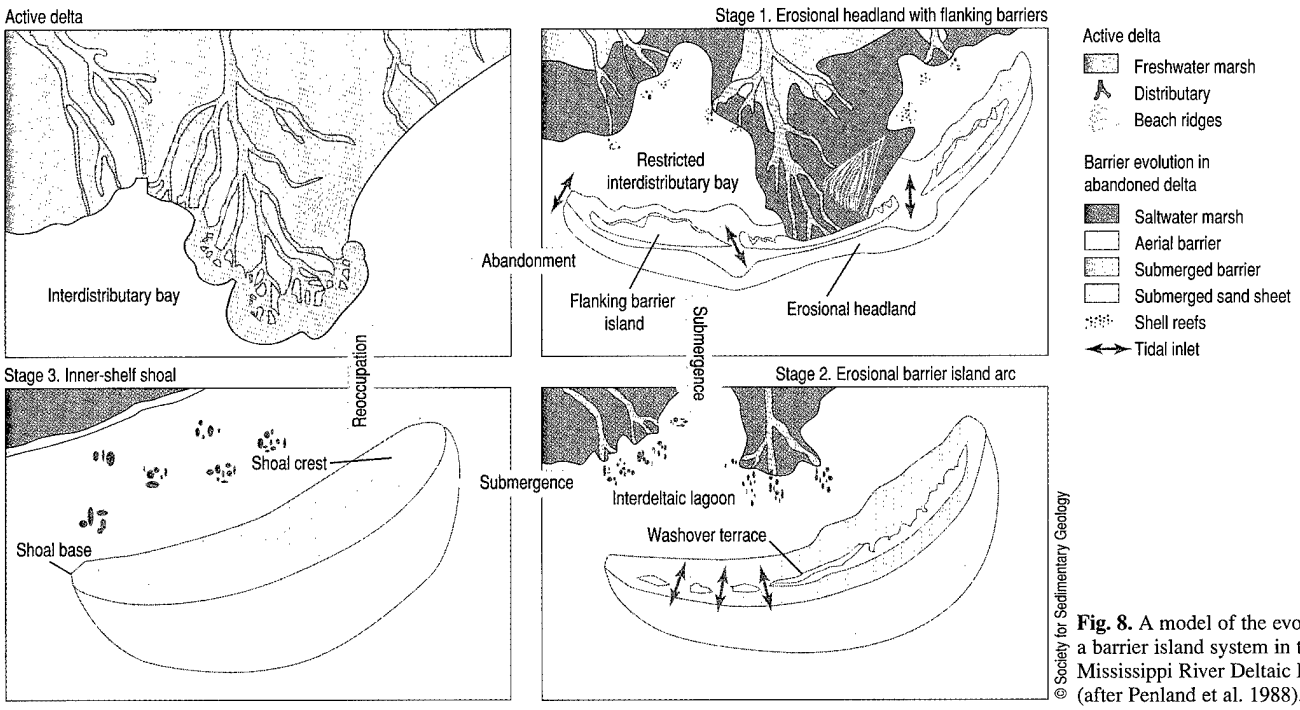


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Fig. 8. A model of the evolution of a barrier island system in the Mississippi River Deltaic Plain (after Penland et al. 1988).

shoreline (Kemp 1986). When the active channel of the river moved eastward and the Chenier Plain lost most of its sediment supply, erosion reworked the mud deposits, winnowing out the finest materials and forming beachfront ridges (cheniers) along the coast, with the remnants of the old mudflats (now marshes) behind them. The present topography reflects multiple river-mouth ridges converging to form a single beachfront ridge between the river inlets (Gosselink et al. 1979a,b,c; Fig. 9).

With the increase in this century of flow in the Atchafalaya River close to the western edge of the delta, fluvial processes are again dominating the Chenier Plain, and mudflat development is occurring along its eastern coast (Kemp 1986).

Accretion and Subsidence

The only active deltaic areas on the coast today are the Balize delta at the mouth of the Mississippi River and the actively expanding Atchafalaya River delta. Even within the Balize delta, much of the heavy sediment load of the Mississippi River is entrained by levees and navigational structures and is deposited in deep water on the edge of the Continental Shelf. Today, destructional processes far outweigh constructional processes over the Mississippi delta as a whole. The Chenier Plain, although protected on the marine edge by chenier ridges, is also rapidly losing wetlands, probably as an indirect result of human activities that have altered hydrology and allowed saltwater to invade freshwater marshes.

Net submergence is a dominant process in this destructional phase. It is a complex process with three components: subsidence, sea-level rise, and accretion of the surface through mineral sediment deposition and organic matter production (for example, see Cahoon et al. 1995). Subsidence of the substrate and eustatic sea-level rise lead to submergence of the land surface. Vertical growth via mineral sediment deposition and underground plant growth counter the effect of submergence. Net submergence occurs when subsidence and sea-level rise exceed vertical growth. Net submergence is taking place in most of the marshes in this destructional phase of the delta cycle, where submergence rates average about 1 centimeter per year, whereas vertical growth averages only about 0.6 centimeters per year. These subsidence estimates may actually be underestimates for many areas because they do not include subsidence that is occurring in the upper few meters of the substrate (Cahoon et al. 1995).

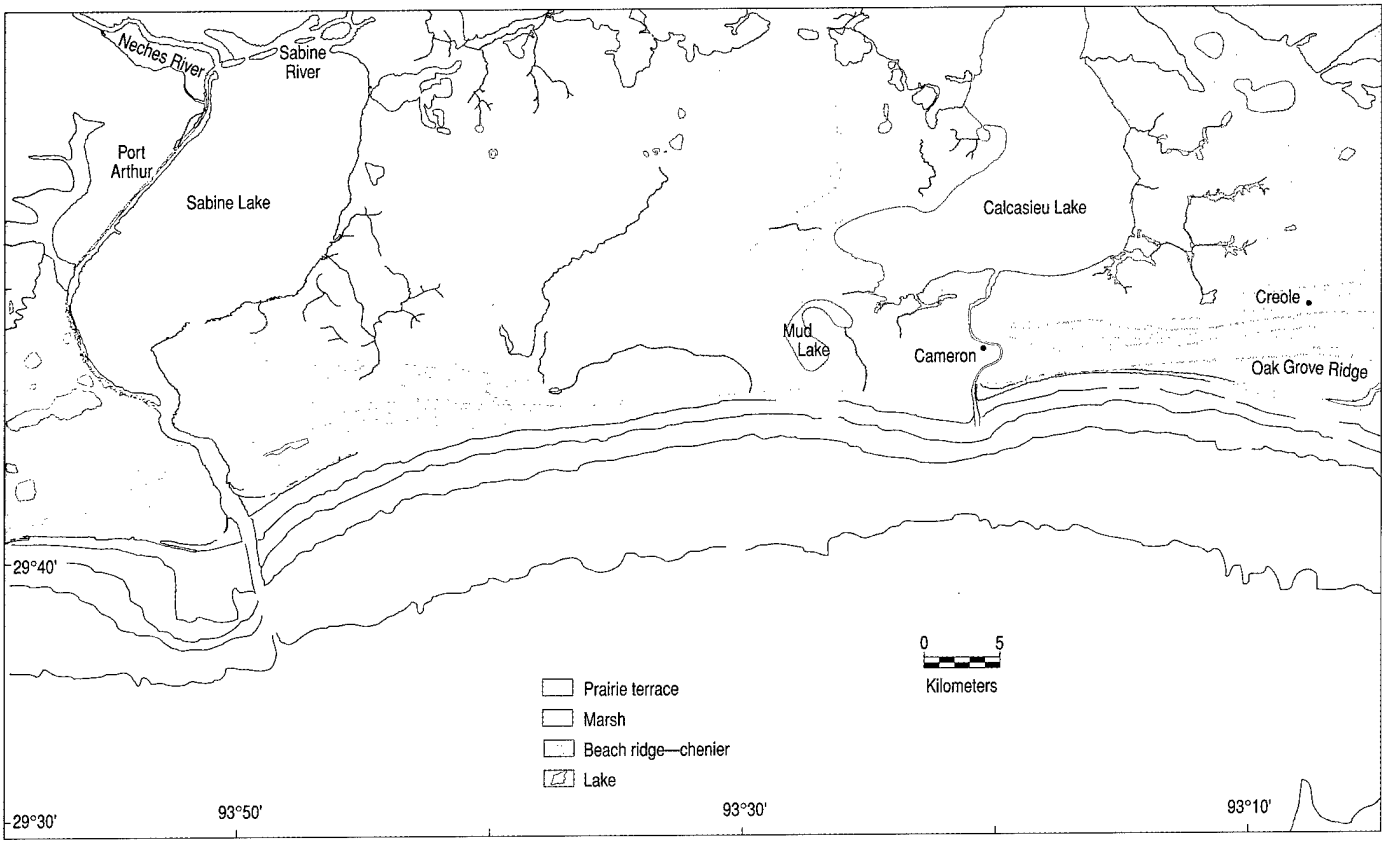
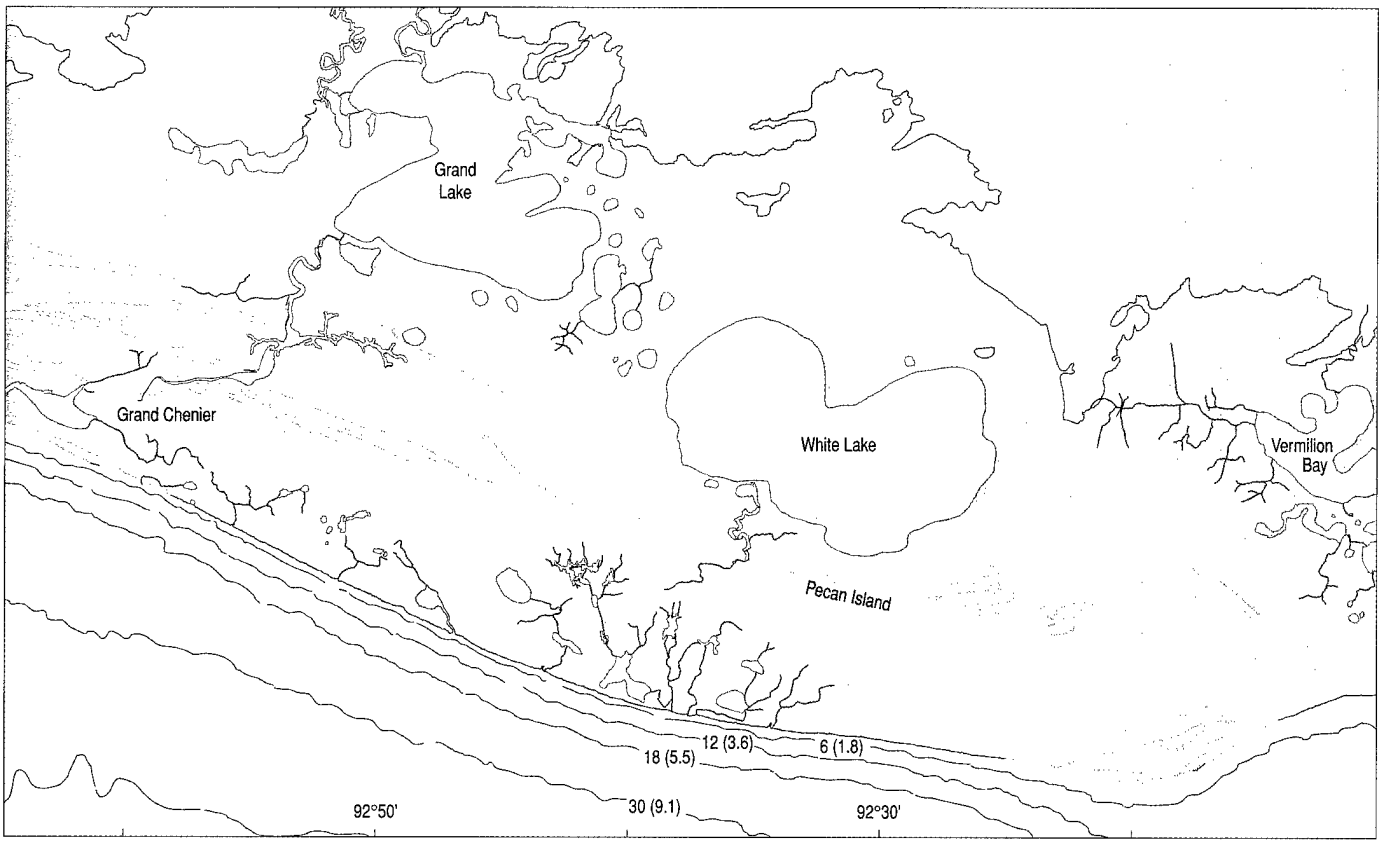


Fig. 9. The regional geomorphology of the Mississippi River Chenier Plain (after Penland and Sutter 1989). Bottom depths are in feet (meters in parentheses).

Along the northern gulf coast, eustatic sea-level rise is a minor component of submergence, about 0.23 to 0.24 centimeters per year (Gornitz et al. 1982; Penland et al. 1989), less than 10% to 50% of the total submergence rate. Most observed submergence is thus related to subsidence (Penland et al. 1994), and the subsidence rate is extremely variable across the coast (Fig. 10). The age and thickness of Holocene (recent) deposits are a contributing factor to the subsidence rate because thick deposits have more potential for compaction than thin ones and because younger deltaic deposits subside faster than older deposits, reflecting the progressive consolidation of sediments. The thickest Holocene sediments (nearly 100 meters; Penland et al. 1994) are within the incised valley of the Mississippi River; this valley spans the area between the Atchafalaya River on the west and New Orleans on the east, the largest portion of the coast. Thus, this part of the coast is generally subsiding faster than other sections. Peats, organic-rich sediments, prodelta clays, and bay clays have the greatest consolidation potential (Kuecher et al. 1993).

Most of the compaction occurs in the upper 2 meters of the sediment profile, reflecting the biological process of peat decomposition during the first few years after production. After that, sediment compaction and soil dewatering appear to dominate (Turner 1991).

Until recently, most of the emphasis on accretionary processes that counterbalance subsidence has focused on the introduction of mineral sediments by fluvial and marine processes, which occurs during the constructional phase of a delta cycle. However, in the destructional phase of a delta, organic material—primarily live and dead plant roots still in place—is the major structural component of the substrate, and plant underground production is the major expansion force (Nyman et al. 1990; Nyman et al. 1993a). Inadequate organic matter accumulation results from a decrease in root production of flood-stressed plants as a marsh subsides. Mineral sediments counteract this flooding stress, as shown by the positive relationship between soil bulk density and plant biomass (DeLaune et al. 1979; Nyman et al. 1994; Fig. 11). The role of sediments, however, is not structural but is indirect through stimulation of plant growth by mineral nutrients (Broome et al. 1975; DeLaune and Pezeshki 1988), precipitation of toxic sulfides (King et al. 1982; Mendelssohn and McKee 1988), and buffering of low reduction/oxidation potentials (Ernst 1990).



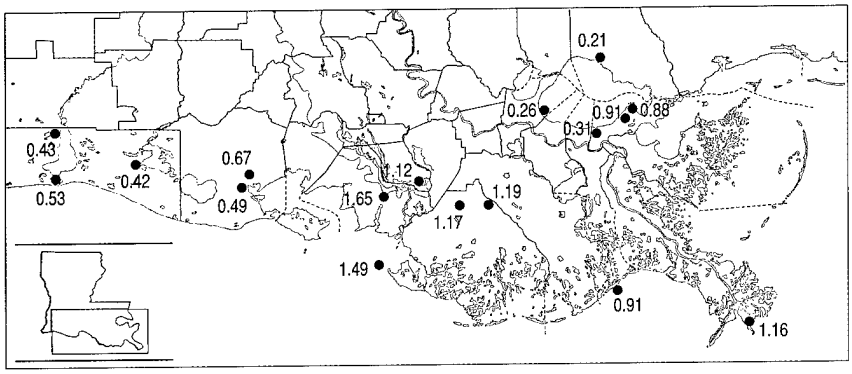


Fig. 10. Coastal Louisiana subsidence rates, centimeters per year (modified from Ramsey and Penland 1989; Penland and Ramsey 1990).

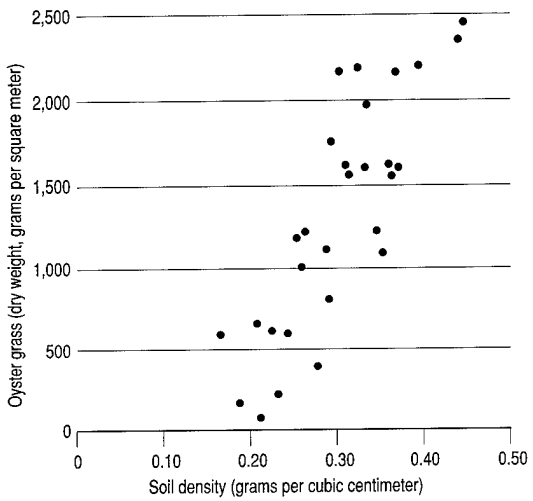


Fig. 11. Relationship between soil bulk density and aboveground biomass of smooth cordgrass in saltwater marshes (after DeLaune et al. 1990). Reprinted courtesy Elsevier Science, Catena, Volume 17, p. 282 (DeLaune et al. 1990). Processes governing marsh formation in a rapidly subsiding coastal environment. © 1990, Elsevier Science N L, Sara Burgerhartstraat. 25, 1055 KV Amsterdam, The Netherlands

The Present Environment of Coastal Louisiana

Climate

In the Mississippi River delta region, at about 30° north latitude, solar energy reaching the Earth's surface varies from about 200 calories per square centimeter per day during the winter to a peak of nearly 600 calories per square centimeter per day in June and July. During the summer, insolation at this latitude is higher than anywhere else on the globe; it falls off both northward toward the Arctic and southward toward the Equator. Therefore, midsummer growth potential in terms of solar energy is as high in the Mississippi delta as it is anywhere else on Earth.

As one might expect, seasonal air temperatures closely follow insolation. Mean monthly temperatures range from a December–January low of about 14°C to a midsummer high of about 30°C. Because of the moderating effect of the water bodies and high humidity, midday temperatures seldom exceed the low 30's (Celsius) despite the high insolation. Frost is infrequent; the annual average number of frost-free days on the coast is about 300. Because most of the inshore waters are less than 1 meter deep, water temperature closely follows air temperature.

Each of the components of the *water budget* (rainfall, evapotranspiration, river inflow, and tides) varies in both time and space. Annual precipitation, usually as rain, averages about 150 centimeters (Fig. 12). October tends to be the driest month and July the wettest, but torrential rains are common at any time. Wax et al. (1978) analyzed the atmospheric circulation of the Louisiana coast and found that high pressure systems moving in from the north and west bring cool, dry air. These systems are easily recognized during the winter as cold fronts but occur throughout the year. The fronts are typically followed by atmospheric conditions that bring warm air in from the coast, usually with heavy cloud cover and rain. About two-thirds of the coastal rainfall is associated with frontal activity of this kind. Ten to fifteen percent of the rainfall is from infrequent, severe tropical storms and hurricanes.

The effect of precipitation depends not so much on absolute amount but on the relationship between rainfall and evaporation from water and plant surfaces. Excess water occurs during the winter, a balance during the summer, and occasional deficits from May through August (Fig. 12), with an annual rainfall surplus of about 75 centimeters. This surplus is important for maintaining salinities well below seawater strength in the estuaries.

Hurricanes and severe winter storms play a major role in ecosystem maintenance and development (see box on Hurricane Andrew in the Natural Processes chapter). These severe events overturn floating marsh mats, decimate forests, kill large areas of vegetation through inundation with saltwater, and account for most of the

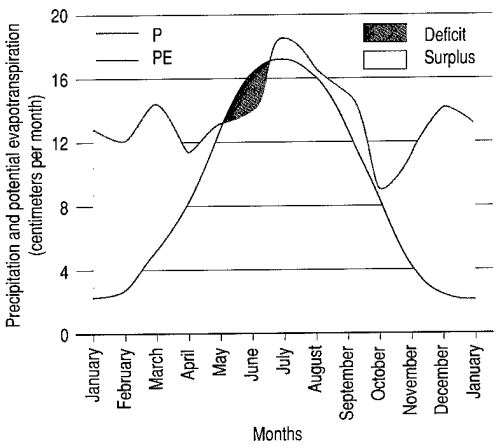


Fig. 12. Average water budget for the upper Barataria estuary, 1914–1978 (modified from Gosselink 1984; Sklar 1983). P = precipitation, PE = potential evapotranspiration.

sediment deposition in interior destructional phase marshes (Baumann et al. 1984; Reed 1995; Guntenspergen and Vairin 1996).

Fluvial Processes

The largest source of fresh water to the Louisiana coast is the Mississippi River and its major distributary, the Atchafalaya River. The combined annual flow of these two rivers averages about 15,400 cubic meters per second. Other, smaller rivers contribute additional water from local watersheds. Flow is strongly seasonal, peaking in late spring, fed by melting snow and spring rains in the Upper Mississippi watershed. River flow can be nearly independent of local rainfall because of the size of the Mississippi River watershed but is often reinforced by spring rains along the coast.

The inactive delta of the Mississippi River (the part that has been abandoned by the river) is isolated from direct riverine input by natural and artificial levees. The Mississippi and Atchafalaya rivers discharge into the Gulf of Mexico through the active Balize and Atchafalaya delta lobes. Most of their waters are carried westward along the coast, freshening the gulf waters that move in and out of the Barataria, Terrebonne, and Vermilion estuaries. Thus, although these three estuaries have almost no direct freshwater inflow except from local runoff, the rain surplus and the moderated salinities offshore keep estuarine salinities much lower than that of seawater.

Marine Processes

Water fluxes in the coastal marshes are driven by the water-level differences across the estuary. These change over the long term, seasonally, and daily (Fig. 13). Since the ocean reached its present level about 6,000 years ago, it has been rising relative to the land at a rate measured in centimeters per decades (Fig. 13a). Superimposed on this long-term trend is a mean water level that varies seasonally by 20 to 25 centimeters, with peaks in the spring and late summer (Fig. 13b). Part of this seasonal variation is related to the dominant variable wind regime over the Gulf of Mexico (Chew 1962). Maximum east and southeast winds in spring and fall move water toward the shore. During winter and summer, westerly winds (southwest in summer, northwest in winter) strengthen the Mexican Current and draw a return flow of water from the estuaries (Baumann 1980).

Superimposed on the seasonal water level change is a diurnal tide (Fig. 13c), which averages about 30 centimeters at the coast. Because of the broad, shallow expanse of the coastal estuaries, the tides decrease inland. The normal tide range decreases from saltwater to freshwater marshes (Fig. 13c); in the example in Fig. 13c, tides are still perceptible 50 kilometers inland from the tidal passes because of the extremely gradual slope of the land.

Water levels do not always follow predictable daily and seasonal cycles; they are modified strongly by unpredictable weather fronts with winds that push water in or out of the estuaries. Such effects are clearly shown in Fig. 13c, where gradually decreasing water levels are associated with a cold front beginning on 12 October 1972. The water levels suddenly rose on 19–22 October, when the wind changed to the south. The magnitude of these wind effects is often 40–50 centimeters, which, when combined with astronomical tides, can result in water-level shifts of more than a meter within

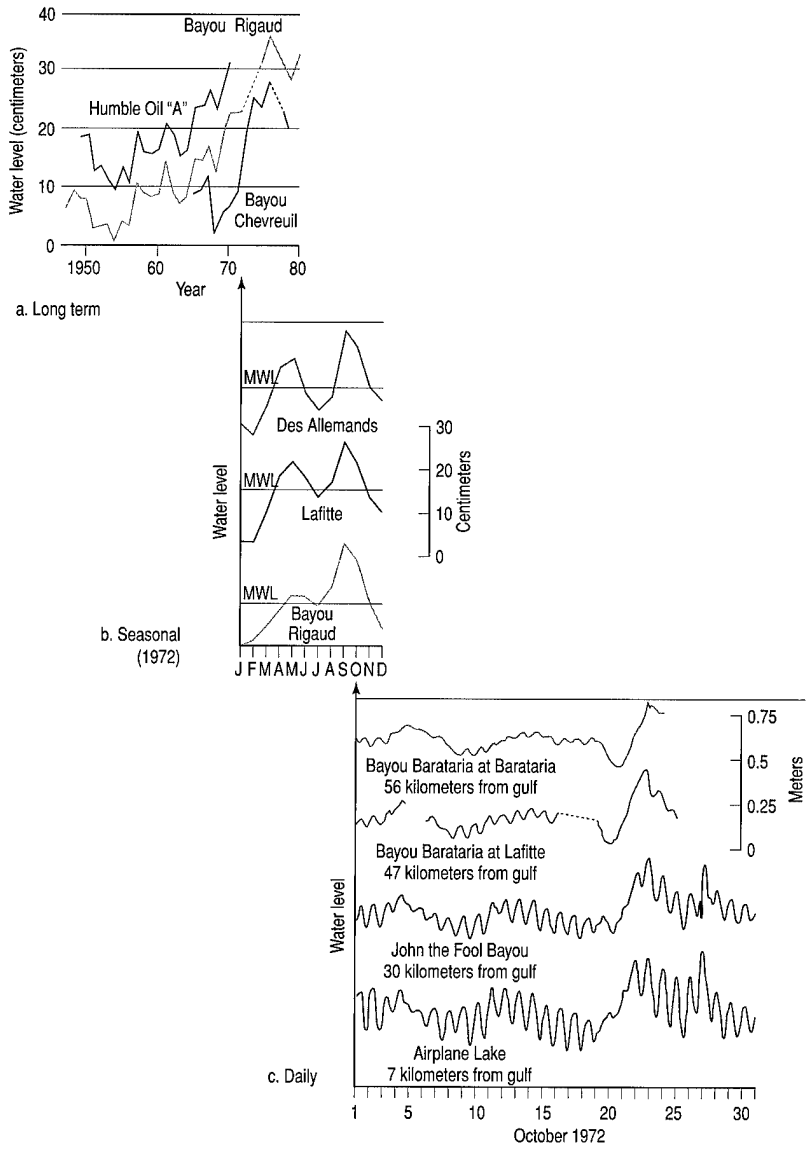


Fig. 13. Water-level trends in Louisiana coastal marshes: a) long term, b) seasonal, and c) daily. MWL = mean water level (Gosselink 1984).

