Status Review of the Marbled Murrelet *(Brachyramphus marmoratus)* in Alaska and British Columbia

Open File Report 2006–1387

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

Report Documentation Page	*Form Approved* *OMB No. 0704-0188*

1. REPORT DATE **2006**	2. REPORT TYPE **N/A**	3. DATES COVERED **-**

4. TITLE AND SUBTITLE **Status Review of the Marbled Murrelet (Brachyramphusmarmoratus) in Alaska and British Columbia**	5a. CONTRACT NUMBER 5b. GRANT NUMBER 5c. PROGRAM ELEMENT NUMBER
6. AUTHOR(S)	5d. PROJECT NUMBER 5e. TASK NUMBER 5f. WORK UNIT NUMBER
7. PERFORMING ORGANIZATION NAME(S) AND ADDRESS(ES) **U.S. Department of the Interior 1849 C Street, NW Washington, DC 20240**	8. PERFORMING ORGANIZATION REPORT NUMBER
9. SPONSORING/MONITORING AGENCY NAME(S) AND ADDRESS(ES)	10. SPONSOR/MONITOR’S ACRONYM(S) 11. SPONSOR/MONITOR’S REPORT NUMBER(S)

12. DISTRIBUTION/AVAILABILITY STATEMENT

Approved for public release, distribution unlimited

13. SUPPLEMENTARY NOTES

The original document contains color images.

14. ABSTRACT

15. SUBJECT TERMS

16. SECURITY CLASSIFICATION OF:			17. LIMITATION OF ABSTRACT	18. NUMBER OF PAGES	19a. NAME OF RESPONSIBLE PERSON
a. REPORT **unclassified**	b. ABSTRACT **unclassified**	c. THIS PAGE **unclassified**	**SAR**	**276**	

Standard Form 298 (Rev. 8-98)
Prescribed by ANSI Std Z39-18

COVER PHOTOGRAPH

A stylized form of a Marbled Murrelet (*Brachyramphus marmoratus*) adorns the top of a Tlingit Murrelet Hat, with feathering of human hair, and wings and tail cocked as if ready to dive. Two more murrelet images are carved onto the hat surface, each on opposite sides of a human face, and all upside down. Clan hats such as this one represent the history and strengths of the Kaagwaantaan Clan of southeast Alaska, the most powerful of the Tlingit Wolf moiety. This particular hat was acquired by Louis Shotridge from Daqu-tonk, the leader of the Kaagwaantaan Clan's Drum House at the Alaskan village of Klukwan in the spring of 1917. The hat is much older.

The Marbled Murrelet represents an important figure in Tlingit clan history and mythology. As a result, the Murrelet is represented on Tlingit clan regalia or clan *at.oow* (such as clan hats), and in Tlingit artwork. Some accounts that share the significance of the bird (who is often a being that combines animal and human forms) for the Tlingit people are available in English. "*The First War in the World*", by J.R. Swanton in his Tlingit Myth and Texts (1909), is but one example.

Even a cursory glance at just a few Tlingit resources indicates that today, as in the past, the Murrelet is a significant crest for several clans of the Eagle Moiety. The Naasteidí Clan of Kooyu Kwáan or Kuiu Island, holds the Murrelet and the Flicker as their crests, and has a house named the Ch'eet Hit (Murrelet House); the Nees.ádi Clan of Kake holds the Flicker, Killerwhale, and the Murrelet as their primary crests; the Wooshkeetaan Clan (in several Tlingit communities) holds the Shark, Wolf, Murrelet, Mud Shark, and Dog Fish as their important crests; the Yanyeidi Clan holds the Wolf, the Murrelet, Halibut, Hawk, Bear, Shark, and Marten as their important crests, and may have a Murrelet hat today. In addition, the Kagwaantaan (Wolf) Clan of Sitka has a house named Ch'eet Hit (Murrelet House).

According to the Federal Register, another Murrelet Hat was repatriated in 1996 by the Eiteljorg Museum of Indianapolis. The hat was returned to the Brown Bear House of the Kaagwaantaan Clan.

Information contributed by Lucy Fowler Williams, The Jeremy A. Sabloff Keeper, American Collections, University of Pennsylvania Museum.