12 hours. Such meteorologically driven changes in water level are common events. Tropical storms are much more unusual and may elevate water levels dramatically. The water-level height/frequency curve for Shell Beach, southeast of New Orleans, for example, shows that wind tides as high as 3.5 meters have been recorded and that 1.5-meter tides occur about once every 8 years. On a coast with a slope of about 0.2 centimeters per kilometer (Byrne et al. 1976), a 1.5-meter tide can flood hundreds of kilometers inland.

Human Effects

Before European settlement along the Mississippi River, the Coastal Plain gradually increased in area and elevation, supporting a wetland area of about 16,000 square kilometers. Dominant fluvial processes not only built new delta lobes but also nourished the deteriorating lobes through overbank flooding during high water in spring. During this century, though, the balance between land-building processes and destructional processes has tipped in the direction of land loss, resulting in a net conversion of 4,000 square kilometers of wetland to open water.

Continental-scale manipulation of the Mississippi River and its tributaries for flood control and hydropower has significantly influenced coastal ecosystems. After a major flood occurred in 1927, the U.S. Congress initiated a massive effort to levee the river, seal off the crevasses, and cut off long meanders to increase the gradient and accelerate runoff. Because of the levees, the river has built its present active delta to the edge of the Continental Shelf, where most of the sediments are lost in deep water and can no longer build land. A control structure constructed 480 kilometers above the mouth of the river has halted the imminent capture of the main flow of the Mississippi River by the Atchafalaya River; this structure limits the diversion to one-third of the combined flow of the Mississippi and Red rivers. The levee systems on both rivers limit overbank flow during spring floods to the lower Balize delta and to the Atchafalaya bay and its adjacent marshes (Louisiana Coastal Wetlands Conservation and Restoration Task Force 1993).

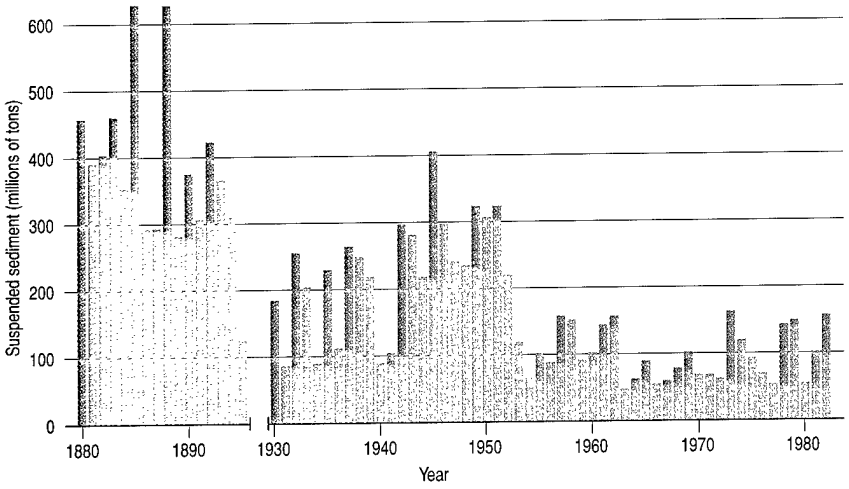


Fig. 14. Historical record of the suspended sediment load of the Mississippi River at New Orleans (Kesel 1987). Historical period = before 1900, pre-dam period = 1930–1952, and post-dam period = 1963–1982.

Before these artificial modifications, the Lower Mississippi River had an estimated average annual sediment discharge of 270 million cubic meters per year of suspended load, and bedload that may have been as high as 130 million cubic meters per year (Kesel et al. 1992). Since 1850, however, the sediment supplied by the Mississippi River and its tributaries has decreased by almost 80%. This reduction can be divided into three phases: a historical period before 1900, a pre-dam period (1932–1952), and a post-dam period (1963–1982). The suspended sediment load declined by 43% from the historical to the pre-dam periods and by 51% from the pre-dam to the post-dam periods (Fig. 14). At the same time, the particle size of the suspended sediment load has decreased. At 170 kilometers above the mouth of the river, the sand fraction decreased by 72% from the late 1800's to 1983 (Kesel 1989). The particle size distribution in the bedload also declined during this period. Presumably, dams on the tributaries, particularly the Missouri River, act as sediment traps, especially for the heavier sediment fraction, and are partly responsible for the decrease in both load and coarse fraction delivered to the delta. Clearing of the watershed for agricultural and urban development undoubtedly contributed to the suspended load during the last century, but clearing may have occurred before there were good records of sediment loading rates. Efforts to reduce erosion from agricultural fields in recent years are not reflected in the record.

Development projects within the coastal basins themselves also affect the rates of wetland loss. Early in this century more than 800 square kilometers of wetland were cleared, leveed, and pumped out to create agricultural and suburban lands (Harrison and Kollmorgen 1947). Draining the organic wetland soils resulted in rapid oxidation, subsidence, and reversion to open water when subsequent storms breached the levees. Many of these "reclamation" projects are still visible as large rectangular lakes (Fig. 15). More recently, structural management for marsh restoration has controlled the exchange of water through levees and control structures such as flumes and gates, which are typically managed to reduce flooding frequency and duration and to restrict

saltwater input. The effectiveness of this type of management is a source of considerable controversy.

Artificial canals also significantly affect coastal wetlands. Formerly, rain runoff from adjacent uplands flowed across the wetlands, dropping its load of sediment and nourishing the marshes. Now a network of drainage canals along the marsh–upland interfaces of the coastal estuaries carries this runoff directly into estuarine lakes and bays, bypassing the swamps and marshes (Conner and Day 1982). If runoff flowed across the wetlands, the trapped sediment would allow the vertical accretion of the marsh surface and would help minimize wetland subsidence. Additionally, the quality of the runoff water would be improved before it entered the lakes and bays because wetlands act as natural filters. Instead, the portions of the estuaries near urban areas are becoming increasingly turbid and enriched by nutrients (Craig et al. 1977; Gael and Hopkinson 1979).

At the seaward edge of the estuaries, navigation canals, especially those that cross the shoreline, disrupt water circulation. These canals are straight and deep in estuaries where the average depth is otherwise only 1 or 2 meters. They capture flow from smaller channels and allow the intrusion of saltwater deep into the estuary. Saltwater accelerates the conversion of freshwater and low-salinity marshes to saline marshes. When salt increases are sudden, salt-intolerant vegetation is often killed, and the marsh may erode before other vegetation can become established (Reed 1995).

An extensive network of medium-sized canals, dredged to provide access to oil and gas well sites (Fig. 16), links the navigation canals to the inner marsh and to the elaborate system of drainage canals constructed to drain floodwaters from the adjacent uplands. The canals themselves act in the same manner as the navigation canals and, in combination with them, change circulation patterns. For example, in the Leeville oil field (Terrebonne basin), the density of natural channels declined as dredged channels captured the flow of water. The canals also allow saltwater intrusion into formerly freshwater marshes and brackish-water marshes. In addition, the spoil banks of these canals block the flow of water across marshes, depriving them of sediments and nutrients, an effect that is especially noticeable where canals intersect and their spoil banks interlock to impound or partially impound an area (Turner 1987; Turner and Cahoon 1987a,b,c; Turner and Rao 1987, 1990; Reed 1995).

A linear relationship exists between canal density and marsh loss rate (Turner et al. 1982; Turner and Cahoon 1987a,b,c), although there is considerable unexplained variation in the

a.

Courtesy National Aeronautics and Space Administration (NASA)

b.

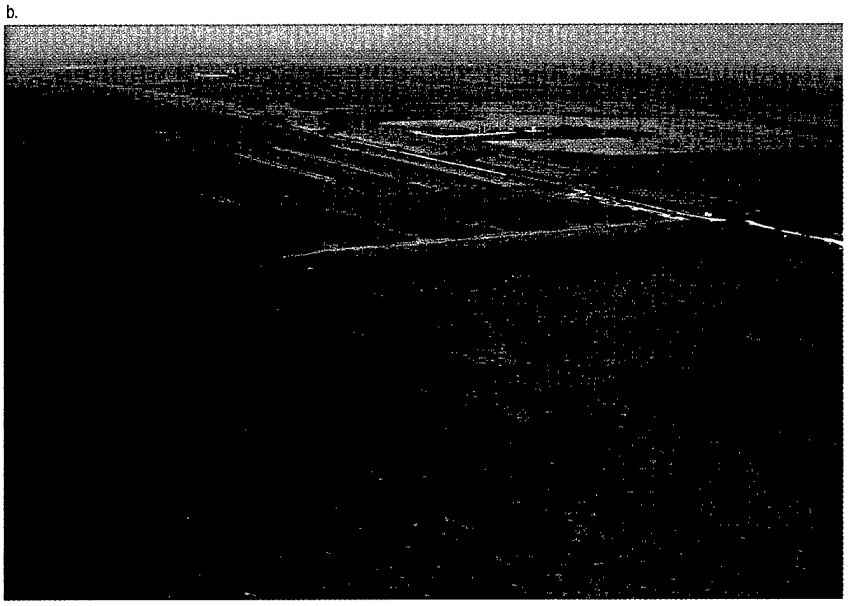


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Fig. 15. Freshwater wetlands were drained for residential and agricultural development in the early part of the century. The infrared aerial photograph a) depicts: (1) Delta Farms, now a large, rectangular lake that was the result of such agricultural development along (2) Bayou Lafourche, an abandoned distributary of the Mississippi River; (3) artificial canals that are straight and deep; (4) natural channels that are meandering and shallow; and (5) Clovelly Farms, sugarcane fields that are still in production. At Delta Farms, levees were breached by a severe storm and the reclamation was abandoned. The soil surface inside the levees at Delta Farms is now about 2 meters below the surrounding water level as a result of compaction and oxidation of the organic substrate. At Clovelly Farms, however, levees are still intact and water is continually pumped out to allow agricultural production. b) The northeast corner of Clovelly Farms is shown at a lower altitude in this aerial view; the sugarcane fields in the background are contrasted with the adjacent natural marsh in the foreground.

Fig. 16. An oil field in the Louisiana coastal wetlands. The extensive network of artificial canals provides access to oil and gas wells. The canals are bordered by elevated deposits of dredged materials that block the natural flow of water to the remaining wetlands.

data, and therefore, considerable controversy surrounds the effect of canals on marsh loss. The rate of loss per unit of canal is higher in recently formed deltas where the sediments are less consolidated (Deegan et al. 1983), and it seems to be highest where freshwater marshes experience salt intrusion (Dozier 1983). Turner et al. (1982) found that in places where canal density was zero, marsh loss was always less than 10% of the total loss and was usually nearly zero. This finding indicates that if there were no canals, the marsh loss rate would be less than 10% of the present rate. The area actually dredged out of the marsh for a canal is less than 10% of the total loss. If the spoil area is three to five times the size of the canal area (Johnson and Gosselink 1982), the direct loss of marsh due to canals is less than half of the total loss. The rest of the loss is attributed to indirect effects of circulation disruption by the canal and its spoil deposits, unintended impoundment of wetlands, and saltwater intrusion into freshwater wetlands (Turner 1987; Turner and Cahoon 1987a,b,c).

Land Loss Rates

A recent study conducted by the U.S. Army Corps of Engineers Waterways Experiment Station (Britsch and Kemp 1990; Dunbar et al. 1990; Dunbar et al. 1992) analyzed wetland loss rates over the entire Louisiana Coastal Plain for four periods, from the early 1930's to 1990 (Table 1). These results show that loss rates were relatively low, about 38 square kilometers per year from the 1930's to 1958, before major human effects were detected on the coast. A peak loss rate of about 108 square kilometers per year occurred during the 1958–1974 period; the loss rate has fallen off since to a 1990 rate of about 66 square kilometers per year. A concurrent mapping study by the National Wetlands Research Center of the U.S. Geological Survey, in cooperation with the Louisiana Department of Natural Resources (Barras et al. 1994), generally supports this trend (Fig. 17), although the absolute values are different because of overlap in census dates in the late 1970's and 1980's, different scales of photographic coverage, and differences in methodologies of map interpretation and boundaries. In both studies, however, most wetland loss occurred because of degradation to open water, rather than by drainage for human use.

Table 1. Wetland loss rates in the Louisiana coastal zone, 1930's to 1990.

Interval	Loss rate (square kilometers per year)
1930's–1958	38[a]
1958–1974	108[a]
1956–1978	102[b]
1974–1983	79[a]
1978–1988/1990	90[b]
1983–1990	66[a]

[a] Dunbar et al. (1992).

[b] USGS, Biological Resources Division, National Wetlands Research Center, Lafayette, Louisiana.

Pattern of Loss

Wetland loss does not occur uniformly across the Louisiana coast. Local loss rates are determined by the interaction of several processes and characteristics, including the thickness of recent sediments; the pattern of distributaries of earlier delta lobes; the withdrawal of oil, natural gas, and other minerals; subsurface faulting; the type of marsh vegetation present; the intrusion of marine waters into the estuary; and the size of water bodies relative to wind direction and intensity, fetch, and tide surges.

There are two categories of marsh loss, shoreline loss and interior marsh loss (Wayne et al. 1993, 1994). Shoreline loss due to erosion by storms and boat wakes represents only about 31% of the total loss. Nearly all the rest (67%) is associated with interior marsh loss. Although dredging channels through marsh is a significant source of interior marsh loss (Craig et al. 1979; Turner et al. 1982; Scaife et al. 1983), most loss is associated with the development of small ponds that gradually coalesce into large shallow lakes (Wayne et al. 1994). The most rapid wetland losses occur in the low-salinity interior marshes (Lee and Turner 1987), possibly because the influences of subsidence and saltwater intrusion stress the marsh vegetation beyond its ability to survive.

Status and Trends of Ecosystems and Associated Biota of the Louisiana Coast

The cyclic geological development of the Louisiana coast leads to plant associations or communities that are determined by the stage of development or degradation of each delta lobe (Gagliano and Van Beek 1975; Fig. 18). Following a period of rapid wetland formation during the progradational phase of a delta lobe, a longer period of lobe degradation follows the shift of the river to another location. Overlapping natural environments develop and decline as the lobe ages. The sequence begins

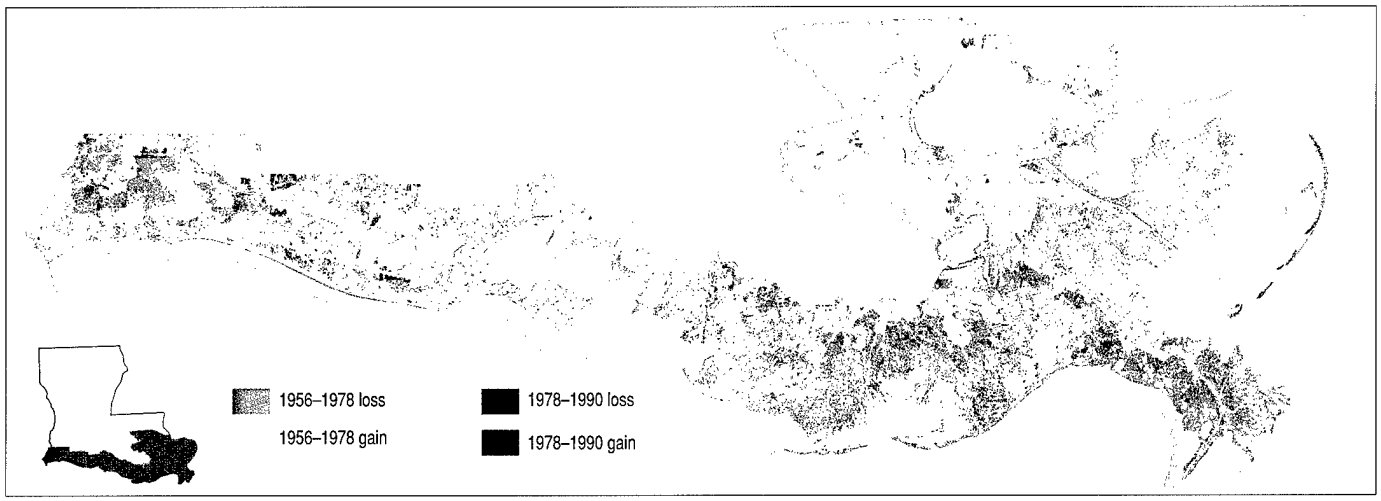

Fig. 17. Coastal land loss and gain in Louisiana, 1956–1990 (from Johnston et al. 1995).

with a shallow open bay into which the river begins to pour sediments. Infilling of the bay results first in subaerial mudflats, which later become freshwater marshes and swamps (Fig. 19). The natural levees along the major distributaries are elevated by sediment deposition during the largest floods and form a skeletal network of high ground that becomes terrestrial habitat amid the wetlands and lakes.

As the delta lobe expands and the river's course is channelized, portions of the lobe that receive little direct freshwater input come under the influence of marine forces, and freshwater marshes slowly change to brackish and then to saline marshes. The river abandons the lobe slowly over many years, and the system becomes progressively more saline. The compaction of recently deposited sediments and the loss of a mineral sediment supply begin a period of net subsidence, during which time the land surface gradually sinks beneath the water, the plant cover dies, the substrate disperses, and the area reverts to a shallow bay. At the marine interface, reworking of the shoreline by waves, longshore currents, and storms forms beaches and headlands that become detached from the mainland when the interior marshes are lost. Thus, a barrier island system is one of the last expressions of a degrading delta lobe.

Neill and Deegan (1986) showed that habitat diversity increases with age of a delta lobe. Gagliano and Van Beek (1975) speculated that biological diversity also increases (Fig. 18), with maximum diversity occurring during the middle of the destructional decay phase. As oceanic forces impose a strong salinity gradient, the landscape pattern increases in complexity, creating more and more habitat types (Fig. 20). Of a total of about 16,000 square kilometers of wetlands in Louisiana, marshes occupy about 10,000 square kilometers and forested wetlands about 6,000; of this 6,000, about 600 are shrub–scrub (U.S. Geological Survey, National Wetlands Research Center data base, 1990).

The net result of a series of overlapping delta lobes is a row of estuaries from east to west along the coast, each bounded on the east and west by the natural levees of old distributaries and on the seaward edge by a barrier headland or island system. The interdistributary basin is

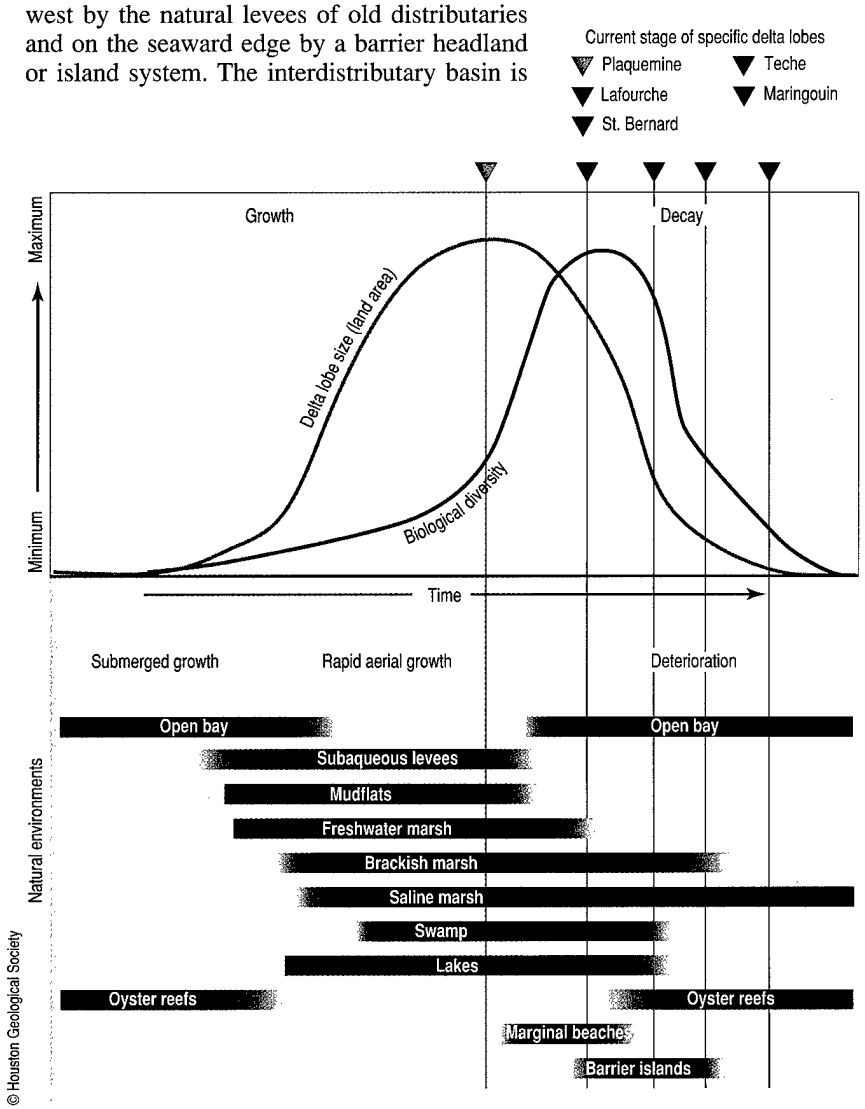

Fig. 18. Graphical depiction of the growth and decay of a delta lobe (adapted from Gagliano and Van Beek 1975; Neill and Deegan 1986). Habitat and biological diversity peak in the early to middle stage of the decay phase.

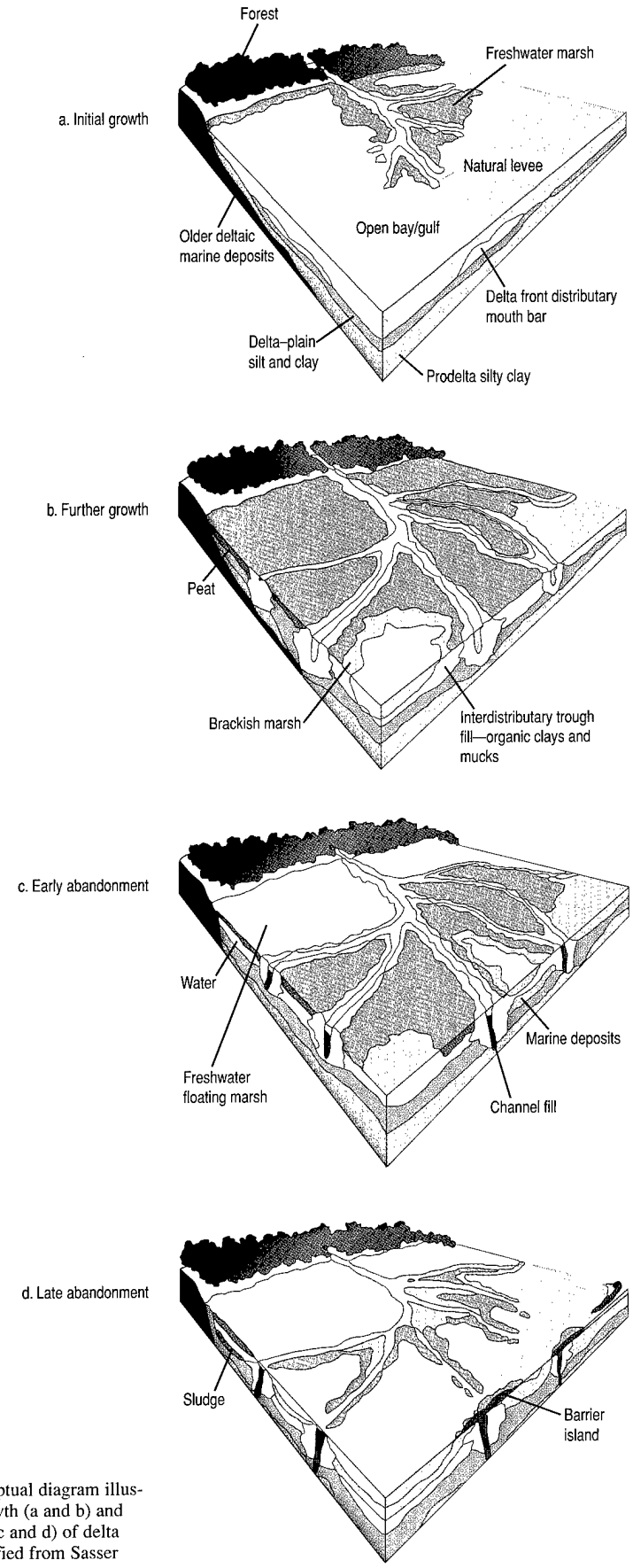

Fig. 19. Conceptual diagram illustrating the growth (a and b) and abandonment (c and d) of delta marshes (modified from Sasser 1994).

flanked by the degrading lobes of earlier deltas, and the interior is a series of bays and freshwater lakes.

The water regime of each estuary is fairly isolated. The natural levees of the old major distributaries confine the small flows they now receive, so that the estuary has little direct freshwater input except from local runoff and rain. The elevated remnants of the natural levees of the minor distributary network fork out across the degrading delta lobe like the branching system of an old tree. When the remnants are young, they support oak forests, which are replaced by shrubs and finally, as they subside, by vascular marsh plants. The stark silhouettes of dead trees across a flat marsh is a common signal of the remnants of an old natural distributary.

Marshes lie between the branches of the distributary system, and as subsidence progresses they grow over and obliterate the lower ends of the distributaries with a thick skin of organic peat. The broad natural levees at the landward edge of the estuary are nearly all developed for human occupation. They were once terrestrial forests dominated by live oaks, but few patches of forest remain, as most are replaced by villages, sugarcane fields, shipyards, and seafood processing plants.

As natural levees slope downward away from the stream that formed them, the terrestrial vegetation is replaced by flood-tolerant vegetation, first by bottomland forests, then by deep swamps dominated by baldcypress and tupelo gum. Seaward, the forests give way to freshwater marshes, many of them on a floating organic mat thick enough to support a mature man with ease (Sasser 1994). Runoff from adjacent uplands and rain falling on the estuary tend to freshen the system, while marine tides bring saline water in through the barrier island passes. These processes maintain a strong salinity gradient that fluctuates seasonally and spatially under the influence of evapotranspiration, storms, and frontal systems. Freshwater marshes give way to brackish and then to saline marshes seaward.

The barrier islands fronting the Gulf of Mexico are typically low and sandy, with poor dune development. They are dominated by salt-tolerant xeric grasses and succulent herbs on the dune face and crest, grading into brackish and salt marshes on the bay side (Visser and Peterson 1995). Barrier headlands form with the reworking of river-mouth sediments. The coastal ridges of the Chenier Plain often have higher relief than the barrier islands, and historically they supported maritime forests dominated by live oaks. Only remnants of these forests remain, the rest lost to subsidence and human development.

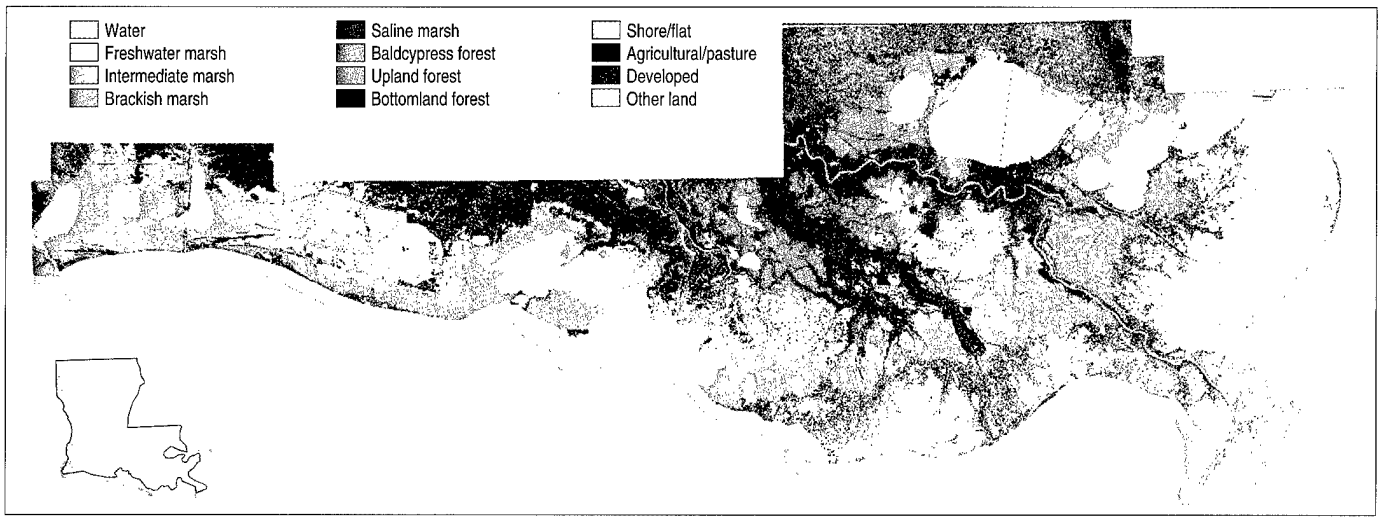

Fig. 20. Map of major coastal habitats of Louisiana, 1988–1990 (data from U.S. Geological Survey, National Wetlands Research Center data base).

The two major rivers of the coast, the Mississippi and the Atchafalaya, flow between the estuaries as if through large closed pipes. The Mississippi River's area of active deposition is now so far out to sea that most of its sediments are deposited in deep water on the Continental Shelf, and its surface expression is small. Where exposed wetlands do occur, however, both sediment deposition and subsidence are rapid, and the cycle of growth and decay of crevasse splays (mini-deltas formed as water goes through a break; see Fig. 6) is short. Because of the enormous volume of river water, the environment is almost entirely fresh water. The large nutrient load of the river results in rapid growth of willows on the levees of the channels and a wide spectrum of marsh vegetation on the mudflats (White 1993), including extensive stands of common reed. Farther west along the coast, the Atchafalaya River flows into the shallow Atchafalaya bay. This new delta lobe is similar to the Balize delta but differs in its slower sedimentation rate and generally lower river energy. Nevertheless, plant invasion of the new mudflats and subsequent community development and change are extremely rapid, reflecting a complex mix of physical and biological factors (Shaffer et al. 1992).

Marshes

Intertidal marshes (Fig. 21) are the most abundant landform on the Louisiana Coastal Plain. They stretch in a broad band across the entire state, covering 10,192 square kilometers (Table 2), about 40% of all U.S. coastal marshes (Field et al. 1991). The first thorough description of major coastal wetland plant communities in Louisiana was made by Penfound and Hathaway (1938). They described baldcypress–tupelo gum swamps; freshwater marsh

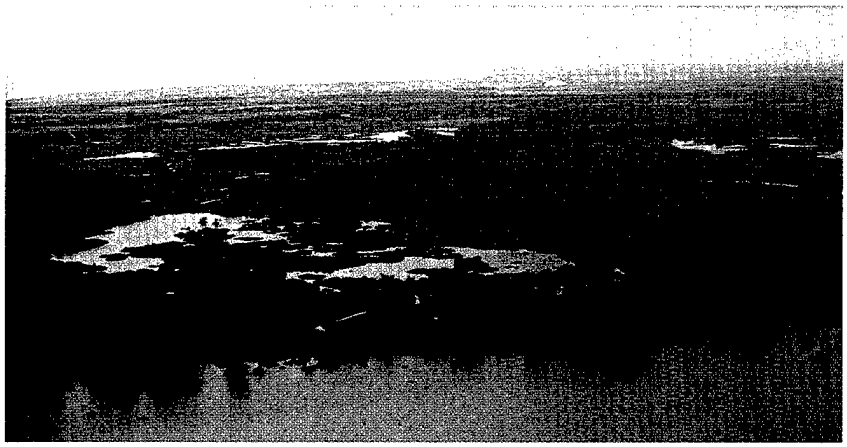
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Fig. 21. Fingers of swamp forest on slightly elevated land fan out into a freshwater marsh.

dominated by cattails, giant bulrush, sawgrass, and maidencane; a cane zone adjacent to levee areas dominated by common reed in the freshwater areas and by big cordgrass in the more saline areas; saltwater marshes dominated by saltgrass and smooth cordgrass; and brackish marshes dominated by wire-grass, saltgrass, and needlegrass rush. O'Neil (1949) published the first vegetation map of the Louisiana coast, but since his book was primarily about muskrats, his vegetation zones reflect the vegetation most important as muskrat food. The map delimits marsh zones by species and salinity tolerance and is the first (and until recently, the only) map to identify freshwater and brackish floating marshes.

The most comprehensive vegetation surveys of the coastal marshes were carried out in 1968 by Chabreck and other scientists from the Louisiana Department of Wildlife and Fisheries (Chabreck et al. 1968). The maps were updated in 1978 and 1988 (Chabreck and Linscombe 1978, 1988), although the detailed vegetation transects of previous surveys were not repeated

Table 2. Areas of major ecosystem types in the Louisiana coastal zone in 1988–1990 (data from U.S. Geological Survey, National Wetlands Research Center).

Ecosystem	Area (square kilometers)
Marsh	10,192
Fresh	3,829
Intermediate	1,495
Brackish	3,209
Saline	1,659
Forested wetland	5,935
Baldcypress forest	2,541
Bottomland/scrub–shrub	3,393
Upland	7,656
Forest/scrub–shrub	2,022
Developed	1,649
Pasture/agriculture	3,943
Barren	41
Water bodies	10,491
Submerged aquatics	306
Shore–flat	87
Other	2
Total	34,668

for the whole coast. These maps show adjacent bands of salt, low-salinity (Chabreck divided this zone into brackish and intermediate), and freshwater vegetation lying parallel to the coast in a landward direction. The maps were updated in 1990, based on high-altitude color-infrared photography and remotely sensed imagery (Landsat Thematic mapper; U.S. Geological Survey, National Wetlands Research Center and Louisiana Department of Natural Resources; Fig. 20).

As Penfound and Hathaway (1938) showed, three primary environmental factors control plant species distribution throughout the marsh: salinity, flood frequency, and flood duration. The broad vegetation bands in Figure 20 reflect such salinity differences. Flooding is an important species selector in areas where drainage is artifically controlled, and in areas adjacent to coastal streams, where slightly elevated natural levees allow less flood-tolerant species to grow.

Table 3 shows the percent cover of dominant plant species in the different salinity zones from Chabreck's 1968 survey (Chabreck 1972). Species richness predictably increases from saltwater to freshwater environments. Although many vascular plants apparently can tolerate a periodically flooded substrate, not many can tolerate the combined stresses of flooding and high salinity. Chabreck's salinity zones and plant associations were based on his broad experience in the field and on the precedents of Penfound and Hathaway (1938) and O'Neil (1949). Recently Visser (*in* Reed 1995) carried out a cluster analysis of Chabreck's 1968 data. Chabreck's freshwater, brackish, and saltwater marsh associations are identified in Visser's cluster analysis, but the low-salinity *intermediate* marsh is not as clearly seen. Generally, Visser's analysis refines Chabreck's classification, identifying a number of distinct plant clusters within each salinity zone.

What is particularly interesting about Visser's analysis is the rapid change in species dominance over the period of about 25 years since Chabreck's first survey in 1968 (Fig. 22). The constant percentage of open water showed that marsh loss was negligible in a freshwater to brackish area of the coastal wetland on the eastern flank of the Atchafalaya River that receives considerable sediment from the river during floods. However, there has been a steady replacement of about half of the maidencane during this period, primarily by spikerushes. The maidencane was growing on thick, apparently stable, floating substrates, many of which have become thin, insubstantial floating mats dominated by spikerush.

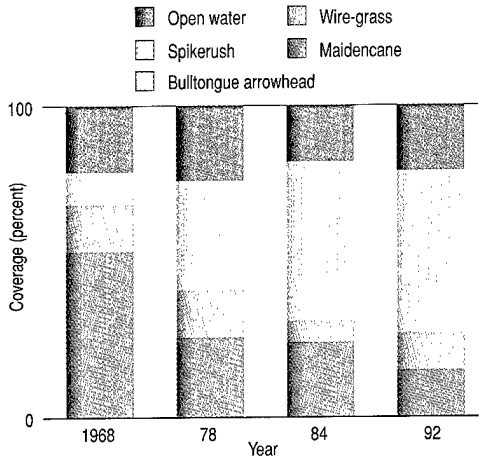

Fig. 22. Changes in dominant plant species in a freshwater to brackish marsh adjacent to the Atchafalaya River, coastal Louisiana, from 1968 to 1992. Data collected by Chabreck and Linscombe: Chabreck et al. 1968; Chabreck and Linscombe 1978, 1988. Data analyzed by J. V. Visser, Louisiana State University, Baton Rouge.

Table 3. Percent cover of dominant plant species in major marsh zones of the Louisiana coast (Chabreck 1972). Numbers may not sum because of rounding.

Species	Marsh zone (percent cover)			
	Salt	Brackish	Intermediate	Fresh
Alligatorweed	0	0	2.5	5.3
American bulrush	0	5	3.3	0.5
Bulltongue arrowhead	0	0	6.5	15.2
Coastal waterhyssop	0	0.9	4.8	1.4
Common reed	0	0.3	6.6	2.5
Dwarf spikerush	0	2.5	0.5	0.5
Leafy threesquare	0.7	1.8	0.7	0
Maidencane	0	0	0.8	25.6
Manyflower marshpennywort	0	0	0	1.9
Needlegrass rush	10.1	3.9	0.7	0.6
Saltgrass	14.3	13.3	0.3	0.1
Saltwort	4.4	0	0	0
Seashore paspalum	0	1.4	4.5	0.4
Smooth cordgrass	62.1	4.8	0.9	0
Spikerushes	0	0.8	3.3	10.7
Variable flatsedge	0	0.8	2.2	1.6
Walter's millet	0	0.4	2.7	0.7
Widgeongrass	0	3.8	0.6	0
Wire-grass	6	55.2	34	3.7
Other plants	2.4	5.1	25.1	29.1
Total	100	100	100	98.8
Number of species	17	40	54	93

Freshwater Marshes

Freshwater marshes cover 3,829 square kilometers of the Louisiana coastal zone (Table 2) and are the most abundant habitat type. These marshes look and function quite differently in the active delta than in the inactive delta. In the former, they occur in an actively accreting, sediment-rich, high-energy riverine environment. Sediment introduction and water level are strongly seasonal, with spring floods and late summer low-water periods. Freshwater marshes are sites of primary succession, as new land is produced in an expanding delta lobe. Though spring floods are the rule, expansion of the delta is episodic. In the Atchafalaya basin, for example, expansion occurs only in years when river discharge exceeds about 7,000 cubic

meters per second (Roberts and van Heerden 1992; Fig. 23).

Details of colonization and early succession are given by Shaffer et al. (1992) and Johnson et al. (1985) for the Atchafalaya delta and by White (1993) for inner deltaic splays caused by natural or intentional crevassing in the Balize delta. Johnson et al. (1985) described the vegetation of the Atchafalaya delta 7 years after the first occurrence of subaerial land in 1973. A typical river-mouth bar island (Fig. 24) is formed from a submerged bar that divides the flow of the river. During floods, this incipient island is submerged, and because the water slows as it passes over the island, it drops coarse sediments. This process creates an arrowhead-shaped island, with the highest elevations and coarsest sediments at its upstream apex and along its flanks and finer sediments at the interior and distal ends of the island. When the head of the island is high enough, black willow invades, stabilizing the substrate and protecting the downstream island, which is colonized by broadleaved cattails and a mixture of flatsedge, broad-leaved arrowhead, dwarf spikerush, and purple ammania. The low island mudflats are colonized by broad-leaved arrowhead and delta duckpotato, often in expansive stands of plants of the same genus.

White (1993) sampled vegetation during the first 7 years after a crevasse initiated a cycle of mudflat accretion in the Balize delta. He observed colonization in the first summer by a mixed group of "primary colonizers," including several species of sedges, and many of the same species observed by Johnson et al. (1985) in his mixed association. These are mostly annual plant species that propagate rapidly with widely dispersed seeds. Willows did not invade until the island elevations were about 11 centimeters above the mudflat. White (1993) found the same pattern of plant distribution in the Balize delta as Johnson et al. (1985) had found in the Atchafalaya delta, but an elephant's ear association replaced the Atchafalaya delta cattail association, and American bulrush dominated the flats at the lower ends of the islands. Elephant's ear is an introduced species that is now becoming common in the Atchafalaya delta.

Apparently, physical processes determine vegetation zonation patterns; elevation is the dominant factor, and sediment coarseness is secondary. Sediment grain size, however, is related to elevation, and both are determined by hydrology. White (1993) noted that on one island, the American bulrush-dominated association was replaced by broad-leaved arrowhead (vegetation similar to that of the Atchafalaya back-island flats) when the pass feeding water to the site was blocked by formation of a shoal, so that sediments no longer reached the island.

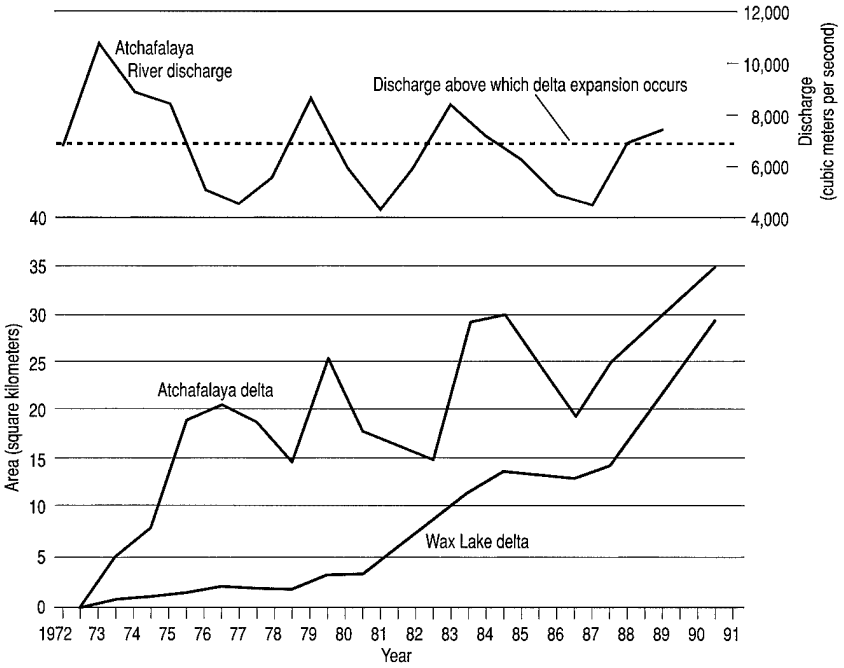

Fig. 23. The relationship of growth of the Atchafalaya and Wax Lake deltas to river discharge.

Subsidence apparently lowered elevation where the American bulrush grew, leading to its replacement by broad-leaved arrowhead.

In the years following the study by Johnson et al. (1985), vegetation changes in the Atchafalaya delta continued at a rapid rate. Most of the large expanses of broad-leaved arrowhead died, leaving bare mudflats (Shaffer

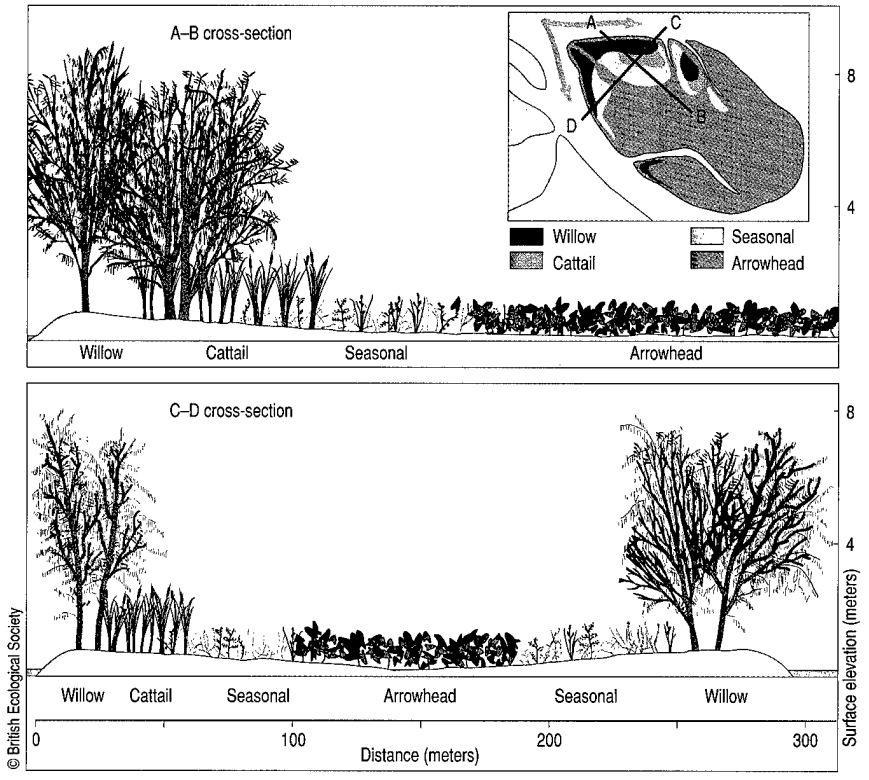

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Fig. 24. Illustration of a typical mouth-bar island in the Atchafalaya River delta, Louisiana, showing both aerial and cross-sectional views. Arrows represent direction of predominant water flows (Johnson et al. 1985).

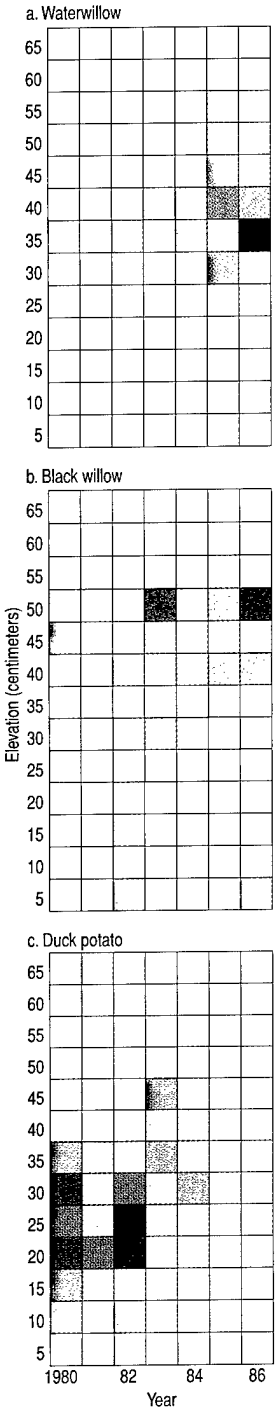


Fig. 25. Relative cover (proportional to color intensity; the deeper the intensity, the higher the coverage) of selected plant species with respect to time (*x*-axis) and elevation (*y*-axis) in the Atchafalaya delta, Louisiana. Examples illustrate species that a) increase in cover through time and stabilize on certain elevational zones, b) are relatively stable over time, and c) occur over a wide range initially but eventually disappear at low elevations (modified from Shaffer et al. 1992).

et al. 1992). From 1980 to 1986, vegetation was structured into more distinct groupings, and species richness increased. The mean cover per species peaked in 1981, falling off in later years, but total cover in the vegetated areas increased because there were more species. Species richness was directly related to elevation. Shaffer et al. (1992) identified three patterns of change:

- Species increased in cover through time (Fig. 25a). For example, the area occupied by looseflower waterwillow increased as the species became established in circular patches in the mudflats, apparently through dispersal of stem and root segments. The plant formed dense, monospecific stands that appeared to trap sediments efficiently.
- Species were relatively stable over time (Fig. 25b). Once established, willow seedlings grew into trees, regardless of changes in elevation, but spread little to other sites.
- Species are present over a wide range initially but eventually disappear at low elevations (Fig. 25c). Broad-leaved arrowhead was the dominant species on the delta islands in 1980, forming large, nearly monotypic stands at low to medium elevations on the islands. In 1983, this species began to decline in abundance and by 1986 had decreased by 90%. In places where broad-leaved arrowhead had occurred at elevations with more than 4,000 hours of flooding per year, no vascular plant species replaced it, but at higher elevations, most of the plots were revegetated by other species. Broad-leaved arrowhead is probably susceptible to grazing by nutria and waterfowl, and its disappearance can be linked to the high density of nutria, a nonindigenous species, on the delta islands (Fuller et al. 1985; Evers et al. 1988; Llewellyn and Shaffer 1993).