Status Review of the Marbled Murrelet (*Brachyramphus marmoratus*) in Alaska and British Columbia

By J.F. Piatt, U.S. Geological Survey, K.J. Kuletz, U.S. Fish and Wildlife Service, A.E. Burger, University of Victoria, S.A. Hatch, U.S. Geological Survey, V.L. Friesen, Queen's University, T.P. Birt, Queens University, M.L. Arimitsu, U.S. Geological Survey, G.S. Drew, U.S. Geological Survey, A.M.A. Harding, Alaska Pacific University, and K.S. Bixler, U.S. Geological Survey

Open-File Report 2006–1387

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

U.S. Department of the Interior
DIRK KEMPTHORNE, Secretary

U.S. Geological Survey
Mark D. Myers, Director

U.S. Geological Survey, Reston, Virginia: 2007

For product and ordering information:
World Wide Web: http://www.usgs.gov/pubprod
Telephone: 1-888-ASK-USGS

For more information on the USGS--the Federal source for science about the Earth, its natural and living resources, natural hazards, and the environment:
World Wide Web: http://www.usgs.gov
Telephone: 1-888-ASK-USGS

Suggested citation:
Piatt, J.F., Kuletz, K.J., Burger, A.E., Hatch, S.A., Friesen, V.L., Birt, T.P. , Arimitsu, M.L., Drew, G.S., Harding, A.M.A., and K.S. Bixler, 2007, Status review of the Marbled Murrelet (***Brachyramphus marmoratus***) in Alaska and British Columbia: U.S. Geological Survey Open-File Report 2006-1387, 258 p.

Contents

Contents—Continued

Contents—Continued

Contents—Continued

Figures

Figures–Continued

Figures–Continued

Tables

Tables—Continued

Tables—Continued

Conversion Factors and Abbreviations, Acronyms, or Symbols

Conversion Factors

SI to Inch/Pound

Multiply	By	To obtain
centimeter (cm)	0.3937	inch (in.)
cubic meter (m^3)	0.0008107	acre-foot (acre-ft)
gram (g)	0.03527	ounce, avoirdupois (oz)
hectare (ha)	0.003861	square mile (mi2)
kilometer (km)	0.6214	mile (mi)
meter (m)	3.281	foot (ft)
metric ton (Mt)	1.102	ton, short (2,000 lb)
millimeter (mm)	0.03937	inch (in.)
square kilometer (km^2)	247.1	acre

Inch/Pound to SI

Multiply	By	To obtain
acre	4047	square meter (m^2)
barrel (bbl), (petroleum, 1 barrel = 42 gal)	0.1590	cubic meter (m^3)
cubic foot (ft^3)	0.02832	cubic meter (m^3)
foot (ft)	0.3048	meter (m)
gallon (gal)	3.785	liter (L)
gallon (gal)	0.003785	cubic meter (m^3)
gallon (gal)	3.785	cubic decimeter (dm^3)
mile (mi)	1.609	kilometer (km)
mile, nautical (nmi)	1.852	kilometer (km)
pound, avoirdupois (lb)	0.4536	kilogram (kg)
square mile (mi^2)	259.0	hectare (ha)
square mile (mi^2)	2.590	square kilometer (km^2)
ton, short (2,000 lb)	0.9072	megagram (Mg)

Temperature in degrees Celsius (°C) may be converted to degrees Fahrenheit (°F) as follows:

$$°F=(1.8×°C)+32.$$

Conversion Factors and Abbreviations, Acronyms, or Symbols—Continued

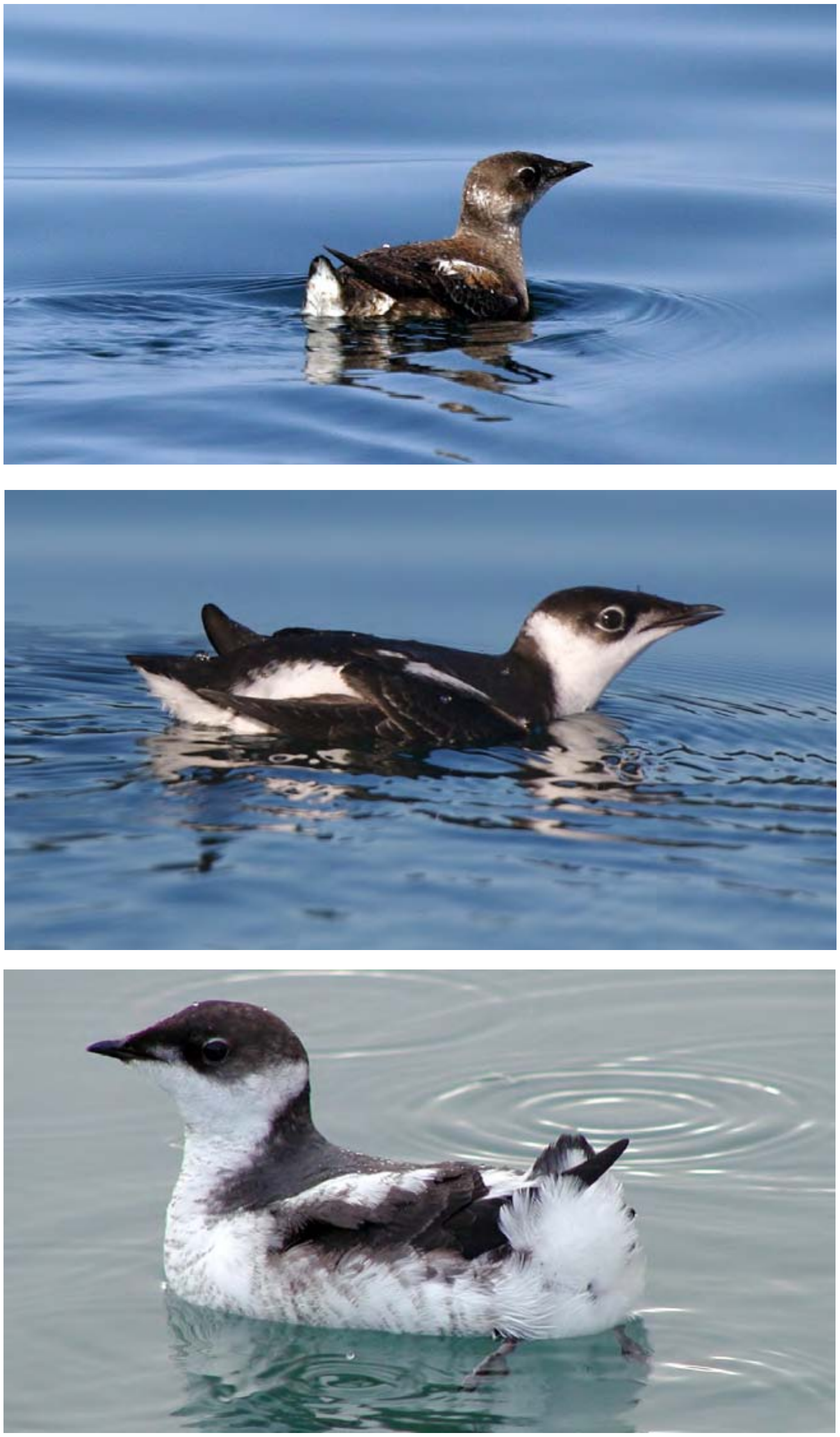
Abbreviation, Acronym, or Symbol

Abbreviation, Acronym, or Symbol	Meaning
ADEC	Alaska Department of Environmental Conservation
ADFG	Alaska Department of Fish and Game
ADNR	Alaska Department of Natural Resources
AHY	After-hatching-year (adult birds)
ANCSA	Alaska Native Claims Settlement Act
ANILCA	Alaska National Interest Lands Conservation Act
AOU	American Ornithologists' Union
BLM	Bureau of Land Management (U.S.)
bp	Base pair
CBC	Christmas Bird Count
CLMP	Chugach Land Management Plan
CMMRT	Canadian Marbled Murrelet Recovery Team
COSEWIC	Committee on the Status of Endangered Wildlife in Canada
CWS	Canadian Wildlife Service
DBH	(Tree) diameter at breast height
DFO	Department of Fisheries and Oceans (Canada)
DPS	Distinct Population Segment (U.S.)
EC	Environment Canada
ENSO	El Niño-Southern Oscillation
ESA	Endangered Species Act (U.S.)
EVOS	*Exxon Valdez* oil spill
EVOSTC	EVOS Trustee Council
FAO	Food and Agriculture Organizaiton (UN)
FIA	Forest Inventory and Analysis
FPB	Forest Practices Board (British Columbia)
FR	Federal Register (U.S.)
FRPA	Forest and Range Practices Act (British Columbia)
GBNPP	Glacier Bay National Park and Preserve
HSI	Habitat suitability index
HY	Hatching-year (juvenile birds)
IUCN	World Conservation Union
IWMS	Identified Wildlife Management Strategy (British Columbia)