In the upper reaches of abandoned delta lobes, freshwater marshes have developed under quiet conditions of slow flows and low suspended sediment, beyond the reach of marine processes. Water levels vary, but lunar tides are replaced by wind tides that raise water levels when the wind is from the south and lower them when the north winds of winter fronts come through. As a result, periods of flooding and drainage are longer in freshwater marshes than in tidal marshes, and the frequency of flooding is lower. When the river abandons a delta lobe and the sediment supply is lost, further marsh development occurs primarily through peat formation. Such marshes have organic substrates.

J. Visser (Louisiana State University, Baton Rouge) described six freshwater marsh plant associations from Chabreck et al.'s 1968 survey (Reed 1995). This is a simplification of freshwater marsh diversity, as Chabreck (1972) described 93 plant species in freshwater marshes, Conner et al. (1986) listed 154 species, and Johnson et al. (1985) identified 46 marsh species in the Atchafalaya delta alone. The most frequently encountered plant association is dominated by common spikerush and smooth beggartick. Several species of spikerush are common in freshwater marshes. Although Chabreck did not identify the specific species in his 1968 study, in an unpublished description of a similar plant association he recently identified it as common spikerush. Smooth beggartick is common in marshes and forested wetlands, and its distribution has increased over the past 20 years. Its fruit is often disseminated by attaching to a host animal. Nutria, for example, are abundant in freshwater marshes and frequently come in contact with smooth beggartick, thus disseminating the seeds. The achenes, with their barbed awns, however, may pierce the nutria's skin, causing a chronic dermatitis that destroys the commercial value of the fur (Chabreck et al. 1977).

Maidencane is probably the species most closely associated with freshwater coastal marshes in Louisiana. It dominates so many stands that other species are not noticed at a casual glance, but in such a marsh Sasser and Gosselink (1984) listed 67 other species. Maidencane is also found in associations as a codominant with arrowhead species, though it is not as common in the Chenier Plain, where bulltongue arrowhead-dominated stands and alligatorweed replace it.

Except in the active deltas, much of the freshwater marsh appears to be floating. According to O'Neil (1949), a floating marsh develops from an anchored marsh that builds up an organic substrate over many years. As the original marsh surface subsides and the organic layer becomes thicker, the buoyancy of the mat increases until during some high-water period the mat tears loose from the substrate and floats. Sasser et al. (1996) observed that some floating marshes can become anchored during periods of low water and may take months to break loose again. They estimated that as much as 70% of coastal freshwater marsh may be floating. Three plant associations are maidencane dominated, one is dominated by bulltongue arrowhead, wire-grass, and spikerush, and one is dominated by dwarf spikerush and Baldwin's spikerush. Some wiregrass dominated marshes also appear to be floating (Sasser et al. 1996). Species characteristic of a floating maidencane mat include royal fern, southern marsh fern, snowy orchid, and tuberous grasspink. Wax myrtle bushes may develop on maidencane marshes anchored in the floating mat and may grow to 4–8 meters tall. When the floating mat begins to sink under the mass of the wax myrtles, the trees die and

the cycle begins again (Williamson et al. 1984; Sasser et al. 1994).

Maidencane is well adapted for life in a floating marsh because it has an extensive, strong, fibrous, and intertwined root mass that makes up about three-fourths of total plant biomass (Sasser et al. 1994). Floating mats are about 50–60 centimeters thick, with the top 25 centimeters composed of a thick mat of intertwined live and dead roots; the bottom half is peat in progressive stages of decomposition with depth (Fig. 26). Under the mat, there is typically a layer of clear water, its thickness dependent on the water level in the adjacent lake or stream. Below the water column, a layer of highly decomposed sludge often forms, apparently derived from decomposing peat that falls from the overlying mat. A clay layer typically lies under the sludge; researchers believe this layer is the original surface upon which the marsh was formed.

A plant association dominated by dwarf spikerush and Baldwin's spikerush in the spring and by anglestem primrose willow, common fogfruit, and smooth beggartick in the summer is apparently expanding. This association forms a thin floating mat and has replaced some thick maidencane mats over the past 20 years. Despite observations of the disappearance of maidencane-dominated marshes, on the whole they appear to be stable through time. Sasser et al. (1995a,b), for example, found no change in vegetative composition in one such marsh over an 11-year period. Biomass, however, has varied from year to year, which could be accounted for by a combination of climatic variables and water level.

In a developmental sense, floating marshes are at the opposite extreme from the freshwater marshes of the active delta. Whereas the active delta marshes are almost completely structured by abiotic forces, the highly organic substrates of floating marshes enable them to maintain a constant water level in the marsh substrate, regardless of how high water rises around them. Thus they are unaffected by flooding, the major variable that appears to control species distribution in other freshwater marshes. The surface of a well-developed mat floats about 5 centimeters above the water level, and the root system develops in this damp but unflooded upper 5 centimeters of substrate, creating an ideal plant environment—full sunlight without water limitations.

Table 4. The annual duration and frequency of inundation of marshes in the Barataria basin, Louisiana (Gosselink 1984).

Marsh zone	Reference	Duration[a] (hours per year)	Frequency (number per year)	Duration of event (hours)
Salt				
Inland	Baumann 1980	4,396 (50)	263	16
	Byrne et al. 1976	4,400 (50)	200	22
	Sasser 1977	4,100 (47)	150	27
Streamside	Byrne et al. 1976	1,050 (12)	160	7
Brackish	Byrne et al. 1976	3,700 (42)	75	50
	Sasser 1977	3,500 (40)	125	28
Intermediate[b]	Sasser 1977	2,300 (26)	32	29
Fresh	Byrne et al. 1976	3,700 (42)	32	115

[a] Figures in parentheses indicate the percentage of the year a marsh is inundated.

[b] Wire-grass and bulltongue association.

Saltwater Marshes

At the coastal edge of the estuary, 1,650 square kilometers of saltwater marshes (Fig. 27) provide a contrast to interior freshwater marshes. These saltwater marshes are characterized by daily tidal flushing rather than wind-driven, periodic water-level changes and by saline marine water rather than fresh river or rainwater. Table 4 compares flooding frequency and duration in different marsh zones in the Barataria basin. Although the total annual hours of inundation does not vary much across marshes (except for streamside saltwater marshes that are flooded for a relatively short time), the number of inundations decreases sharply as tidal influence wanes. Hence the average length of a single flooding event decreases from about 100 hours in the freshwater marsh to about 20 hours in a saltwater marsh. These differences in flooding duration and salinity result in dramatic geomorphic and biological differences between saltwater marshes and freshwater marshes. Daily inflow and outflow of tidal water carve bidirectional streams out of the marsh, and the higher water energy supports a heavier load of suspended sediment, which is deposited along the marsh edge as tides overflow the surface. Compared with broad expanses of unbroken freshwater marsh, saltwater marshes present a surface highly dissected with streams, whose

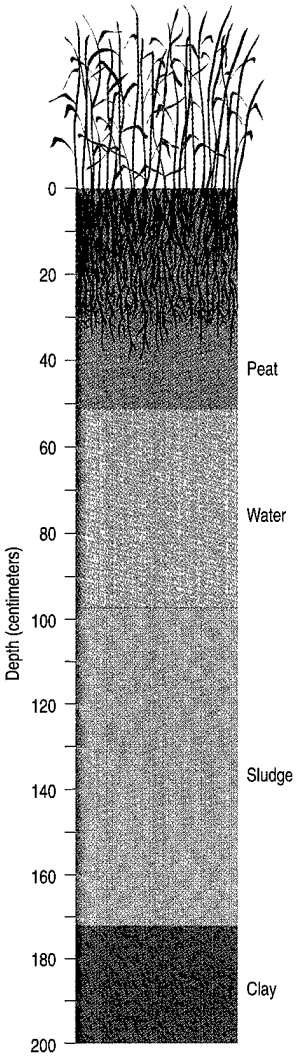
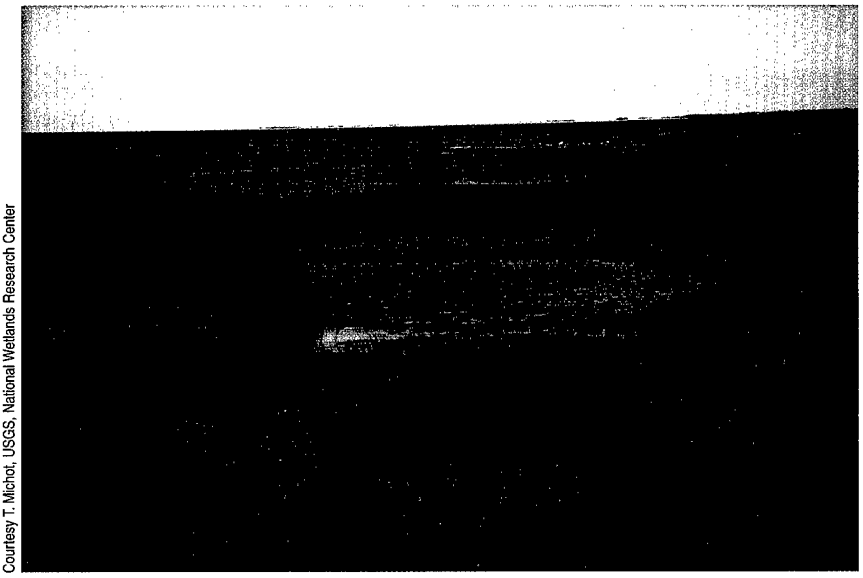


Fig. 26. Vertical depth profile of substrate in a maidencane-dominated floating marsh (modified from Sasser et al. 1995a).



Courtesy T. Michot, USGS, National Wetlands Research Center

Fig. 27. A Louisiana saltwater marsh.

banks have a slightly elevated streamside surface that supports more vigorous plant growth than can be found farther into the marsh. This is the *tidal subsidy* effect described by Odum and Fanning (1973).

Plant species richness is markedly lower in saltwater marshes than in freshwater marshes because few vascular plants can survive the combined stress of salt and flooding. Chabreck (1972) reported only 17 plant species in Louisiana saltwater marshes, and Conner et al. (1986) identified 25 species. Visser (*in* Reed 1995) listed only two plant associations, both dominated by smooth cordgrass, one with saltgrass and the other with needlegrass rush. In much of the saltwater marsh, smooth cordgrass is virtually the only species present, except along the slightly elevated stream edges where the codominants (wire-grass, leafy American bulrush, and sometimes big cordgrass) and the salt-tolerant shrubs bigleaf sumpweed and sea-oxeye are found. Sea-oxeye is often covered with the orange-tinted vines of the epiphyte called dodder. In pockets of high salinity the succulents saltwort and pickleweeds are found. Black-mangrove, at the northern limit of its natural range in Louisiana saltwater marshes, usually grows as a large bush that is periodically killed by winter frosts. This species provides excellent nesting habitat for some coastal birds, including the eastern brown pelican.

Because coastal Louisiana winters are mild, smooth cordgrass grows year-round (Kirby and Gosselink 1976). Shoot senescence also occurs throughout the year but peaks in late fall after the maximum production of live biomass. Dead shoots do not accumulate on the marsh. Instead, as shoots decompose and fragment, they are swept into adjacent streams by flood tides, where large aggregations of decaying organic material (locally called "coffee grounds") accumulate along the edges of streams and tidal lakes.

Not much is known about nonvascular plants in salt marshes. The regularly flooded bases of smooth cordgrass shoots support a vigorous epiphytic population of algae, including the filamentous forms *Enteromorpha* and *Ectocarpus* in the winter and *Bostrichia* and *Polysiphonia* in the summer, as well as a diverse population of diatoms (Stowe 1982). These epiphytes are net producers only along the stream edge where adequate light is available. The microflora of the marsh surface has not been studied in Louisiana, but cyanobacteria *Lyngbya* and *Rivularia* and the green algae *Ulothrix, Rhizoclonium, Chaetomorpha, Ulva, Enteromorpha*, and *Monostroma* are distributed in saltwater marshes around the world (Chapman 1960; Ursin 1972). In Georgia, saltwater marshes support hundreds of species of diatoms, dominated by *Cylindrotheca, Gyrosigma, Navicula*, and *Nitzschia*, which make up 75%–93% of the benthic algal biomass (Williams 1962).

Marshes are detritus-based ecosystems. In Louisiana, the trophic structure and energy flow of saltwater marshes are much better understood than for other marsh types. Energy flow in saltwater marshes was described by Montague and Wiegert (1990) and Gosselink (1984). Probably 90% of the net energy from plant photosynthesis reaches animals higher in the food web through decomposition by bacteria and fungi on the surface of the marsh and through ingestion by micro- and meiofauna in the sediments (Fig. 28). Flooding of the marsh surface provides access by aquatic animals, and tidal flushing of decaying material and microorganisms delivers food to the adjacent streams. In both cases the detritus and microfauna are available to benthic feeders: crabs, shrimp, snails, and filter feeders, which in turn are fed upon by bottom-feeding fish, wading birds, and small mammals. It is estimated that about 10% of primary production is grazed by insects (Smalley 1960).

In Louisiana, saltwater marshes are not grazed much by mammals and herbivorous waterfowl, but in freshwater and brackish marshes, muskrats, nutria, and a number of duck species can do serious damage to marshes as they feed on underground roots and rhizomes (R. G. Linscombe and N. Kinler, Louisiana Department of Wildlife and Fisheries, Baton Rouge, unpublished manuscript). It is unlikely that the direct ingestion of plant material is the major cause of the damage; rather, the destruction of plants by the animal's movements while grazing is extensive. This dead material enters the detrital food chain.

Primary production and plant biomass are also highest along the edge of the marsh (Kirby and Gosselink 1976; Mitsch and Gosselink 1993). *Edge effects*, the concentration of physical energy and biological activity at the interface of habitat types—in this instance the marsh and adjacent water—are most clearly evident in saltwater marshes. Tidal energy is focused at the marsh edge; as rising water spills over the marsh, the edge receives the coarsest sediments and the most nutrients, with finer sediments deposited farther into the marsh. Also, because of the many tidal streams, the length of edge per unit of marsh is highest in the saltwater marsh (Fig. 29). As the dead plant matter decomposes, it accumulates both on the marsh edge and in the adjacent water as fine particles of decaying organic matter. Macroinvertebrates, nematodes, and benthic infauna concentrate in this detritus, and the larger invertebrates—shrimp and crabs—feed there, both in the edge of the

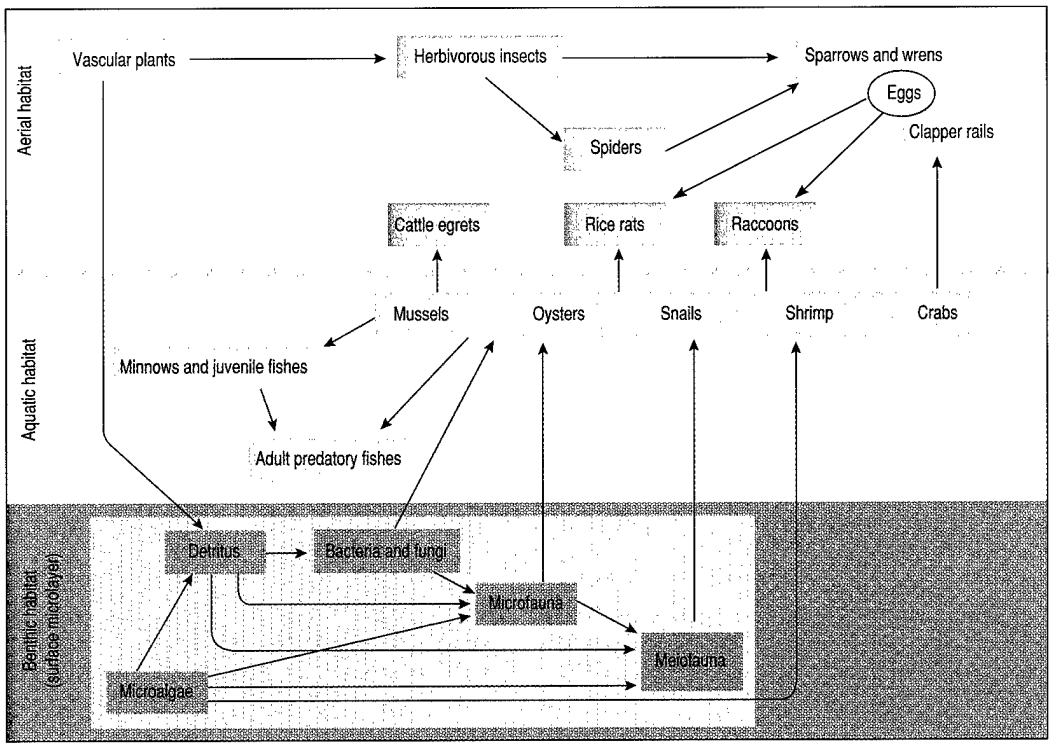


Fig. 28. Saltwater marsh food web, showing the major consumer groups of aerial, benthic, and aquatic habitats (modified from Mitsch and Gosselink 1993).

stream and on the marsh when it is flooded (Zimmerman et al. 1990). It is no wonder that the top carnivores—such as wading birds, seatrout, and redfish—also congregate there. Concentrated activity at marsh edges is also seen in other marshes (Odum et al. 1984) but is not as strongly expressed as it is in saltwater marshes.

Low-Salinity Marshes

Low-salinity marshes are those classified by Chabreck et al. (1968) and Chabreck and Linscombe (1978, 1988) as brackish and intermediate. Such marshes cover 4,704 square kilometers (Table 2), ranging in salinity from as low as 1 part salt per thousand to as high as 10 parts salt per thousand. Because salinity is a continuous gradient in nature, this group of marshes overlaps with both freshwater and saltwater marshes, and the boundaries are not sharp, especially at the freshwater edge.

Visser's analysis of Chabreck's data (see Reed 1995) identifies four brackish plant associations; only three have broad distribution. These three are dominated by wire-grass, with saltgrass, American bulrush, and yellow cowpea as codominants. At the saltwater marsh end of the gradient, other common species are smooth cordgrass and needlegrass rush, whereas at the freshwater end, dwarf spikerush, coastal waterhyssop, Walter's millet, and seashore paspalum are common. Species that seem most characteristic of low-salinity marshes are wire-grass and American bulrush. Yellow cowpea, an annual vine, is common but is also widely distributed in freshwater environments. Chabreck (1972) identified 40 plant species in brackish marshes, whereas Conner et al. (1986) found 23 species.

Chabreck's intermediate salinity marshes are at the freshwater end of the salinity gradient, apparently supporting freshwater species that can tolerate occasional salt spikes of up to about 8 parts per thousand. Penfound and Hathaway (1938) classified these marshes as slightly brackish, and they are probably the same kinds of marshes that Odum et al. (1984) described on the south Atlantic coast as tidal freshwater marshes (R. H. Chabreck, Louisiana State University, Baton Rouge, personal communication). In Visser's analysis, this group probably coincides with the wire-grass–cowpea and the freshwater arrowhead associations.

Functionally, low-salinity marshes are probably the least understood marsh group. They have an organic substrate ranging from nearly pure organic matter (some sites are floating) to mineral soils similar to those of saltwater marshes. Low-salinity marshes are generally low-energy systems, and because they are located some distance from both a strong tide and local upland drainage, they probably receive few sediment and nutrient inputs. Despite this, aboveground production and standing biomass can be extremely high in these marshes (Hopkinson et al. 1978). The root systems of intermediate marshes are fine and shallow, and underground live root mass is small; only about a third of production is allocated to the roots, compared with about half for maidencane (Sasser et al. 1994). Beneath the root mat, the substrate is often an unconsolidated, semifluid muck.

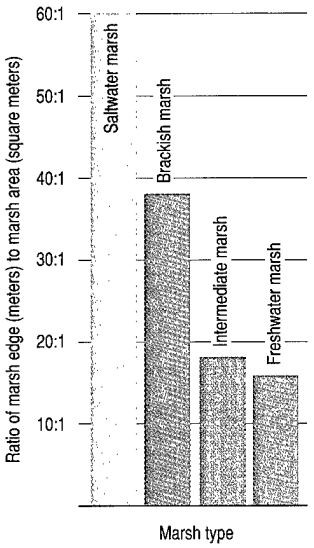


Fig. 29. The relative length of marsh edge to area in saltwater, brackish, intermediate, and freshwater marshes along the Louisiana coast (data from Gosselink et al. 1979a,b,c).

In much of the low-salinity marsh, accretion does not balance subsidence, and consequently the marshes are the most rapidly degrading type in the coastal zone. From the air, low-salinity marshes have a clumpy appearance caused by large, apparently vigorous individual plants separated from each other by bare mud (Nyman et al. 1993a). The plant clumps are elevated above the rest of the marsh; the root system is very shallow, and often the clump with its intact roots can be lifted with little apparent disturbance of the substrate.

Physiological and growth characteristics of wire-grass may make it particularly susceptible to subsidence. This species grows vigorously at upper elevations in the tidal zone and is a good competitor under these circumstances, as is demonstrated by its wide distribution. Most wetland plants respond to increased flooding by producing root aerenchyma (a gas-filled tissue produced in some plants in response to flooding and which sometimes aids in oxygen flow), which enable the roots to maintain their oxygen supply directly from the aerial portions of the plant (Webb and Jackson 1986; Burdick 1989). In wire-grass, however, aerenchyma production does not compensate for oxygen deprivation associated with flooding as shown by a simultaneous increase in anaerobic fermentation (Pezeshki et al. 1991; Naidoo et al. 1992). Although species like smooth cordgrass produce many roots that grow downward into the soil (like most plants) in response to flooding, wire-grass produces few roots and these protrude up out of the substrate (Naidoo et al. 1992).

Wire-grass is apparently physiologically unable to cope with increased flooding associated with net subsidence. As a result, its growth is curtailed and fewer roots are produced to counter subsidence. The net subsidence rate increases, setting up a positive feedback loop that accelerates marsh degradation (Nyman et al. 1993b). Though root production apparently provides the structural framework that controls the accretion rate, mineral sediments strongly influence accretion. Nyman and DeLaune (1991) found that wire-grass marshes require about 1,000 grams per square meter per year of mineral sediment to accrete 1 centimeter per year. Many are accreting at only about half to two-thirds of this rate.

Forested Wetlands

Forested wetlands on the Louisiana coast are located at the landward edges of the estuaries that flank the Mississippi River and its major distributaries. They fall into two broad vegetation zones, baldcypress–tupelo swamps and bottomland hardwood forests. Because dry terrain is at a premium in the coastal zone, much of the land firm enough to develop was long ago cleared for agriculture, industry, and urban use. Most of the remaining forest, therefore, is wetland, most of it swamp and low bottomland sites. A diagrammatic elevation profile of the Mississippi River Deltaic Plain region illustrates the relationship of wetland forests to adjacent marshes on one side and the developed levees on the other (Fig. 30).

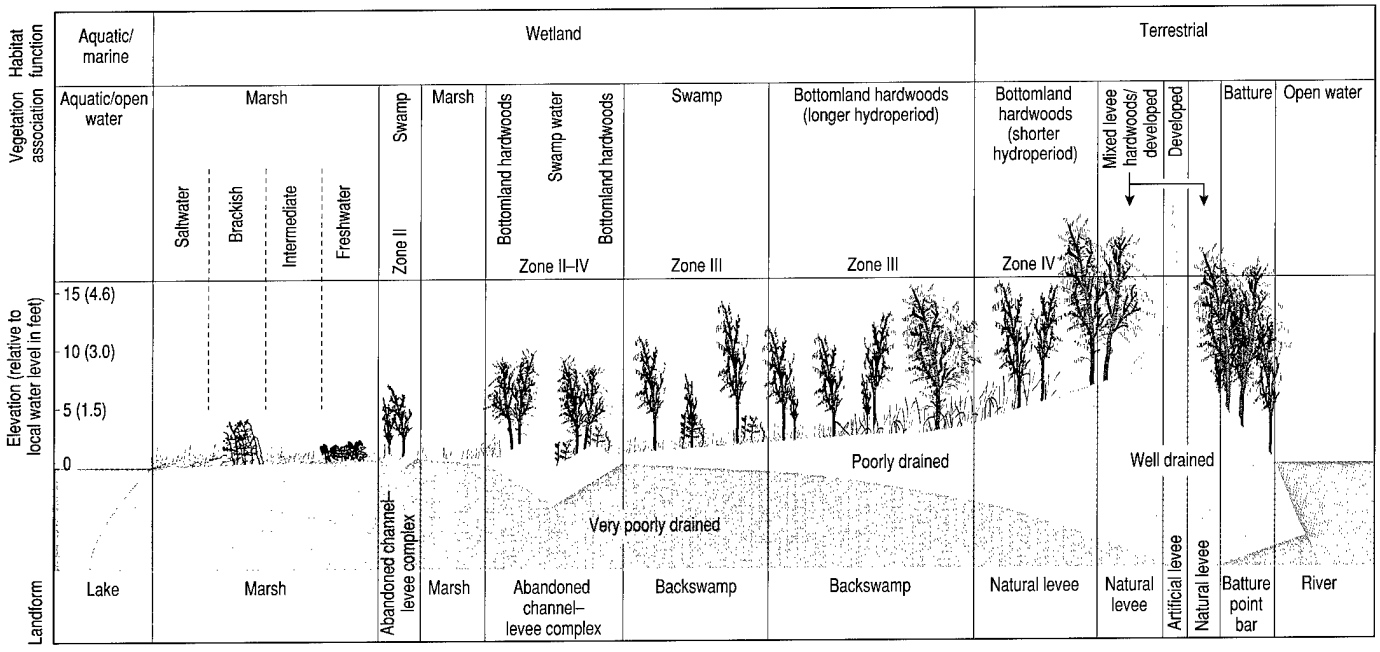


Fig. 30. Relation of habitat and vegetation associations to landforms in the Mississippi River Deltaic Plain region (Wicker 1980). Elevation relative to local water level is given in feet (meters in parentheses).

Larson et al. (1981) classified bottomlands into five forest zones based on elevation and flooding frequency. Nearly all the forested wetlands in the Louisiana coastal zone fit into Zones II, III, and IV; Zone I is permanently flooded and supports no woody vegetation. Zone II is the wettest area of flooded forest habitat, including wet flats, sloughs, swales, and backswamps (shown as backswamp only in Fig. 30). Flooding and soil saturation are constant year-round except for periods of extreme drought. Soils are highly reduced, high in organic matter, and nutrient-rich, although nutrient availability is limited by the anaerobic conditions. This is the classic deep swamp environment, dominated in Louisiana by baldcypress and water tupelo (Table 5), which are often found either in nearly pure stands or in mixed stands of the two species. Other overstory trees include green ash, pumpkin ash, and red maple. Buttonbush, Virginia-willow, and American and red maple are common understory species. The presence of standing water nearly year-round allows for the growth of numerous floating aquatic and emergent plants. Duckweeds, water hyacinth, Carolina mosquitofern, and American frog's-bit are common floating plants. Lizard's tail and water smartweed are the most common emergent herbaceous plants, which, along with woody seedlings, can be found growing on logs, stumps, baldcypress knees, and even on the buttresses of the baldcypress trees.

Zones III and IV, the natural levee environment (Fig. 30; Table 5), are slightly more elevated than Zone II (swamp in Fig. 30). Flooding occurs for extensive periods during the growing season, and saturated soils that are prevalent most of the year are mottled gray, indicating periodic reduced conditions. However, soils surrounding the root are commonly dry in summer. In early stages of succession, these zones support black willow, red maple, and sometimes eastern cottonwood (Table 5). American elm, sweet gum, sugarberry, and red maple become dominant. The woody understory is composed of red maple and boxelder saplings. In places where light can penetrate, a thick tangle of vines and herbs grows, including poison ivy, greenbriers, peppervine, and Virginia creeper.

These are extremely diverse environments, in terms of both microhabitats and plant species. The meandering of the river across the floodplain creates old oxbows, sloughs, ridges, ponds, mudflats, and other areas of slightly differing elevation and soil characteristics (Mitsch and Gosselink 1993). It is no surprise then that Conner et al. (1986) listed 146 species associated with bottomlands and 140 species with swamps.

The extent of the area occupied by forested wetlands in the Louisiana coastal zone is unknown. Recent detailed studies of coastal wetland change (for example, Britsch and Kemp 1991; Johnston et al. 1995) have focused on marsh loss, and forested wetlands were not included in the Waterways Experiment Station study of wetland loss discussed previously (Dunbar et al. 1992); other inventories used different coastal zone boundaries. One of the largest areas of bottomland forest in the United States occurs in the Atchafalaya basin, which is usually considered an inland basin and is not a part of the jurisdictional coastal zone. Without including this basin, Wicker et al. (1992) reported 3,820 square kilometers of swamp in the Louisiana coastal zone in 1955 and 3,530 square kilometers in 1978. The National Wetlands Research Center estimated 5,930 square kilometers of forested wetland from 1990 aerial imagery (L. R. Handley, U.S. Geological Survey, National Wetlands Research Center, Lafayette, Louisiana, personal communication). Regardless of the absolute area of forested wetland, the direction of change is clear. A period of intensive logging occurred from the mid-1800's until about 1920, overlapping a period of forest clearing for crop production, which continued into the 1980's. In recent years, sea-level rise and coastal subsidence seem to have threatened the future of coastal forested wetlands.

The early history of baldcypress logging is recounted by Conner and Toliver (1990). To early settlers, swamps were dangerous and forbidding, and the best use for them was drainage and agricultural production. In the meantime, the vast baldcypress forests were the main cash crop of the colonists, especially in southern Louisiana. Baldcypress logs were first harvested by girdling, allowing them to dry in place, then felling and floating them out of the forest. Low levees were often piled around a forest patch to maintain water levels deep enough to float the logs. Some of these levees remain today. During the 1890's, the pullboat, and later the overhead-cableway skidder and railway system, increased the range of the loggers and consequently the amount of timber that could be brought out of the forest. Logging continued to accelerate until the peak year of 1913, when more than 1.7 million cubic meters of lumber were processed in 94 mills (Mattoon 1915; Fig. 31). As the last of the old-growth timber was harvested during the 1920's, production crashed, and by the early 1930's production had decreased by 95% from its peak. The last major baldcypress logging operation closed in 1956 (Conner and Toliver 1990).

Table 5. Selected tree and shrub species of bottomland forests in the southeastern United States (Larson et al. 1981). Zone II, also known as swamp, is the wettest area, generally saturated almost permanently throughout the growing season (see Fig. 30); Zone III is slightly more elevated and is inundated or saturated more than 25% of the growing season; Zone IV is the least frequently flooded swamp area, typically inundated between 12.5% and 25% of the growing season.

Species	Ecological zone		
	II	III	IV
American elm		X	X
American snowbell		X	
Baldcypress	X	X	
Black willow	X	X	
Boxelder		X	X
Buttonbush	X	X	
Carolina ash		X	X
Cedar elm		X	
Common persimmon		X	X
Dwarf palmetto			X
Eastern baccharis		X	X
Eastern cottonwood		X	X
Green ash		X	X
Green hawthorn			X
Hazel alder			X
Honeylocust		X	X
Laurel oak		X	X
Leadplant		X	X
Live oak			X
Nuttall oak			X
Overcup oak		X	X
Possumhaw		X	X
Red maple		X	X
River birch		X	X
Sugarberry		X	X
Swamp dogwood		X	X
Swamp-privet	X	X	
Sweet gum		X	X
Sycamore			X
Virginia-willow		X	
Water-elm	X	X	
Water hickory		X	X
Water locust	X	X	
Water tupelo		X	X
Water viburnum		X	
Willow oak			X
Winged elm			X

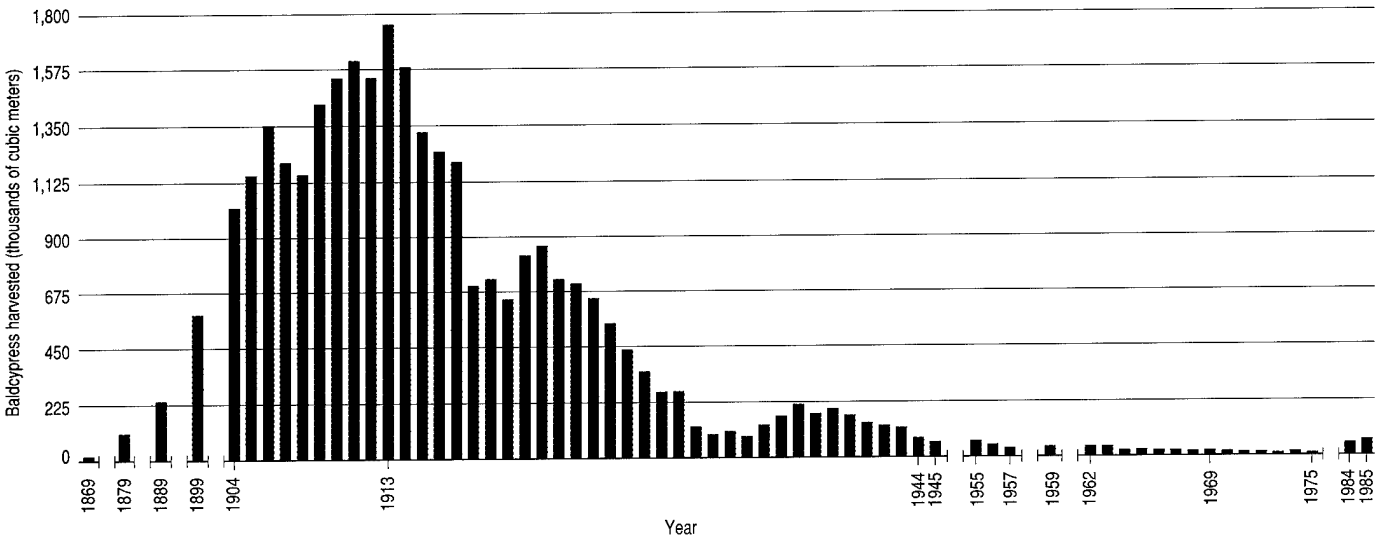


Fig. 31. The volume of baldcypress logged in Louisiana (Conner and Toliver 1990; data from Anonymous 1943, 1956–1976, 1957; Steer 1948; Mistretta and Bylin 1987). Solid wood, converted as 423.8 board feet = 1 cubic meter.

Second-growth forests have regenerated after the logging, and many stands are now about 80 years old. Estimates from various sources of growing stock (Conner and Toliver 1990) suggest a volume of about 15 million cubic meters in 1954, increasing to about 40 million cubic meters in 1984. In recent years, because of the large reserves and new techniques of logging, baldcypress logging has once again become attractive (Marois and Ewel 1983).

The second period of human activity that affected wetland forests was the clearing of bottomlands for agriculture. In the colonial period, agriculture was confined to the natural levees that were dry during the growing season. These rich soils were replenished with mineral nutrients when the adjacent river overflowed its banks during spring floods, and no fertilization was needed to grow vigorous crops. With the development of powerful tractors and equipment and of crops (especially soybean varieties) that would mature even if planted as late as early July, there was a strong economic incentive to clear bottomlands for agriculture. In the Mississippi River alluvial floodplain, clearing was linked to flood-control projects funded with tax dollars. The result was a rapid clearing of the floodplain from about 1930 through about 1980. The Nature Conservancy (1992) estimated that before European settlement, the Mississippi River alluvial floodplain contained about 80,000 square kilometers of riparian forests; fewer than 20,000 square kilometers remained in 1991.

Surveys that depend on aerial imagery to determine habitat changes are not particularly effective in discerning the slow, subtle change threatening the remaining coastal wetlands. Conner and coworkers (Conner and Day 1988a,b, 1989, 1991; Conner and Toliver 1990) and Pezeshki et al. (1990, 1993) have described the effects of rising sea level and substrate subsidence on wetland forests. In impounded forests with elevated water levels, regeneration stops because seed germination almost always requires exposed soil. The less flood-tolerant species, such as green ash, slowly die. Baldcypress and water tupelo survive, and basal area is not greatly affected at first because as some trees die, the flood-tolerant ones continue to grow (Conner et al. 1981). These changes are not evident on aerial photographs, but the forest is in decline—it is not reproducing itself. Coastal forested wetlands are subsiding at a rate of about 0.85 to 1.4 centimeters per year (DeLaune and Patrick 1987; Conner and Day 1988b), whereas accretion is only about 0.3 to 0.6 centimeters per year. The forests are thus slowly sinking. As flooding frequency and depth increase, the trees will respond as they do in impoundments. Regeneration is nearly absent in many coastal swamps.

The density of nutria in many coastal forests and their consumption of baldcypress seedlings complicate regeneration. Seedling survival seems to depend on the density of nutria near the plantings; sleeves over the seedlings have been ineffective in preventing nutria damage (Conner and Toliver 1987; Conner 1988).

Natural Levees, Ridges, Cheniers, and Barrier Islands

Several maritime communities occur along the Louisiana coast. All are linear and elevated above the coastal wetlands. To describe them as upland communities would be to stretch the definition of uplands; most are only a meter or two above the ambient water level and are flooded during any moderate storm surge. These communities fall into two groups. The first includes

natural levees of major and minor distributaries (Fig. 32) that diverge from larger distributaries as they trend toward the coast, and it also includes the cheniers that run parallel to the coast, are part of the mainland coast, and are separated from the beach by intervening marshes. Deposits of mostly linear dredged material that crisscross the coast also mimic natural levees in some respects (Monte 1978). The second group of communities includes the barrier islands and headlands fronting the Gulf of Mexico.

These communities do not encompass a large area compared with the coastal marshes, but in coastal basins they play an important ecological role through their function as barriers between the ocean and the estuary and as water regime barriers within an estuary and because they present the only elevated, sometimes forested land within a plain of wetland and water. They provide periodic or continuous habitat for nearly all mammals and birds in the coastal zone.

Fig. 32. Natural levees along an abandoned distributary of Bayou Lafourche. Most of the surrounding marsh has degraded, leaving the old distributary streambed with remnants of the natural levee on each side.

Trends

All the maritime communities are decreasing in area, primarily as a result of the geomorphic processes described earlier. The larger levee communities have the potential to be forested, but most have been cleared. The remaining forests occur mainly along the inland edge of the coastal zone, and some forests remain on the high coastal cheniers, particularly in the Chenier Plain. Many are used for cattle grazing and others are modified by human occupation, but they still provide habitat for many birds.

Older residents of Leeville, a community near the seaward end of the subsiding Bayou Lafourche natural levee, can remember when rice was raised nearby on the back slopes of the levee. The land is now too low and too saline for rice cultivation. Flood-control dikes and pumps along the backswamp edge of the natural levees have been constructed to keep the towns and pastures dry, but recently the bayou itself has begun to flood over the highest part of the natural levee with the occurrence of almost every minor tropical disturbance. On unprotected natural levees out in the marsh, the trees have been replaced, first by woody shrubs such as bigleaf sumpweed and wax myrtle, then by marsh grasses and other herbs, and finally by shallow ponds.

The cheniers are settling, but many are still as much as 3 meters above sea level, and they are still major elements of the landscape. The barrier islands are also rapidly degrading, as are barrier islands around the rest of the United States (Williams and Johnston 1995). The U.S. Department of the Interior identified 2,055 kilometers of undeveloped shoreline in its Coastal Barrier Resources System. Louisiana has 287 kilometers of undeveloped shoreline, or about 14% of the U.S. total, but the total length of the barrier system in Louisiana is about 600 kilometers of undisturbed shoreline (Penland et al. 1990). Still, Louisiana's coastal barrier retreat rate is the highest in the nation, averaging 4.2 meters per year over the past 50 years. The rate is not constant through time nor across the coast—at different locations, barrier retreat rates range from +3.4 meters per year to -15.3 meters per year. Most of the retreat occurs during major storms and hurricanes and can be as great as a loss of 20–30 meters over a 3- to 4-day storm (Penland et al. 1990).

In addition to beach retreat, the total area of Louisiana's barrier shoreline is decreasing. In 1880 the total barrier island area was 98.6 square kilometers. By 1980 the total area had decreased by 41%, to 57.8 square kilometers (Penland and Boyd 1982). The barrier island system is now a series of arcs of isolated islands formed by fragmentation of earlier large islands. The relief on these islands is low; dunes are seldom more than 2–3 meters high, and overwash occurs during even moderate storms. Except for Grand Isle and Grand Terre, the largest island remnants of the Lafourche delta lobe, the islands are treeless.

Vegetation

The larger cheniers and natural levees still support some groves of live oaks, formerly the dominant tree species. Other common species include sugarberry, American elm, red maple, waterlocust, prickly-ash, common persimmon, and water oak. Baldcypress is found in low areas. Palmetto is a common understory species, as are haws, buttonbush, possumhaw,

and eastern baccharis. On heavily grazed cheniers, chickasaw plum, saltcedar, and prickly pear dominate. Vines, especially grape, are ubiquitous (Gosselink et al. 1979a,b,c).

Vegetation on the Louisiana coastal islands is generally similar to that found on barrier islands of the south Atlantic coast and the rest of the Gulf of Mexico coast (Stalter and Odum 1993), except that sea oats, which dominate those areas, are replaced by wire-grass in Louisiana (Barbour et al. 1987). Surveys of the *beach face* (from the beach edge of the vegetation line to the point where beach vegetation is mixed with stabilized dune, forest, marsh, or inland species) identified a Louisiana beach association distinct from those to the east and the west (Barbour et al. 1987). Gulf beaches everywhere have a number of species in common: saltgrass, beach morning glory, and gulf croton. In addition, two species of heliotropes are found only on Louisiana beaches, and coast sandbur is found only on Louisiana, Texas, and south Florida beaches.

On transects extending across an entire barrier island, Visser and Peterson (1995) identified 12 plant species dominated by smooth cordgrass, saltwort, black-mangrove, coastal dropseed, perennial pickleweeds, and sea-oxeye. The species were distributed according to elevation and degree of exposure to the ocean, with the succulent species and vines on the lower beach face, wire-grass at highest elevations, and smooth cordgrass and black-mangrove on the protected bayside flats.

The Isle Dernieres system, the remnant of the headlands of the Teche delta lobe, is an example of a typical barrier island system. In 1853 this system consisted of a single large island and one small island, separated from the coast by a narrow bay (Fig. 33). In the 1850's the large island was a popular beach resort for the residents of New Orleans and other Louisiana cities, who fled the summer heat and humidity (and the mosquitoes that transmit yellow-fever) for the hotel and beach cottages of Last Island (Sothern 1980). The island supported a thriving community, especially during the summer. On 9 August 1856, at the height of the resort season, a severe hurricane ravaged the island, killing about 200 of the approximately 500 people on the island. One account (*in* Sothern 1980:p. 69) by a member of a rescue party that reached the island several days later said, "There were about one hundred houses on the island, not one was left, nay not a sill nor sleeper, not any part of their foundations to indicate that buildings had once been there."

The islands have never recovered from the storm. For a while, the curious came to view the ruins, but with time the waves and shifting sands erased all traces of human habitation. In 1890 the island system had an area of 3,360

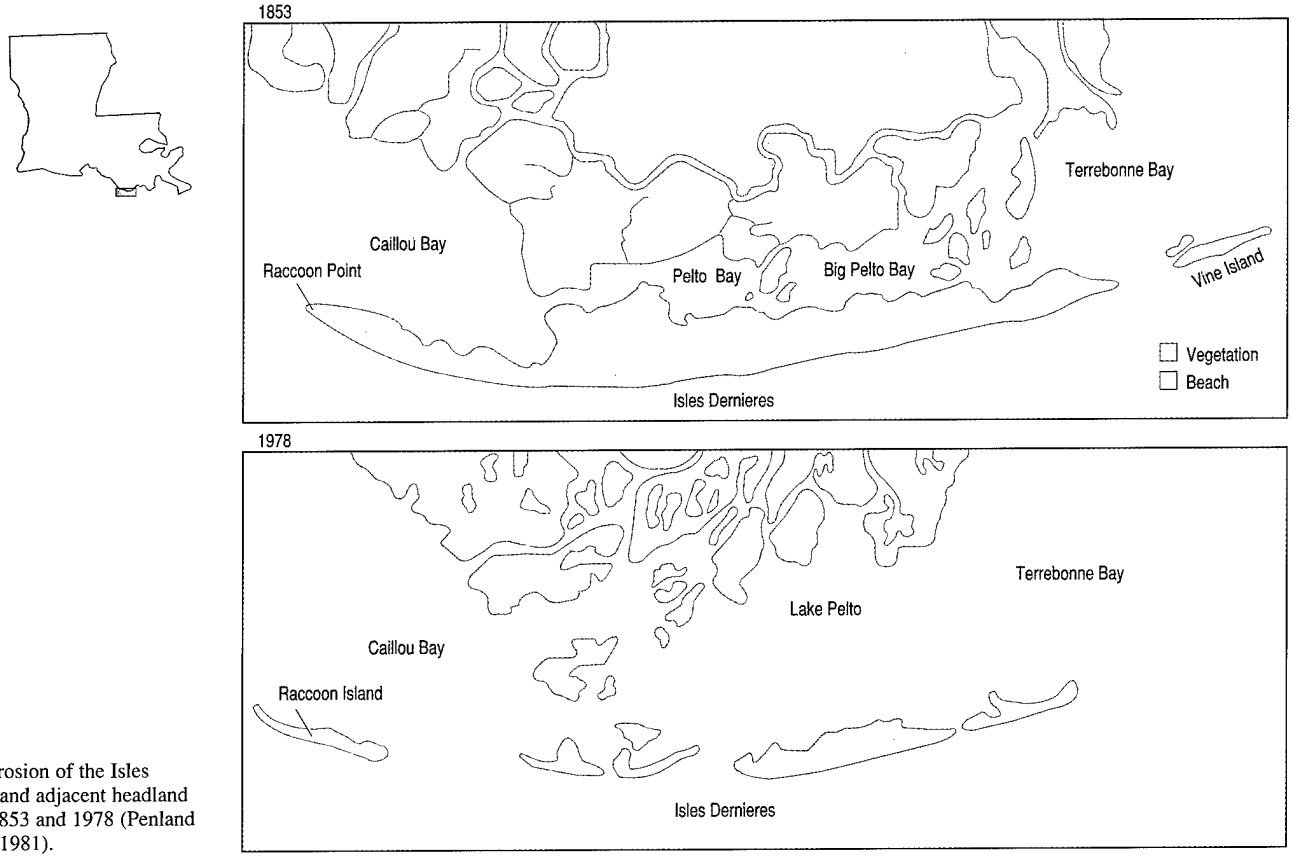


Fig. 33. Erosion of the Isles Dernieres and adjacent headland between 1853 and 1978 (Penland and Boyd 1981).

hectares. By 1978 the Isles Dernieres had eroded to a series of small island fragments well separated from the mainland, with an area of less than 8 square kilometers. In the intervening years, the center of the barrier arc retreated at a rate of 19.1 meters per year (Penland et al. 1990). Before the 1856 hurricane, most of the buildings were clustered at the western end of the island. That site is now known as Raccoon Island, and the vegetation map (Fig. 34) indicates how the forces of storms and waves have changed the island.

Aquatic Ecosystems

Aquatic ecosystems of the Louisiana coast include those described by Moore (1992) as low-salinity lagoons, as well as the brackish to saline estuarine systems described by Dardeau et al. (1992). Chabreck (1971) inventoried the bays, lakes, and ponds of the Louisiana coastal zone. In 1968 the estuarine system was dominated by marsh ponds of less than 0.5 hectares (Table 6). A more recent comprehensive inventory showing the effects of 25 years of marsh degradation does not exist, but because most marsh loss starts with small ponds that later coalesce, the probability is that the small ponds still dominate, although there must have been an increase in the total area of larger ponds. Small ponds are concentrated in the low-salinity marshes, probably because these marshes are breaking up most rapidly. As marsh degradation occurs, the area of open water in the coastal zone increases, mostly in ponds within the marsh, but as these grow in size and coalesce, they open into adjacent bays and lakes. In addition, the edges of water bodies large enough to have significant wave fetch are eroding slowly. Virtually all the wetland loss documented in Table 1 appears as open water gain.

Several characteristics of Louisiana coastal aquatic ecosystems determine the composition and distribution of species and the trends in species' populations through time:

- Most populations that have been studied (chiefly commercially important species) are stable at present (Condrey et al. 1995), but marsh loss and marsh–water interface changes are expected to be major factors in the future. The size of the offshore harvest of commercial fishes and shellfishes that use the estuary as a nursery is directly related to the area of marsh in the estuary (Turner 1977, 1982) because the young of these species concentrate at the marsh–water interface (Zimmerman et al. 1990, 1991; Minello and Zimmerman 1992). As a marsh fragments, the marsh–water interface increases until about half of the marsh is gone, after which the loss of wetlands then decreases the length of this interface (Browder et al. 1989). The total edge length is still climbing, but Browder et al. (1989) estimated that it will reach its maximum around the turn of the century, after which the interface length should decline rapidly. Shellfish and fish populations are expected to follow the interface trend (Condrey et al. 1995).
- Fishing pressure is the cause of population declines of commercial species all over the world. However, in Louisiana most of the commercial species have short life cycles and are harvested during their first or second year of life. The interannual variation in population size is high, related to environmental conditions, but because of the short life cycle, fishing pressure has had little apparent effect on the stocks of all but one or two species (Perret et al. 1993).
- Eutrophication of the estuaries may result in hypoxic and anoxic conditions and shifts in populations of primary producers that are food for fishes and shellfishes (Rabalais et al. 1995). In particular, the closing of shellfish beds because of high coliform bacteria counts is a constant threat to the oyster industry (Kilgen et al. 1985).
- Marsh management or water-level management by construction of levees and water-control structures is practiced in the Louisiana coastal zone as a means of protecting marshes from saltwater intrusion and excessive water currents. However, the control structures limit access to marshes by the larval and juvenile stages of commercial species; thus, yields of these species are seriously reduced (Herke et al. 1987; Herke and Rogers 1989). Because marsh management projects now cover a significant area in the coastal zone and permit requests for many more have been filed (Day et al. 1990), there is concern that such management may be deleterious to commercial fish yields.

Two additional factors that determine the composition and distribution of nektonic species are discussed in subsequent sections. First, salinity is probably the most important determinant of species distribution and composition, especially when freshwater areas are compared to salt-influenced ones. Second, migration between the Gulf of Mexico and estuaries is characteristic of almost all of the commercially important fishes and shellfishes. *Temporal niche* or *habitat sharing* is often associated with these migration patterns.

Table 6. Number and area of ponds and lakes along the Louisiana coast by size classes (Chabreck 1972).

Size class (hectares)	Number of ponds and lakes	Total area included (hectares)
<0.004	2,950,000	11,478
0.004–0.04	1,889,000	30,468
0.04–0.40	425,800	53,571
0.40–4.05	43,460	49,960
4.05–32.4	5,472	59,997
32.4–259.2	722	61,009
259.2–1,296	149	90,032
1,296–6,480	15	46,494
6,480–25,920	7	145,476
>25,920	1	173,503
Total	5,314,626	721,988

Primary Producers

Waters in the coastal zone are shallow: only 1–2 meters deep in the largest bays, except for the major tidal channels. The muddy, shallow bottom sediments are easily suspended by winds, and the water is typically turbid except in small ponds. As a result, bottom-dwelling filamentous algae and submerged vascular aquatic plants are found only in small, shallow ponds. Most of the aquatic producers are small filamentous or single-celled algae. The algal flora

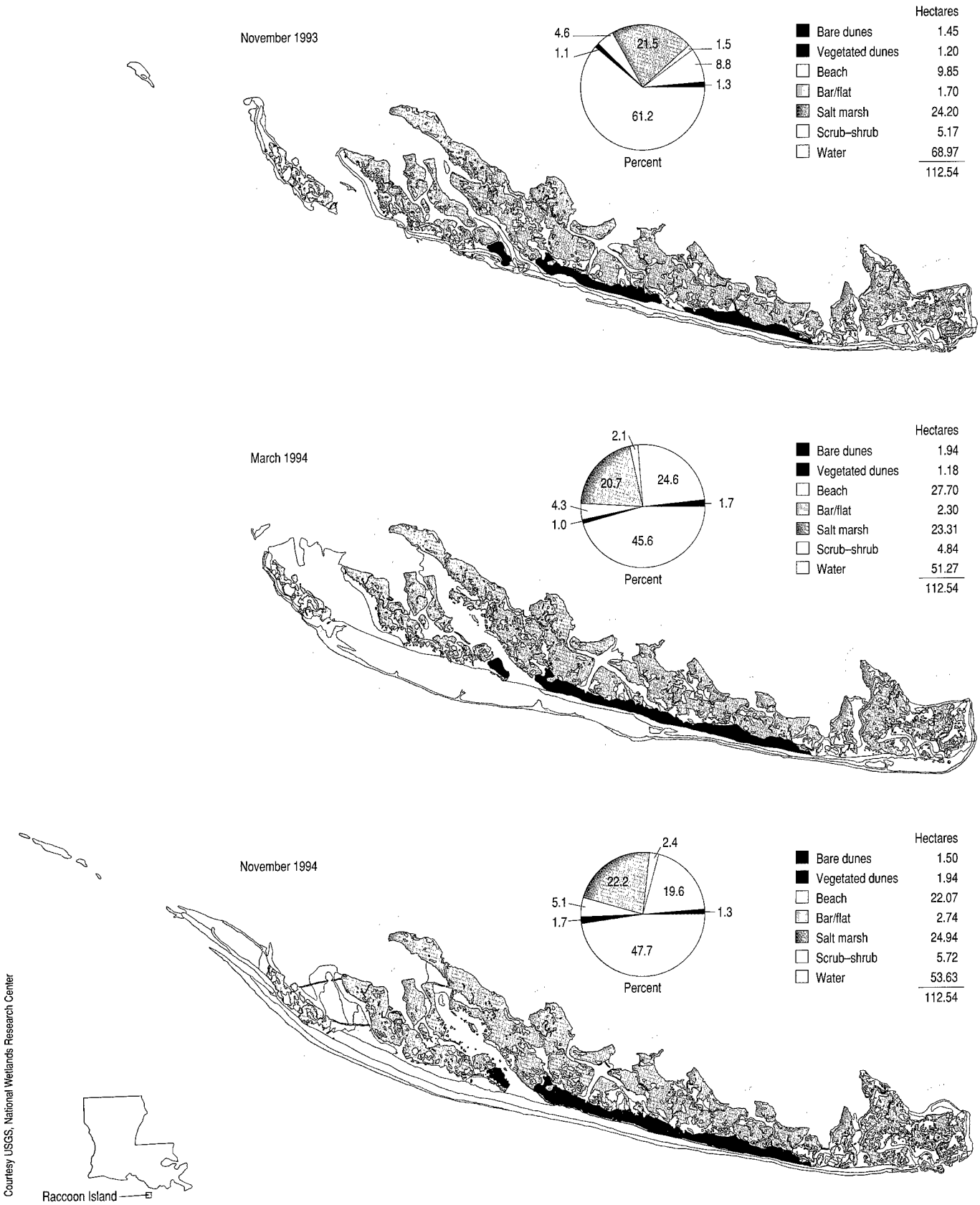


Fig. 34. These vegetation maps of Raccoon Island show how vegetation recovers from storms over time. The state of Louisiana began a beach restoration and nourishment program to reestablish the portions of the island that had been swept away by Hurricane Andrew in 1992. The long-term stability of these newly restored areas may be significantly improved by the establishment of vegetative cover.

of Louisiana estuaries has not been much studied, except to measure the magnitude of primary production (Day et al. 1973, 1977; Stowe 1982; Moncrieff 1983; Shaffer 1986). Day et al. (1973, 1977) found that although gross production in bays and lakes is high, the systems are generally heterotrophic—that is, respiration exceeds production—probably because of the inflow of organic matter from the adjacent marshes and swamps. Production depends strongly on water clarity. In one shallow saline lake studied, benthic production was greater than water column production, but only when light penetrated to the bottom. Salinity and degree of eutrophication determined which species were dominant (Table 7). Freshwater lakes were dominated by blue-green algae, filamentous forms in the spring and unicellular and small colonial species in the summer. Diatoms dominated the winter flora. In low-salinity areas, green algae, dinoflagellates, and diatoms were more important under eutrophic conditions than in less eutrophic conditions where colonial and single-cell coccoid cyanobacteria (blue-green algae) were dominant. The algal flora of a small saline lake was dominated by diatoms during the winter and by dinoflagellates during the summer (Day et al. 1973).

Table 7. Some dominant microorganisms in Louisiana estuaries (Sp = spring; Su = summer; F = fall; W = winter; Y = year-round; x = present). Data from Conner and Day (1987).

Species group	Salinity zone		
	Fresh	Low salinity	Saline
Blue-green algae			
Anabaena species	Su		
Anabaenopsis elenkinii	Su		
Chroococcus species	Sp	Y	
Gloeocapsa species	Sp	Su,F	
Gomphospheria species		Su,F	
Lyngbya contorta	Su		
Merismopedia species	Sp	Su,F	
Microcystis aeruginosa		Su,F	
Green algae			
Chlamydomonas species		F	
Chlorella vulgaris		F	
Pediastrum biradiatum	Su		
Scenedsemus quadricauda	Su		
Staurastrum americanum	Su		
Diatoms			
Actinoptychus undulatus			W
Biddulphia aurita			W
Chaetoceros breve			W
Coscinodiscus species			W
Cyclotella species	W	W	
Diploneis elliptica		W	
Nitzschia species	W	W	
Surirella robusta		W	
Dinoflagellates			
Ceratium hircus			Su
Gymnodinium species		x	Su
Peridinium cinctum		x	Su
Prorocentrum species			Su
Cryptophytes			
Cryptomonas species		Y	
Chrysophyte			
Ochromonas species		Y	
Euglenoids			
Trachelomonas hispida		Y	

Submerged vascular plants are concentrated in shallow marsh ponds of less than 4 hectares (Chabreck 1971). None occur in the saline zone, and widgeongrass is nearly the only species found in brackish areas. Species richness increases from brackish to freshwater areas, with coontail, Eurasian watermilfoil, and southern waternymph appearing in low-salinity areas, and with many additional species present in freshwater ponds (Table 8). A green algal species, *Chara vulgaris*, forms large submerged mats in low-salinity areas during the spring. Floating duckweed solidly carpets forested waterways and flooded swamps, and water hyacinth mats are common obstructions in freshwater lakes and waterways. Water hyacinth, alligatorweed, hydrilla, and Eurasian watermilfoil are all introduced species that have spread widely in Louisiana and are nuisance plants that cause economic damage and are expensive to eradicate.

Table 8. Submerged aquatic plant species in ponds and lakes by marsh zone along the Louisiana coast, August 1968 (Chabreck 1971).[a]

Plant species	Marsh zone (percent cover)			
	Entire coast	Brackish	Intermediate	Fresh
Alligatorweed	0.9	0	0	1.3
American frog's bit	0.8	0	0	1.1
American lotus	1.3	0	0	1.9
American white waterlily	3.4	0	0	5
Blue waterhyssop	0.2	0	0	0.4
Bulltongue arrowhead	0.9	0	0	1.2
Carolina fanwort	2.5	0	0	3.6
Carolina mosquitofern	0.4	0	0	0.6
Carolina spiderlily	0.3	0	0	0.5
Chara vulgaris	8.8	0	32.5	8.1
Coastal waterhyssop	2.5	5	11.7	0.4
Coontail	7.7	0	0	11.2
Creeping primrosewillow	0.2	0	0	0.2
Dwarf spikerush	7	23	10.1	1.6
Eurasian watermilfoil	9.1	3.1	8.9	11
Giant bulrush	0.1	0	0.8	0
Greater duckweed	0.7	0	0	0.9
Horned bladderwort	4.1	0	0	6
Largeleaf pennywort	0.1	0	0	0.1
Lesser duckweed	10.8	0	2.4	15.3
Long-leaf pondweed	0.2	0	0	0.2
Manyflower marshpennywort	1.2	0	0	1.7
Pennywort	0.4	0	0	0.6
Small pondweed	2.3	0	4.9	2.7
Southern waternymph	4.9	0	8.9	5.8
Spikerushes	9.3	4	6.8	11.3
Twoleaf watermilfoil	0.3	0	0	0.5
Water hyacinth	3.1	0	0	4.5
Watershield	1.5	0	0	2.2
Widgeongrass	14.7	62.3	13	0.2

[a] No vegetation in salt marsh zone.

Zooplankton

Zooplankton are an important link in the marine food chain. In the coastal estuaries, for example, the most abundant fish, the bay anchovy, depends largely on zooplankton throughout its life cycle (Darnell 1961). There

are relatively few detailed studies of zooplankton from estuarine Louisiana (Stern and Stern 1969; Bouchard and Turner 1976; DeNoux 1976; Gillespie 1978; Stone et al. 1980). The zooplankton community is dominated by the copepod genus *Acartia*, especially *Acartia tonsa*, which accounts for about 50% of the total zooplankton count from low-salinity lakes near the offshore zone. Other copepod species are also common, and Gillespie (1971) reported that ctenophores are often the most conspicuous zooplankters in high-salinity waters. Fish larvae and fish eggs are also abundant (Raynie and Shaw 1994).

Rotifers, copepods, and cladocerans dominate freshwater environments. Rotifer populations peak once or twice a year, when they may constitute almost the entire zooplankton community. Copepods are represented by *Diaptomus dorsalis*, *D. reighardi*, *D. siciloides*, and *Osphrantieum labronectum*. Cladocerans are the most diverse group, with 17 species, all but 2 of them inhabiting fresh water.

Total numbers of zooplankton species are greatest in nearshore and offshore waters (Table 9). Saline areas have large zooplankton populations but low species richness. Fresh water supports many species, but for reasons not understood, population size and species richness are much lower in brackish zones (Bouchard and Turner 1976; Gillespie 1978; Conner and Day 1987).

Table 9. Zooplankton concentrations and species richness counts within Barataria Bay (cited *in* Conner and Day 1987).

Zone	Bouchard and Turner (1976)		Gillespie (1978)	
	Individuals per cubic meter (mean)	Species richness	Individuals per cubic meter (mean)	Species richness
Coastal water (offshore/nearshore)	83,960	16	9,227	37
Inshore saltwater	19,158	28	5,246	31
Brackish water	1,427	21		
Freshwater	12,682	68		
Backswamp	29,078	59		

At least four factors regulate zooplankton densities: predation by nekton and ctenophores; duration of the larval stages of meroplankton, such as crab zoeae, shrimp, and fish larvae; changes in the aquatic environment brought about by the populations themselves; and externally determined environmental fluctuations (Darnell 1962; Bouchard and Turner 1976). For example, *Acartia tonsa* thrives in a wide range of salinities, and the low salinities in the estuary probably limit competition from other copepods, but ctenophores probably control copepod populations because ctenophores feed voraciously on copepods. When nutrient levels are low, rates of reproduction and densities of organisms decline.

The migration of planktonic phases of fishes and shellfishes is a subject of particular concern because of its importance to the commercial fisheries of the Louisiana coast. Fish larvae seem to move with flood tides from offshore into estuaries, especially deep in the water column. On the ebb tides, larger larval bay anchovies are transported along the pass edges. These observations suggest that the fish and shellfish larvae modify their behavior to enable their transport into the estuary or to stay within it (Raynie and Shaw 1994).

Benthic Organisms

Vittor and Associates, Inc. (1995) reported on a 14-year survey of the benthic infauna in both a low-salinity and a high-salinity area of the Barataria estuary, Louisiana. The number of taxa and density of organisms varied greatly, both seasonally and annually, obscuring any fine differences. Both locations were dominated by annelid worms (oligochaetes and polychaetes), mollusks (bivalves), and arthropods (luciculous amphipods and chironomids). Dominant taxa in the low-salinity zone were the oligochaete worms; *Mediomastus*, *Streblospio*, and *Hobsonia* (polychaete worms); the family Chironomidae (a group of midges); and *Corophium* and *Gradidierella* (amphipods). In the high-salinity zone, some of the same organisms were common—oligochaetes, *Mediomastus*, *Streblospio*, and *Corophium*, as well as the bivalve mollusks surfclams and tellins, and the amphipod *Ampelisca*. Besides the effects of salinity on population composition, the populations appeared structured by sediment grain size. This is particularly apparent in the low-salinity zone, where a long-term trend toward coarser sediments was correlated with an increase in the proportion of arthropods to annelid worms and mollusks.

In a more spatially comprehensive study (32 stations from freshwater to saline environments, each sampled once), Philomena (1983) found that crustaceans, polychaetes, oligochaetes, nematodes, and insects represented nearly 90% of all organisms collected. Abundance of organisms was highest in stations near the marsh edge and in shallow bayous, and it increased from saline sites to freshwater ones. Crustaceans and mollusks were found basinwide; insects, nematode worms, and oligochaete worms were reported mostly in freshwater and low-salinity environments; and polychaete worms and nemerteans were prevalent in brackish and marine environments. Overall, crustaceans were the most abundant group, with 44 genera represented. They appeared at 94% of the stations and contributed 3% of the total biomass. The most important orders were amphipods, cladocerans, ostracods, and isopods. Polychaete worms (13 genera)

were found in 46% of all stations and made up about 1.5% of the total biomass. One species, *Hobsonia florida*, accounted for almost 40% of the total number of worms. Mollusks, with 18 genera, were found in 78% of the stations and made up 93% of the biomass, mostly because of the large size of the Atlantic rangia clam. The narrowmouth hydrobe was the species represented by the largest number of individuals. Oligochaete worms were found at 60% of the stations but constituted only 0.5% of the total biomass. Chironomids were the most abundant insects but only made up about 0.5% of the biomass and 5% of the total number of organisms collected.

The best-known mollusk in Louisiana estuaries is the eastern oyster, which has been extensively studied because of its commercial importance (Fig. 35). At the seaward end of the estuary, oysters are being pushed inland by encroaching saltwater, which favors oyster predators and parasites. Conner and Day (1987) cited evidence that most of the observed summer oyster deaths in the lower (more saline) estuary are related to the protozoan *Perkinsus marinus* rather than to predators such as conchs, stone crabs, boring sponges, and oyster piddocks. At the landward end of the estuary, oysters are being pushed seaward by pollution from developed areas (Van Sickle et al. 1976; Kilgen et al. 1985). Despite this squeeze, the area of substrate potentially suitable for eastern oyster production is increasing as wetlands degrade, and the area leased for oyster production is also increasing (Condrey et al. 1995).

Oysters build extensive reefs or beds. The fauna associated with these structures is diverse, and its biological organization is complex. Bahr and Lanier (1981) reported a total of 42 species of macrofauna representing seven phyla associated with oyster reefs in Georgia, but this is only a fraction of the 303 species listed by Wells (1961) in a monograph on subtidal and intertidal oyster beds.

Fig. 35. Eastern oysters are a commercially important species and are being adversely affected by encroaching saltwater and pollution.

Nekton

This group of organisms includes those that can actively swim independently of current movements. In coastal Louisiana, it comprises numerous fishes; invertebrates such as squids, portunid crabs, and penaeid shrimps; and marine mammals such as bottle-nosed dolphins. Most of these species are a part of the planktonic community for the early stages of their life cycles (Thompson and Forman 1987). Numerous studies (Sabins and Truesdale 1974; Guillory 1982; Herke et al. 1987; Thompson and Forman 1987; Perret et al. 1993; Rogers et al. 1993), as well as a number of excellent theses and dissertations, have documented the composition of nektonic species in Louisiana's coastal estuaries and the major factors controlling their distribution.

A total of 237 species of fish and nektonic invertebrates has been recorded from the Louisiana deltaic plain alone. The estuaries in the inactive delta tend to support similar fish communities. The active deltas of the Mississippi and Atchafalaya rivers are usually fresh water and support a diverse nektonic fauna dominated by freshwater species. During periods of low river flows, however, these deltas have a strong estuarine–marine component. Thompson and Forman (1987) divided coastal nekton into four groups: freshwater, estuarine, estuarine–marine, and marine. Although marine species dominate the inshore fish community, migratory estuarine–marine species (Deegan and Thompson 1985) are by far the most numerically abundant group in the system.

The ten most abundant fish species caught in trawls are bay anchovy, Atlantic croaker, Atlantic bumper, Gulf menhaden, spot, hardhead catfish, sand seatrout, Atlantic threadfin, striped anchovy, and gafftopsail catfish. All but three of these species (Atlantic bumper, striped anchovy, and Atlantic threadfin) have estuarine–marine life histories and a strong affinity for high-salinity estuarine areas. Table 10 compares the relative abundance and biomass contributions of the dominant fish species of the upper, low-salinity (less than 8 parts per thousand) estuary with the lower reaches of the high-salinity (10–27 parts per thousand) estuary. Bay anchovy is the dominant species in terms of both numbers and biomass almost across the entire estuary. In low-salinity zones, catfishes and alligator gar,

Table 10. Abundance and biomass of fish assemblages[a] of the upper and lower Barataria basin (Conner and Day 1987).

Species	Upper bay[b]		Lower bay[c]	
	Number	Weight (kilograms)[d]	Number	Weight (kilograms)[d]
Alligator gar	25	255.8	3	20.6
Atlantic croaker	12,686	64.1	5,300	22.9
Bay anchovy	557,994	303.8	52,633	34.2
Blue catfish	3,498	80.3	0	0
Channel catfish	27,871	404.5	0	0
Gulf menhaden	8,862	40	14,782	23
Hardhead catfish	414	Trace	2,169	52.5
Inland silverside	2,290	Trace	836	Trace
Rough silverside	1,563	Trace	4,514	20.8
Silver perch	10	Trace	899	31.2
Spot	245	Trace	5,786	20.4
Striped mullet	277	Trace	181	18.4

[a] All sampling gears combined.
[b] Chambers 1980 (study done in 1978).
[c] Wagner 1973 (study done in 1971–1972).
[d] Weight is relative but comparable among samples.

Courtesy I. K. Workman, National Marine Fisheries Service

Fig. 36. In coastal Louisiana and in the southeastern U.S., the by-catch of the shrimp fishery as pictured here includes young and adults of various species, as well as invertebrates and other crustaceans such as blue crab.

Courtesy USGS, National Wetlands Research Center

Fig. 37. Commercial shrimp catch.

which are seldom found in high-salinity zones, can make up much of the biomass (Conner and Day 1987).

Among the most common trawl-caught species are a number of estuarine–marine invertebrates, including brown shrimp and white shrimp (Figs. 36 and 37), which seasonally rank in abundance and biomass with the top ten nektonic fish species. Lesser amounts of pink shrimp and seabob shrimp are also harvested commercially. The latter species is apparently not estuarine-dependent, although it is frequently caught in the lower estuary. Brown shrimp and white shrimp exhibit the marsh–estuarine life cycle typical of most commercial invertebrates and fishes on the Gulf of Mexico coast. Brown shrimp spawn in the Gulf of Mexico, and their larvae move into the lower estuaries in February and March, where the postlarval and juvenile stages develop in shallow ponds and streams deep in the marsh. The young adults emigrate to deeper estuarine waters and the nearshore Gulf of Mexico in early to midsummer (Fig. 38); their emigration is keyed to lunar tides (Blackmon 1974). White shrimp have a similar migration pattern, but inshore recruitment occurs in June through August, and mass emigration is keyed to the passage of cold fronts in late fall and early winter.

Blue crab, the most important commercial crab species in the Gulf of Mexico (Fig. 39), is found from the offshore marine waters to the most inland Louisiana freshwater marshes. In late summer, egg-bearing females emigrate offshore to spawn. The larvae follow the inshore migration pattern of the estuarine–marine fish. The mature males generally stay in fresh water or near freshwater areas for the remainder of their life cycle, unlike the males of a related (noncommercial) species, the lesser blue crab, which emigrate offshore with the females where both complete their adult life cycles on the Continental Shelf. The brief squid is the only nektonic mollusk that occurs in any numbers within the estuaries. It is a true estuarine species, and there is evidence of egg deposition by squids within the estuary (Roper et al. 1984).

The freshwater fish assemblage in estuarine Louisiana is poorly studied (Condrey et al. 1995). A modest commercial fishery harvests blue and channel catfishes. Bluegill, black crappie, white crappie, and largemouth bass are caught by sport-fishers in freshwater lakes. In the freshwater areas of the active deltas, freshwater and saltwater fishes are often found together.

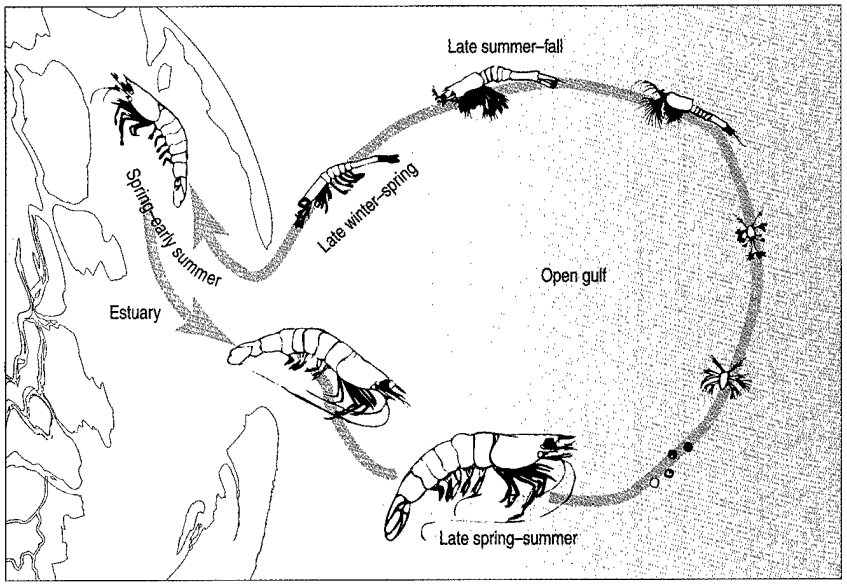
Resident estuarine fishes include minnows, killifishes, silversides, and gobies that spend their entire lives in the estuary. Information on these species is relatively poor; since they

concentrate in shallow marsh ponds and along marsh edges, they are caught relatively infrequently in trawls. Studies using seines have documented that gulf killifish and longnose killifish are among the most abundant estuarine fish species, whereas bayou killifish and the marsh killifish are much less abundant (Thompson 1988). In small saltwater marsh ponds, sheepshead minnow, tidewater silversides, and sailfin molly are common, as well as the killifishes (Ruebsamen 1972).

The most abundant group of coastal Louisiana finfish, which includes most of the commercially and recreationally important finfish on the northern gulf coast, have estuarine–marine life histories similar to the brown and white shrimps (Condrey et al. 1995; Figs. 38, 40, and 41). They are typically euryhaline, and small juveniles often migrate many kilometers up the estuaries. The timing and routes of migration lead to a complex pattern of habitat use in both time and space (Figs. 40 and 41). Most of the commercial catch occurs in the nearshore waters of the Gulf of Mexico, which are the inshore marsh areas that serve as nurseries for the juveniles. The unintended catch of fishes from shrimp trawling is substantial. Studies show a 75% reduction in demersal biomass (that is, the total weight of all species living near the bottom of the water column) occurring within the estuary shortly after the opening of the shrimp-trawling season. Most of these by-catch fish (Fig. 36) are discarded and die, and most are young individuals of the migratory estuarine–marine fishes, including Atlantic croaker, spot, sand seatrout, gulf menhaden, catfishes, and bay anchovy. Many rarer species are taken in smaller numbers. Without the incorporation of turtle excluding devices, trawls also catch endangered sea turtles often enough to threaten their survival (Condrey et al. 1995).

The estuarine-dependent Louisiana fishery is an $875 million (dockside) industry. Shrimp generate the largest share of this income, followed by oysters, menhaden, blue crabs, and striped mullet (Louisiana Coastal Wetlands Conservation and Restoration Task Force 1993; Table 11). The menhaden purse-seine fishery handles the largest volume of catch, but the low price per unit is reflected in the total annual value of about $87 million. In addition, there are important fisheries for estuarine–marine spotted seatrout, black drum, red drum, and southern flounder. Commercial freshwater species include blue catfish, channel catfish, flathead catfish, yellow bullhead, bowfin, carps, gars, and buffaloes. For sport-fishers, primary game species include largemouth bass, yellow bass, black crappie, bluegill, spotted sunfish, redear sunfish, warmouth, and several catfish species in freshwater areas; and seatrouts, red drum, southern flounder, sheepshead, gafftopsail catfish, and Atlantic croaker in estuarine areas.

Most of the commercial and game species are fairly short-lived and are harvested in the first or second year of life. Because of the high recruitment rate, population data do not show any trends that suggest overfishing, and these species are assumed to be stable. Red drum and black drum are long-lived, a characteristic that has led to management strategies to ensure spawning by multiple year-classes (Condrey et al. 1995).



Courtesy USGS, National Wetlands Research Center

Fig. 38. The life cycle of brown shrimp illustrates the typical cycle of an estuarine-dependent fish or shellfish species.

Courtesy USGS, National Wetlands Research Center

Fig. 39. Commercial catch of blue crabs.

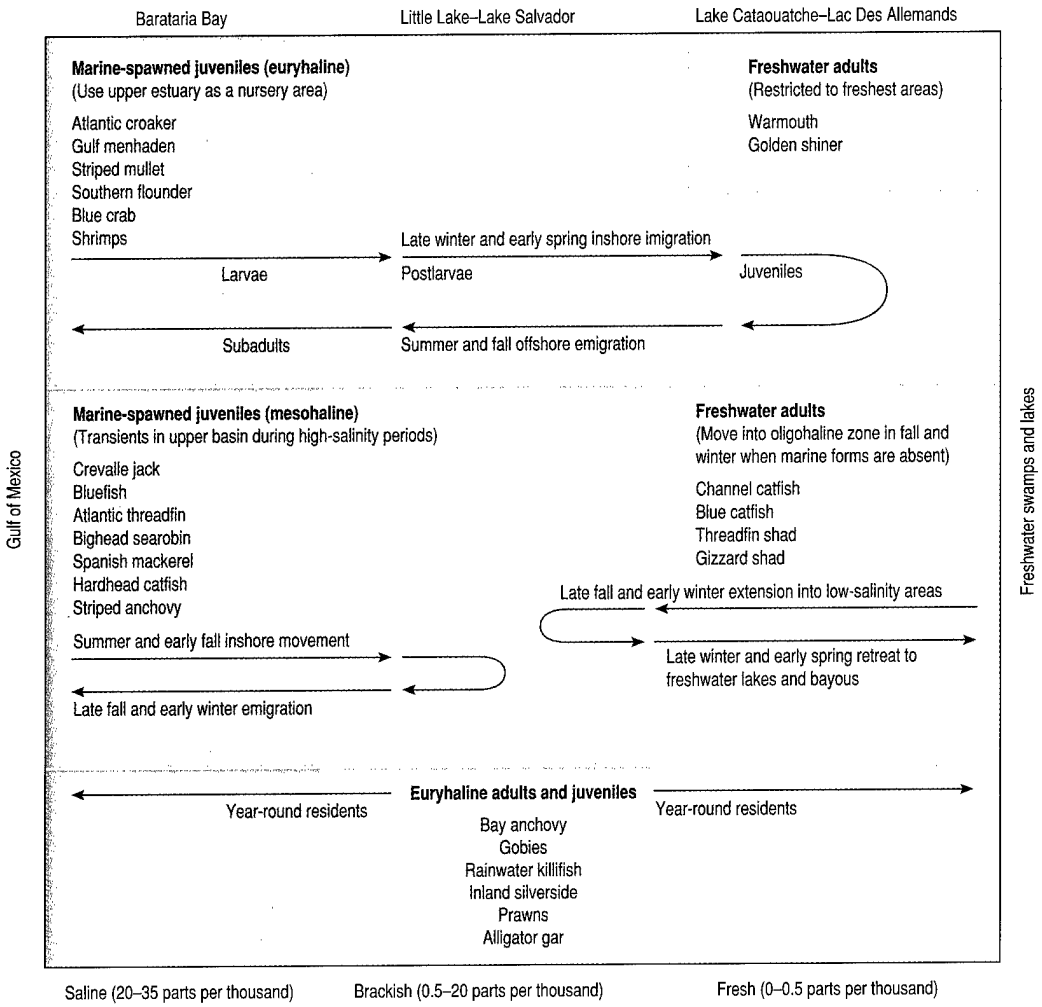


Fig. 40. Patterns of estuarine use by nektonic organisms in the Barataria estuary, Louisiana (modified from Chambers 1980).

Table 11. Harvest and value of the estuarine-dependent commercial fisheries of the Gulf of Mexico and Louisiana coastal area (Louisiana Coastal Wetlands Conservation and Restoration Task Force 1993).

Species	1983–1990 Average corrected landing[a,b] (metric tons)	1992 Gross dockside value[c] (dollars)
Blue crab	56,060	71,618,978
Shrimps	224,779	1,074,386,530
Oysters	18,685	107,187,451
Menhaden	789,708	86,972,225
Atlantic croaker	140	178,282
Black drum	3,193	3,094,473
Red drum	1,589	4,026,099
Catfishes	2,613	3,452,935
Flounders	669	1,532,494
Northern kingfish	304	247,558
Striped mullet	11,355	10,254,730
Sea catfish	62	28,452
Spotted seatrout	1,228	3,137,112
White seatrout	235	278,888
Sheepshead	1,596	808,300
Spot	124	79,143
Finfish	3,075	1,557,835
Total Gulf of Mexico	1,115,415	1,368,841,485
Louisiana coastal area[d]	713,839	876,058,551

[a] Source: U.S. Department of Commerce, National Marine Fisheries Service, published and unpublished data for 1983–1990.
[b] Correction factors based on information provided by the Louisiana Department of Wildlife and Fisheries, Baton Rouge.
[c] Based on 1992 normalized prices and the 1983–1990 average corrected landings.
[d] Gulf of Mexico landings allocated to the Louisiana coastal area are based on the relative abundance of estuarine marsh habitat.

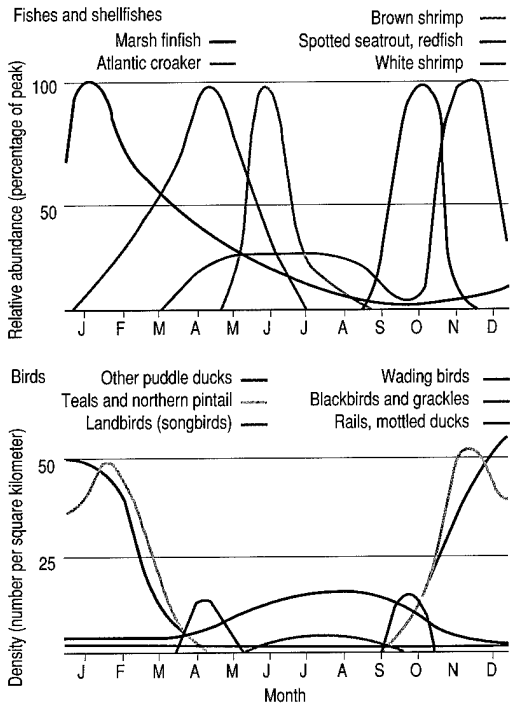


Fig. 41. Seasonal use of wetlands by migratory birds, shellfishes, and fishes (Gosselink 1984).

Status and Trends of Sensitive and Introduced Populations and Groups

Birds

More than 400 species of birds are known to occur in Louisiana, most of them in the coastal region. Coastal Louisiana provides habitat for numerous species of waterfowl, colonial-nesting birds, and other resident and migratory birds. Important nonwaterfowl game species include American coot, clapper rail, king rail, sora, common moorhen, purple gallinule, American woodcock, and common snipe (Michot 1984). Hundreds of nongame species inhabit the coastal marshes, including the wood stork, American white pelican, pied-billed grebe, magnificent frigatebird, black-necked stilt, American avocet, killdeer, black-bellied plover, willet, and various sandpipers, gulls, and terns (Lowery 1974a). The coastal marshes are also of primary importance to large numbers of waterfowl, especially in winter.

Birds and Barrier Islands

Barrier islands and cheniers provide nesting and resting sites for many animals and birds that forage in the marsh. These habitats are particularly important for seabirds, wading birds, and Neotropical migrants. Egg and feather collectors nearly eradicated the abundant bird populations found by early French explorers. Fortunately, these birds responded to conservation measures enacted in the early 1900's. Between 1940 and 1960, however, many seabird populations were reduced by toxic chemicals in coastal waters. The local extinction of the eastern brown pelican is the most dramatic example of the deleterious effects of the pesticide DDT in the food chain. Eastern brown pelicans were reintroduced from Florida and have reestablished a number of colonies (see Endangered Species section in this chapter).

The Louisiana coast has a comparative abundance of seabirds that nest on sandbars, barrier beaches, and marsh islands at the edge of large bays. Most are colonial nesters (for example, pelicans, gulls, terns, and skimmers) which feed on small fishes, primarily within the shallow bays and the near coastal waters. Twenty-eight species of seabirds and wading birds have established nesting colonies in the Louisiana coastal zone (Portnoy 1977; Keller et al. 1984). Louisiana provides the most important breeding area for many species, including Sandwich terns (77% of the United States breeding population), black skimmers (44%), and Forster's tern (52%). Keller et al. (1984) found 188 active bird colonies in coastal Louisiana. In a time-series comparison of colonial bird sites, almost half of the colonies moved between years from one location to another. Because of the rapid loss of barrier islands, nesting habitat is at a premium, and habitat availability is probably the major long-term threat to these populations. Human disturbance of nesting sites is also a serious problem on the accessible islands and headlands (Condrey et al. 1995).

Pelicans nest on the barrier islands, but wading birds—egrets (Fig. 42), herons, and ibises—more often nest inland of the barrier beaches in mangroves, wax myrtle thickets, and other forested areas. These birds are mostly carnivorous, catching frogs, small fishes, snakes, crayfishes, and a wide assortment of worms and insects. Wading birds prefer freshwater and brackish marshes to saline marshes but are common across the entire coast.

Barrier islands and chenier ridges are important to Neotropical migrant songbirds (Fig. 43) for slightly different reasons. Many species use the barrier and ridge habitats irregularly or accidentally during their migrations. Some breed on the Louisiana coast but migrate to Central and South America during the winter. A few breed in the northeastern United States and winter on the Louisiana coast, but most breed in the Northeast and winter in Central and South America. Thus, they must either cross or circumvent a broad ecological barrier, the Gulf of Mexico, during the spring and fall of each year. The majority of migrants fly nonstop for more than 1,000 kilometers to cross the Gulf of

Courtesy USGS, National Wetlands Research Center

Fig. 42. The snowy egret is one species of wading bird that nests in coastal Louisiana in mangroves, wax myrtle thickets, and other forested areas. These birds were almost extirpated from Louisiana in the early 1900's when they were killed for the use of their feathers in the millinery trade, but snowy egrets have recovered and are now common in the state's coastal wetlands.

Courtesy USGS, National Wetlands Research Center

Fig. 43. Prothonotary warbler, a Neotropical migrant that nests in the baldcypress swamps of coastal Louisiana, is one of at least 63 migratory bird species that regularly use woodlands along the Louisiana coast to replenish their energy reserves either before or immediately after crossing the Gulf of Mexico to the Yucatan Peninsula or South America.

Mexico each spring. During the fall, most migrants fly along the coast through Texas and around the gulf. Birds often concentrate in habitats adjacent to ecological barriers during migration, and the geographic position of the Chenier Plain makes cheniers and barrier islands important stopover habitats for enroute migrants. At least 63 species of migratory birds regularly use these wooded habitats to replenish energy reserves necessary to successfully complete their migration before, or immediately after, crossing the Gulf of Mexico. During spring migration, birds usually leave Central and South America at night, making landfall along the northern gulf coast the next midday.

In spite of the difficulty in crossing the Gulf of Mexico, many spring trans-gulf migrants continue flying inland until they reach the more contiguous tracts of forest north of the Chenier Plain. Gauthreaux (1971) found that during fair weather, such as southerly winds and clear skies, approximately 10% of in-transit spring migrants land in coastal woodlands. Under poor conditions of northerly winds or precipitation, however, as many as 80% of the individuals on a trans-gulf flight make landfall in the cheniers and other coastal woodlands, which temporarily support tremendous densities of land birds (Gosselink et al. 1979a,b,c; Condrey et al. 1995; Barrow et al. 1997).

When autumn migrants fly southwesterly around the Gulf of Mexico, the coastal cheniers are important habitat corridors and staging areas for a variety of passerine birds, both those that nest in coastal Louisiana and those that breed farther north, including 180 species of passerines and a few species of cuckoos, swifts, hummingbirds, and goatsuckers. The belted kingfisher and several species of woodpeckers are also residents of the coastal area (Lowery 1974a; Michot 1984).

The Nearctic–Neotropical migratory bird system is complex. Neotropical migrants require a variety of habitats across continents, presenting multiple biological and political challenges. Although increasing international attention is focused on the deforestation of tropical forests and fragmentation of temperate forests, little attention has been given to enroute habitats. Stopover habitats, such as coastal forests near ecological barriers, are undergoing dramatic changes that may threaten Neotropical migrants (Barrow et al. 1997). At present, about one-half of the human population in North America resides in coastal counties (U.S. Department of Commerce 1990); from 1960 to 2010, the coastal population will have grown from 80 million to more than 127 million people, an increase of almost 60% (U.S. Bureau of the Census 1995). As a result, human development will place considerable pressure on remaining coastal habitats. The enroute habitats where migrants tend to concentrate need further quantification, and appropriate conservation and management measures are required.

Waterfowl

Waterfowl are an important commercial resource for the recreational hunting industry: the value of waterfowl hunting to the state of Louisiana is estimated to exceed $10 million annually (Louisiana Coastal Wetlands Conservation and Restoration Task Force 1993). From an ecological point of view, though, waterfowl dramatically illustrate the coupling of ecosystems in the Louisiana coastal region. Although many organisms already discussed move from one ecosystem to another within the coastal zone—or in the case of nektonic fishes, from coastal estuaries to the Gulf of Mexico—waterfowl and other migratory birds link the Louisiana coast with the northern U.S. and Canadian wetlands and with Central American wetlands to the south.

Besides the intrinsic interest in the evolution of waterfowl's complex migratory patterns from an ecological standpoint, the conservation of waterfowl populations also presents major management challenges. The migratory patterns of waterfowl are well studied and understood (see, for example, Bellrose 1980). Generally, waterfowl species nest in northern U.S. or Canadian prairie pothole wetlands in spring and early summer (see chapter on Grasslands). These pothole wetlands are particularly important breeding grounds for ducks. Wetlands as far north as the arctic tundra are used by geese. With the approach of winter, waterfowl migrate along well-established flyways through the heart of the continent to coastal wetlands in the southern United States, where most spend the winter. A few species, such as northern pintail and teals,

continue south to Central America. With the return of spring, the flocks begin the return trip to their nesting grounds (Fig. 44). Although waterfowl winter in coastal wetlands from the south Atlantic coast (Smith and Odum 1981) to Texas and California, Louisiana is at the southern extreme of the major duck and goose migration corridors.

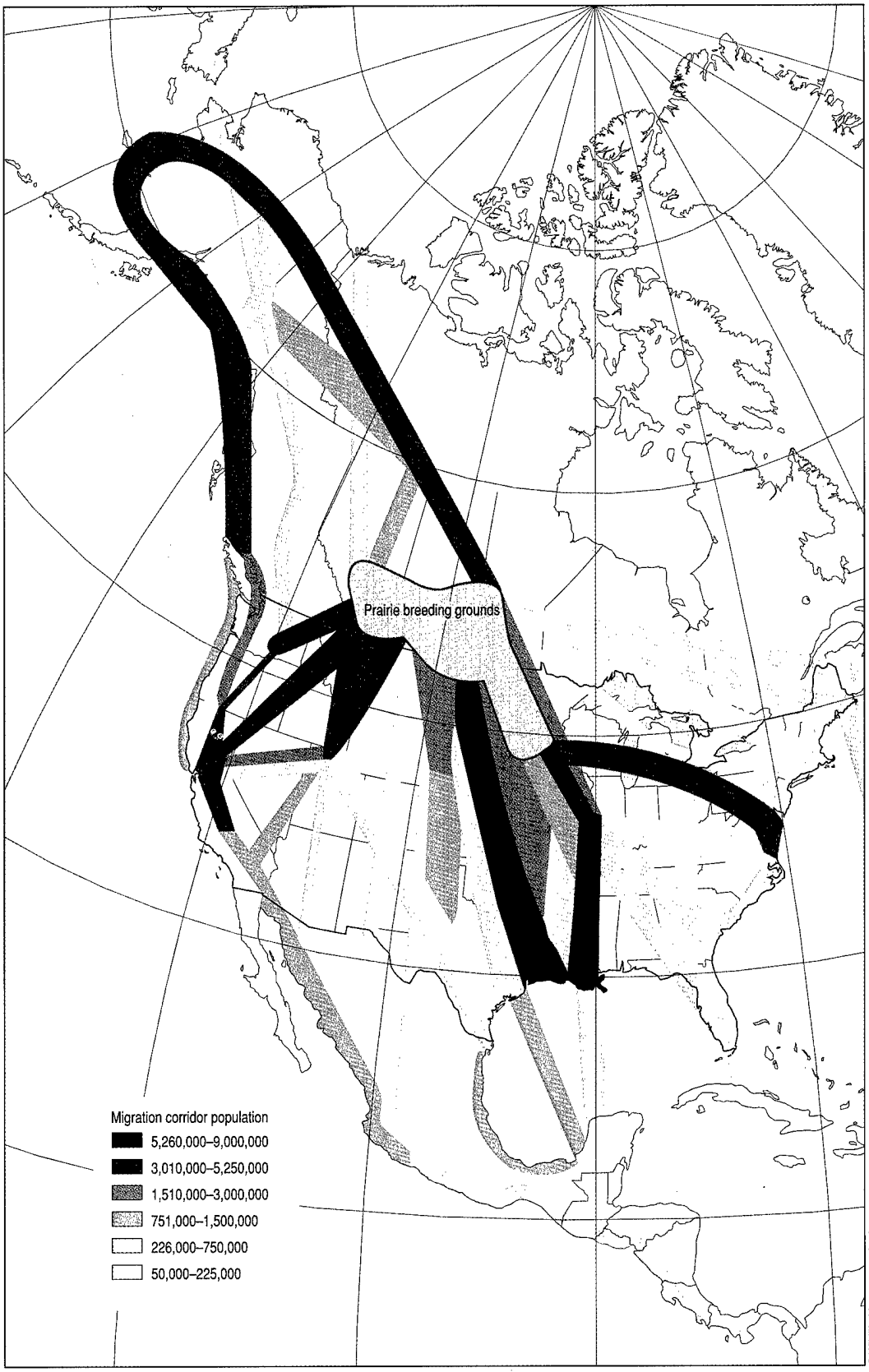


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Fig. 44. Major duck migration corridors to Gulf of Mexico coastal marshes (Bellrose 1980).

Population data gathered from nesting surveys by the U.S. Fish and Wildlife Service and the Canadian Wildlife Service (1994) provide the most reliable estimates of population trends, whereas Louisiana data reflect local population distributions. Ducks and geese are highly opportunistic and will seek superior winter feeding grounds.

Continental populations are influenced by nesting success and recruitment and by mortality, including hunting mortality, throughout the ranges of waterfowl. Population densities of various waterfowl species in Louisiana are influenced by habitat conditions both within and outside the state, winter mortality, local rainfall and weather patterns, and outbreaks of contagious and infectious diseases (Condrey et al. 1995; see box on Duck Plague in Grasslands chapter). In addition, the *short-stopping* of ducks and geese also affects the population densities of some species. Short-stopping occurs when migratory birds "stop short" of their normal wintering grounds because of increased winter food supplies or habitat along their migratory routes.

During the late 1970's through the early 1990's, many waterfowl populations declined precipitously (Michot 1996) because of a severe drought on their breeding grounds. Populations of most species have rebounded in the last few years, primarily in response to wet years and to favorable wetland and upland habitat conditions on the prairies to the far north.

Table 12 and Figure 45 give population estimates for the state's most abundant duck and geese species. Dabbling ducks and geese feed in shallow ponds and flooded freshwater and brackish marshes, although they also frequent adjacent rice fields and other agricultural areas. The birds eat seeds, leaves, shoots, rhizomes, and tubers of emergent marsh plants and submerged aquatic plants; they supplement this diet with insects, mollusks, and other invertebrates. The most abundant dabbling ducks in the Louisiana coastal marshes are gadwall, green-winged teal, mallard, and northern pintail (Fig. 45). The mottled duck, also an important winter species, is one of the three duck species that nest in Louisiana. Mottled duck numbers have increased slightly over the last 25 years in southeast Louisiana (Condrey et al. 1995), but they showed no significant trend over the entire Louisiana coast from 1969 to 1994 (Michot 1996). No other duck population changed significantly during that period, either for all of coastal Louisiana (Michot 1996) or for southeastern Louisiana (Condrey et al. 1995).

Diving ducks feed in large, shallow freshwater lakes and brackish bays, and some species rest offshore in the Gulf of Mexico. Their diverse diet includes emergent and submerged plants, and animals such as fishes, clams, snails,

Table 12. Estimated numbers (mean and standard deviation, in thousands) of ducks and geese in January, 1969–1994, for the Louisiana coastal area, for the U.S. midwinter population, and the percentage of the U.S. midwinter population represented by the Louisiana coastal area population (Michot 1996).

Species or species group	Louisiana coastal area[a]			U.S. total[b]			Percent Louisiana coastal area[c]		
	Number of years	Mean	Standard deviation	Number of years	Mean	Standard deviation	Number of years	Mean	Standard deviation
Dabbling ducks									
Mallard	25	387	230	26	5,911	1,456	25	7	4
Mottled duck	25	67	32	26	104	37	25	63	16
Gadwall	25	734	261	26	1,017	302	25	70	10
American wigeon	25	201	125	26	1,095	306	25	18	8
Green-winged teal	25	617	268	26	1,450	399	25	42	14
Blue-winged teal	25	96	86	26	121	95	25	72	16
Shoveler	25	156	77	26	712	182	25	22	11
Northern pintail	25	372	168	26	3,528	1,538	25	12	7
Total dabblers[d]	25	2,631	754	26	13,928	3,542	25	19	5
Diving ducks									
Redhead	22	15	6	26	389	128	22	4	2
Canvasback	25	21	21	26	269	52	25	7	7
Scaups	25	413	348	26	1,187	337	25	32	25
Ring-necked ducks	24	61	53	26	240	120	24	23	10
Total divers[d]	25	506	355	26	2,085	331	25	23	15
Total ducks[d]	25	3,137	919	26	16,023	3,646	25	19	5
Geese									
Lesser snow	25	345	55	26	1,747	524	25	22	9
Greater white-fronted	25	56	10	26	271	109	25	22	7
Total geese[d]	25	401	48	26	2,018	591	25	21	7
Total waterfowl[c]	24	3,490	913	26	18,041	3,290	24	19	4

[a] Includes all areas south of U.S. Highway 90. Estimates provided by the Louisiana Department of Wildlife and Fisheries, Baton Rouge (all ducks except redhead), and the U.S. Fish and Wildlife Service (redheads and all geese).

[b] U.S. Midwinter Survey data from the 48 conterminous states, all four flyways combined, from the U.S. Fish and Wildlife Service.

[c] For each year (1969–1994), the estimated number of birds for each species for coastal Louisiana was divided by the midwinter estimate (number of birds) for the United States to obtain an estimate of the percentage of the U.S. wintering population that winters in coastal Louisiana. These percentages were then summed over all years and divided by the number of years to obtain a mean percentage for each species over the period of analysis; that mean with its standard deviation is reported in this table. The value for each mean, therefore, differs from a value obtained by dividing the two means presented to the left of it in this table.

[d] Total dabblers, total divers, total ducks, total geese, and total waterfowl include only the species listed in this table; each total presented is a mean of the values for the period of analysis (1969–1994), and thus does not represent a sum of the values presented above it in this table.

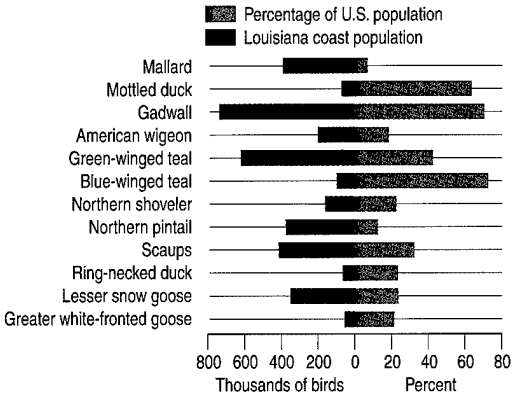

Fig. 45. Number of individuals (1969–1994 mean) of predominant waterfowl species in coastal Louisiana, and for each, the mean percentage of the U.S. wintering population represented by the Louisiana coastal population (Michot 1996).

Courtesy USGS, National Wetlands Research Center

Fig. 46. Lesser scaups. About 25% of the U.S. winter population of scaups are found in coastal Louisiana, where numbers average about a half-million and in some years may approach a million. Scaups feed primarily on the estuarine invertebrates produced in coastal wetlands.

and crabs. Scaups (Fig. 46) are the most numerous diving ducks, followed by ring-necked ducks, canvasbacks, and redheads (Table 12). The wood duck, like the mottled duck, nests in coastal Louisiana and is also present during the winter. About 40% of the wood ducks shot in Louisiana are residents, and the rest are migrants (Bellrose and Holm 1994). Wood ducks nest in tree cavities in coastal forested wetlands (wooded swamp and bottomland hardwoods) and feed primarily on seeds and nuts, although young wood ducks require some animal food, mostly insects.

Enormous numbers of geese occur in coastal Louisiana, primarily in the Chenier Plain, and to a lesser extent in the active delta of the Mississippi River. The abundance of geese in the Chenier Plain region is probably related to the proximity of the coastal wetlands to extensive rice fields and possibly to aggressive management of wetlands for waterfowl in state and national wildlife refuges there. The lesser snow goose is the most abundant goose wintering in Louisiana (Table 12), and white-fronted geese occur in relatively large numbers as well. The Canada goose was formerly abundant in coastal Louisiana, but now only a few thousand winter there while the rest of the population winters farther north. Both snow geese and white-fronted geese increased in the U.S. midwinter population from 1969 to 1994; however, snow geese in coastal Louisiana decreased over that period, whereas white-fronted geese numbers paralleled the national trend (Michot 1996).

Mammals

Fifty-eight species of land mammals are residents of Louisiana (Lowery 1974b), many of them in the coastal marshes. Important game mammals include white-tailed deer, eastern cottontail, swamp rabbit, gray squirrel, fox squirrel, and raccoon; furbearers include muskrat, nutria, raccoon, mink, Virginia opossum, striped skunk, bobcat, beaver, and coyote. Many other land mammals are also found there, including insectivores, bats, rodents, and the nine-banded armadillo. Whales and dolphins inhabit the gulf waters adjacent to the coast, and some, particularly dolphins, enter the estuaries (Michot 1984).

Amphibians and Reptiles

Amphibians are generally found in the freshwater wetlands of the coastal zone. The bullfrog and pig frog are important for commercial and recreational hunting. Other amphibians include lesser siren, three-toed amphiuma, Gulf Coast toad, Fowler's toad, green treefrog, spring peeper, cricket frog, eastern narrow-mouthed toad, and bronze frog.

The commercially important reptiles are found in many freshwater and estuarine habitats; they include the American alligator, common snapping turtle, alligator snapping turtle, smooth softshell, spiny softshell, and diamondback terrapin. Other noncommercial reptiles common in freshwater habitats include the red-eared turtle, painted turtle, common musk turtle, Mississippi mud turtle, green anole, broad-headed skink, diamondback water snake, broad-banded water snake, green water snake, gulf salt marsh snake, western ribbon snake, speckled kingsnake, and western cottonmouth. The gulf

salt marsh snake and diamondback terrapin are also common in brackish to saline marshes (Michot 1984).

Introduced Species

Alligatorweed

Alligatorweed is an introduced nonindigenous plant that has become a major pest. It grows in shallow marsh ponds and on the edges of bayous and sheltered lakes, as well as on the wetland surface. Chabreck (1972) recorded it as having 5% cover in freshwater marshes and 2.5% in intermediate-salinity marshes. In some freshwater marshes, it is codominant with sensitive jointweed. The alligatorweed flea beetle was introduced as a means of biologically controlling the plant and has apparently succeeded in checking its expansion (Gosselink et al. 1979a,b,c).

Water Hyacinth

Water hyacinth is a perennial, aquatic vascular plant that forms floating mats and has a wide distribution in the tropics. It is probably native to Brazil but has spread throughout South America and is now a serious pest in the southern United States. The first authentic account of its introduction is from the Cotton Centennial Exposition at New Orleans in 1884. The plant was apparently introduced as a nonindigenous species "which readily made friends on account of its beautiful bloom and the little difficulty . . . in growing it" (Klorer 1909). The plants were cultivated in ponds at homes around New Orleans and eventually escaped from cultivation. It is an important pest in Florida and has been reported from all the southeastern coastal states as far north as Virginia.

In Louisiana, water hyacinth invades freshwater areas of the coast, including the lower reaches of rivers and freshwater marshes (Penfound and Earle 1948). Its mats become so thick that they obstruct navigation and impede drainage. In the late 1940's damage was as high as $15 million a year (Penfound and Earle 1948). The federal government still spends millions of dollars each year to keep canals and rivers navigable. Fortunately, this tropical plant has little resistance to cold temperatures, and its population is periodically reduced by winter frosts. Mats of water hyacinth may choke out native submerged aquatic plants and can shade and kill marsh plants when high water carries mats into the marsh. The species has been blamed for the death of large areas of floating marshes during the extreme floods of the early 1970's, although this effect has not been verified.

Nutria

O'Neil (1949) discussed the damage done by muskrats in coastal marshes. A related rodent, nutria, was introduced into Louisiana from South America several times during the 1930's. Whether it escaped or was released for fur production is not clear, but the early escaped populations apparently did not become established. However, in 1939, 12 pairs owned by the McIlhenny family on Avery Island (a salt dome surrounded by marsh) escaped, another 150 animals were released during a 1940 hurricane, and landowners began releasing breeding stock into their marshes for fur production and weed control (Lowery 1974b). Two hundred and fifty nutria were transplanted to the Mississippi River delta in 1951, and the population increased so rapidly that the marsh in the delta was completely torn apart by 1957. By 1959 the nutria population in Louisiana was more than 20 million animals (Lowery 1974b). During the 1970's and early 1980's, the population was controlled by trapping, but the demise of the wild fur industry in the United States in the past decade has led to a resurgence of nutrias.

O'Neil (1949) described muskrat *eat-outs* in the marsh that took years to recover. Very little documentation of nutria damage has been available until recently, when a large part of the inactive delta was surveyed. Scientists found widespread damage over an estimated 200 square kilometers of marsh in the Terrebonne and Barataria estuaries alone (Linscombe and Kinler, unpublished report). Effects of nutria on coastal wetlands have been dramatic. Before the introduction of nutria, muskrats were the dominant mammal in freshwater marshes. They are now found primarily in brackish marshes, displaced by the larger and more aggressive nutria (Lowery 1974b). Evers et al. (1988) showed that nutria grazing was a major factor leading to denuding of intertidal flats in the Atchafalaya delta. Linscombe and Kinler (unpublished report) stated that nutria grazing is most destructive in freshwater floating marshes, and there is some evidence that the localized rapid degradation and disappearance of these marshes result primarily from grazing. Nutria are also responsible for the failure of baldcypress regrowth in many coastal baldcypress swamps. Conner and Toliver (1990) reported that nearly all naturally germinating or planted baldcypress seedlings, even if protected with plastic sleeves, were destroyed by nutria in places where their populations were dense.

Endangered and Threatened Species

Many endangered, threatened, and rare taxa in the United States depend on wetlands. Of the 188 animals federally designated in these

categories in 1988, 94 (50%) were associated with wetlands. Of these, 17 were bird species or subspecies. Twenty eight percent of the plants listed were wetland-dependent. Of the estimated 2,500 plants still in need of protection, about 700 may be associated with wetlands (Niering 1988). A publication of the Louisiana Natural Heritage Program (Lester 1988) lists 103 plants and 64 animals of special concern in the Louisiana coastal zone. Although most of these species occur in other states and may have healthy populations elsewhere, in Louisiana they are now rare. Some species, though, have low numbers throughout their range, or even lower populations at the edge of their natural range, but for many species there are local factors that limit their distribution. The highest-profile species are those that are federally listed (Table 13). The following brief descriptions of endangered and threatened animals were compiled from information in Gosselink and Hebrard (1979), Lester (1988), Condrey et al. (1995), Louisiana Department of Wildlife and Fisheries (1995), and U.S. Fish and Wildlife Service (1997), unless otherwise indicated.

Mammals

Although the Louisiana black bear was widely distributed before European settlement, probably only 200–300 remain in Louisiana, and fewer than half of these occur in the coastal zone. Black bears in east Texas, Louisiana, and the southern half of Mississippi are recognized as a distinct subspecies and are listed as threatened under the Endangered Species Act (U.S. Fish and Wildlife Service 1997). Heavy hunting pressure before 1930 and habitat changes—especially the widespread conversion of forests in the Lower Mississippi River valley to row crop agriculture—were the main causes of the bear's decline. Coastal bears extensively use mixed wetland forests and upland habitats on salt domes and canal spoil areas, but bears also occur in wet scrublands, baldcypress swamps, and sugarcane fields. Fragmentation and isolation of wetland forest tracts by development and agriculture make maintenance of a viable population of black bears within the coastal zone of Louisiana difficult.

The red wolf was once found in the Mississippi River valley from Illinois to the Gulf of Mexico coast and from Texas to Florida. Its natural range has shrunk to the marshes and coastal prairies of parts of southwestern Louisiana and southeastern Texas; whether true red wolves remain is uncertain because of their hybridization with coyotes, which have moved into the wolf's range as forests have been cleared. Red wolf populations have declined because of heavy hunting and trapping pressure combined with encroaching agricultural and industrial use of wolf habitat. The species is federally listed as endangered (U.S. Fish and Wildlife Service 1997). By 1980, after a large trapping effort that recovered only 14 pure red wolves, the U.S. Fish and Wildlife Service declared the species extinct in the wild. A coyote-like canid has become established in many of the coastal wetlands once occupied by red wolves and may serve the same ecological function.

Several species of whales frequent Louisiana's coastal waters and are sometimes stranded in its bays or on its barrier beaches. Sightings of West Indian manatee in Louisiana have increased in recent years with about 30 reported sightings from 1975 to 1995; during warmer months individuals disperse from Florida as far west as Louisiana (Louisiana Department of Wildlife and Fisheries 1995).

There are sporadic unconfirmed sightings of the Florida panther, which once ranged across the entire Southeast, but the few animals that remain are probably all in Florida.

Birds

The eastern brown pelican, a large, dark gray-brown waterbird with distinctive white about the head and neck of adults, nests in colonies mostly on small coastal islands (Fig. 47). This species was extirpated from the Louisiana coast during the 1960's, primarily because of thin-shelled eggs and other reproductive failures linked to ingestion of pesticide (chlorinated hydrocarbon) residues in food fishes. A restoration project that was sponsored jointly between the Louisiana Department of Wildlife and Fisheries and the Florida Game and Freshwater Fish Commission introduced 1,276 pelicans at three release sites between 1968 and 1980. In 1995 the Louisiana Department of Wildlife and Fisheries (1996) conservatively estimated that there were 10,000 eastern brown pelican nests and that an estimated 16,000 young were fledged.

The piping plover is endangered throughout its northern U.S. breeding range and threatened along its gulf coast wintering range. Piping plovers are an uncommon to rare winter resident, seen most often on the Louisiana barrier islands. The Chandeleur Islands supported from 3 to 17 birds per kilometer in an early 1991 survey, and the Isles Dernieres and Timbalier Islands supported 9 to 12 birds per kilometer, whereas mainland beaches supported only 2 to 4 birds per kilometer (R. Martin, Louisiana Department of Wildlife and Fisheries, Baton Rouge, personal communication). Wintering habitats have been lost to natural changes in barrier systems due to sea-level rise and lack of a renewable riverine supply of sand to replenish eroding islands. Coastal projects to stabilize

Table 13. Federally listed threatened and endangered vertebrates in Louisiana. T = threatened, E = endangered (Louisiana Department of Wildlife and Fisheries 1995; U.S. Fish and Wildlife Service 1997).

Species	Status
Mammals	
Blue whale	E
Fin whale	E
Humpback whale	E
Right whale	E
Sei whale	E
Sperm whale	E
Florida panther	E
Louisiana black bear	T
Red wolf	E
West Indian manatee	E
Birds	
Brown pelican	E
Peregrine falcon	E[a]
Bald eagle	T
Eskimo curlew	E
Least tern	E
Piping plover	T
Ivory-billed woodpecker	E
Red-cockaded woodpecker	E
Bachman's warbler	E
Attwater's greater prairie chicken	E
Whooping crane	E
Reptiles	
American alligator	T[b]
Gopher tortoise	T
Ringed sawback turtle	T
Green turtle	T
Kemp's ridley	E
Leatherback	E
Loggerhead	T
Hawksbill	E
Fishes	
Gulf sturgeon	T
Pallid sturgeon	E

[a]Endangered due to similarity of appearance.
[b]Threatened due to similarity of appearance.

Courtesy USGS, National Wetlands Research Center

Fig. 47. Eastern brown pelicans. The eastern brown pelican, whose nesting was completely eliminated from Louisiana in the 1960's, was reintroduced and now has several colonies with a total of more than 10,000 nests (Louisiana Department of Wildlife and Fisheries 1996).

inlets, beaches, and shorelines; to reduce overwash; and to allow human development have probably contributed to shifts in wintering ground use and a general reduction in habitat availability.

The least tern nests on barrier beaches and is extremely vulnerable to human disturbance and to severe storms (Visser and Peterson 1994; see box on Western Snowy Plovers and California Least Terns in California chapter). Their populations vary widely from year to year, but they are a fairly common sight on the coast. Two least tern populations occur in Louisiana, and only the northern interior population is actually endangered. Most of the least terns on the coast are part of the southern population.

Populations of both the bald eagle and the peregrine falcon had declined precipitously until recent efforts to restore them. Both are birds of coastal marshes and swamps. The eagle builds nests in large trees in forested wetlands and forages in adjacent marshes. About 100 nests are known in Louisiana (Hess 1996). The peregrine falcon is a winter (nonbreeding) resident, although one nest was reported in 1942 (Lowery 1974a). Populations of both species were probably severely harmed by chlorinated hydrocarbons in the same way as the eastern brown pelican (Lowery 1974a). The arctic peregrine falcon was officially removed from the federal list of endangered species in 1994 and is no longer considered threatened. However, it remains classified as "endangered due to similarity of appearance" to the nearly identical American peregrine falcon, to protect that subspecies (U.S. Fish and Wildlife Service 1997).

The red-cockaded woodpecker and Bachman's warbler inhabit the interior of upland forests and are only peripherally associated with coastal Louisiana. Bachman's warbler was thought to be locally extinct until a recent (1988) sighting in bottomland forests upriver from the coast (R. Hamilton, Louisiana State University, personal communication). The red-cockaded woodpecker was formerly found throughout the state in mature pine forests, but fewer than 400 active colonies remain in Louisiana, most of them in the center of the state. The ivory-billed woodpecker has not been seen in Louisiana for many years, but the Cuban subspecies has recently been identified in the Caribbean.

Attwater's greater prairie chicken and the whooping crane formerly inhabited the Chenier Plain, but current populations are restricted to coastal Texas and no Louisiana sightings have occurred since the 1940's (Lowery 1974a). The eskimo curlew was last recorded in Louisiana in the late 1800's, but there were several sightings near Galveston, Texas, in the 1960's (Lowery 1974a).

Reptiles

The Kemp's ridley, a marine turtle, is federally listed as endangered. It nests primarily near Rancho Nuevo on the northeast coast of Mexico and may have the most restricted distribution of any sea turtle. Juveniles and subadults occur along the Eastern Seaboard of the United States as well as in the Gulf of Mexico, but adults are usually confined to the gulf. Along the Louisiana coast, there are occasional sightings and incidental catches of sea turtles in shrimp trawls, even within the estuaries, and sightings of Kemp's ridley are more frequent along the western coast of Louisiana. With the exception of loggerheads, which have been observed to nest on the Chandeleur Islands (Lester 1988); no other sea turtle species is currently known to nest in Louisiana.

Human-induced mortality appears to be the primary reason for the decline in numbers of Kemp's ridley. From the 1940's through the 1960's, before the nesting area was protected, large numbers of turtle eggs were removed and packed out of the area in mule trains and trucks and by horseback from the Rancho Nuevo nesting beach. The most important factor now affecting the reproductive ability of this species is the growth of the shrimp-trawling industry. The increased entrainment of turtles in trawls associated with the intense growth of the shrimp fishery from the 1940's to the present is the major cause for the population decline of the Kemp's ridley (U.S. Fish and Wildlife Service 1992). During 1994, 457 Kemp's ridleys were found stranded and dead on U.S. shores, and of these, 26% were found on the Louisiana coast (Steiner 1994). The good news is that the

number of turtles nesting at Rancho Nuevo is increasing (Eckert and Eckert 1996), perhaps because of the mandatory use of turtle excluder devices on shrimp trawls.

The ringed sawback turtle, a small animal, is endemic to the Pearl River and its tributary, the Bogue Chitto. It is found in sandy or gravelly riverine beach and bar environments with a moderate current and numerous basking logs. The coastal portion of the Pearl River enters the Gulf of Mexico along the Louisiana–Mississippi boundary, but the turtle is seldom encountered that far south. Surveys using mark–recapture techniques (Jones 1991) indicated that the population ranged between 85 and 341 turtles per kilometer. The population decline of this species is attributed to habitat alteration caused by channel modification for flood control, navigation, and impoundment and to water quality degradation from siltation and pollution (U.S. Fish and Wildlife Service 1992). The species is federally listed as threatened (U.S. Fish and Wildlife Service 1997). The gopher tortoise occurs in sandy, well-drained soils of upland longleaf pine and mixed pine-hardwood forests in the Coastal Plain from South Carolina through Florida to southeastern Louisiana (Louisiana Department of Wildlife and Fisheries 1995).

American alligators are the largest nonmarine reptiles in North America with the exception of the American crocodile. They prefer freshwater marshes, swamps, and associated water bodies and occur across the South from Florida to Texas and as far north as North Carolina. Alligators are prized for their skins, and hunting pressure had reduced the population so dramatically by 1960 that the state of Louisiana declared a moratorium on hunting. In 1967 alligators were declared federally protected over nearly all of their range. With a moratorium on hunting, the Louisiana population rebounded so rapidly that alligators are a frequent sight in the coastal wetlands and are now legally hunted under strict state regulations. For law enforcement purposes, however, the alligators in Louisiana are now classified as "threatened due to similarity of appearance" to American crocodiles. Biologically, alligators are now considered neither endangered nor threatened (U.S. Fish and Wildlife Service 1997).

Fishes

The gulf subspecies of sturgeon is the only anadromous species to spawn in Louisiana. Its range is predominantly east of the state, but it is known to move up the Pearl River to spawn. Both immature and mature individuals participate in freshwater migration. Young fish less than two years of age apparently do not migrate out of rivers and estuaries. Seagrass beds with mud and sand substrates, such as those found behind the Chandeleur Islands, are important marine habitats for the species (Mason and Clugston 1993). The gulf subspecies is federally listed as threatened (U.S. Fish and Wildlife Service 1997). Primary reasons for its decline are habitat destruction and degradation—exacerbated by the potential for overexploitation—including dam construction, dredging, and navigation maintenance, all of which lower river elevations and eliminate deep holes and river substrate; and a decrease in groundwater flow that is thought to offer warmwater refugia. Agricultural, industrial, and urban contaminants may also be a factor in the gulf sturgeon's population decline.

Information Gaps

The Louisiana coastal zone is an immense area of wetlands. For the past two decades, scientists have sounded the alarm about the serious rate of degradation of this resource. In recent years their concern has galvanized citizens of the state and federal agencies in Washington to rise to the challenge of coastal restoration. What is our knowledge of the resource, and how is that related to our ability to retard and possibly reverse the loss of wetlands? Our understanding of geomorphic processes is strong, and spatially based data on rates of wetland change are probably better known for coastal Louisiana than for almost any other area of comparable size. Much of the research in the coastal zone has been process-oriented, as scientists have struggled to understand how wetland loss occurs and how it can be stopped. We know that the biological resources—the fisheries and waterfowl, for example—depend on healthy wetland habitat, and conservation of the habitat has been the major research focus. In the 1970's and 1980's, several reviews of ecosystem function were prepared with federal agency funding (for example, Gosselink et al. 1979a,b,c; Costanza et al. 1983; Gosselink 1984; Conner and Day 1987). More recent studies have generally focused on problems related directly to wetland loss (for example, Turner and Cahoon 1987a,b,c; Cahoon and Groat 1990a,b,c,d; Boesch et al. 1994; Reed 1995).

Although these are excellent summaries of available data, they also reveal serious gaps:

- In the immense area of the Louisiana coast, available field studies are thinly distributed. The coast is notoriously heterogeneous, and this variability has hardly been probed. With the advent of computer capacity to interpret high- and low-resolution aerial photography and satellite-based spatial data, this problem is beginning to be addressed,

although many processes cannot be deciphered with information gained from these techniques.

- The data base documenting the diversity of species in different coastal environments is quite weak, and biodiversity is receiving little attention.
- Water-regime information is vital to understanding coastal ecosystems. However, although a good deal of information has been published about the variation in time and space of gauge data—water levels, flooding duration, and so on—the velocity and pattern of flows are extremely expensive to measure and yet are vital to our management of the estuaries. The development of fine-structured spatial models of hydrology would seem to be the next generation of necessary research in this area.
- Subsidence is a dominant, though geographically variable, feature of these vast coastal marshes, yet accurate benchmarks for elevation and subsidence rates are few.
- Our understanding of biological variability of wetland vegetation and its response to physical and biotic forces is still in its infancy.
- The interaction of vertebrates and invertebrates with these dynamic coastal systems is understood only at the gross level, and detailed relationships required to fully restore these vast marshes are not well understood.
- Landscape-level synthesis of information, including interactive models that can simulate the consequences of proposed projects, is desperately needed. Management is occurring in small projects all over the coast. Both the state and federal governments, through the Coastal Wetlands Planning, Protection, and Restoration Act, are committed to massive coastal restoration. Proposed projects range from small beach and barrier plantings to retard erosion to massive freshwater river diversions to initiate new delta lobe cycles. The cumulative effect of these projects has not been addressed and probably cannot be addressed with our present knowledge limitations. Fortunately, Coastal Wetlands Planning, Protection, and Restoration Act projects are required to include monitoring to ensure their efficacy. Monitoring is overseen by five federal agencies and the Louisiana Department of Natural Resources and is carried out by the Department of Natural Resources and the Biological Resources Division of the U.S. Geological Survey of the U.S. Department of the Interior. The Department of Natural Resources and the U.S. Geological Survey's National Wetlands Research Center, along with Louisiana State University personnel, have begun to develop a coastwide monitoring program to ensure that cumulative restoration can be evaluated. This monitoring program will include periodic mapping of habitats from satellite imagery and ground-based measurements of all important physical and biological processes; it has the potential to be not only a comprehensive source of long-term information but also a model for monitoring programs elsewhere (Steyer and Stewart 1993).

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Acknowledgments

We thank D. Cahoon, D. Frugé, and three anonymous reviewers for helpful reviews of an early draft, and T. Michot for his work on the waterfowl, birds, and endangered species sections, and the overall organization. R. Pace provided comments and additional information on the red wolf and black bear. D. Shaver-Miller provided information on Kemp's ridley, and T. Spengler provided material on Neotropical migrant birds. E. Evers, L. Handley, C. Sasser, and J. Visser provided information and assistance on text and graphics. J. Buys was invaluable in providing information support and assistance. G. Farris made everything happen behind the scenes. Without her this manuscript would never have been written.

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