Conversion Factors and Abbreviations, Acronyms, or Symbols—Continued

Abbreviation, Acronym, or Symbol—Continued

Abbreviation, Acronym, or Symbol	Meaning
KFNPP	Kenai Fjords National Park and Preserve
LRMP	Land and Resources Management Plan (Canada)
LUP	Land Use Plans (Canada)
MMBF	Million board feet
MMS	Minerals Management Service (U.S.)
mtDNA	Mitochondrial DNA
NFMA	National Forest Management Act (U.S.)
NGO	Non-governmental organization
NFMA	National Forest Management Act (U.S.)
NGO	Non-governmental organization
NMFS	National Marine Fisheries Service (NOAA)
NOAA	National Oceanographic and Atmospheric Administration (U.S.)
NPPSD	North Pacific Pelagic Seabird Database
OCSEAP	Outer Continental Shelf Environmental Assessment Program
OGMA	Old Growth Management Area (British Columbia)
PCR	Polymerase chain reaction
RIC	Resource Inventory Committee (Canada)
SARA	Species at Risk Act (Canada)
SSPC	Single-stranded conformation polymorphism
TFL	Tree Farm License
TLMP	Tongass Land Management Plan
TTRA	Tongass Timber Reform Act
USCG	U.S. Coast Guard
USDOT	U.S. Department of Transportation
USFS	U.S. Forest Service
USFWS	U.S. Fish and Wildlife Service
USGS	U.S. Geological Survey
USNPS	U.S. National Park Service
WHA	Wildlife habitat area (British Columbia)



Marbled Murrelet in summer breeding (alternate) plumage (top, © Gerry Sanger/Sound Expressions), winter (basic) plumage (middle, Martin Renner), and juvenile plumage (bottom, Rich MacIntosh).

Status Review of the Marbled Murrelet (*Brachyramphus marmoratus*) in Alaska and British Columbia

By J.F. Piatt[1] , K.J. Kuletz[2] , A.E. Burger[3], S.A. Hatch[1], V.L. Friesen[4], T.P. Birt[4], M.L. Arimitsu[1], G.S. Drew[1], A.M.A. Harding[5], and K.S. Bixler[1]

Abstract

The Marbled Murrelet (*Brachyramphus marmoratus*) is a small, diving seabird inhabiting inshore waters of the Northeastern Pacific Ocean. This species feeds on small, schooling fishes and zooplankton, and nests primarily on the moss-covered branches of large, old-growth conifers, and also, in some parts of its range, on the ground. We reviewed existing information on this species to evaluate its current status in the northern part of its range—Alaska (U.S.) and British Columbia (Canada). Within the southern part of its range (Washington, Oregon, and California, U.S.), the Marbled Murrelet was listed as a threatened species under the Endangered Species Act (ESA) in 1993, and the U.S. Fish and Wildlife Service (USFWS) needed information on the species throughout its range for ESA deliberations. We compiled published information on the conservation status, population biology, foraging ecology, population genetics, population status and trends, demography, marine and nesting habitat characteristics, threats, and ongoing conservation efforts for Marbled Murrelets in Alaska and British Columbia. We conducted a new genetic study using samples from a segment of the range that had not been included in previous studies (Washington, Oregon) and additional nuclear intron and microsatellite markers. We also analyzed available at-sea survey data from several locations for trend. To understand the reasonableness of the empirical trend data, we developed demographic models incorporating stochasticity to discern what population trends were possible by chance. The genetic studies substantially confirmed previous findings on population structure in the Marbled Murrelet. Our present work finds three populations: (1) one comprising birds in the central and western Aleutian Islands; (2) one comprising birds in central California; and (3) one comprising birds within the center of the range from the eastern Aleutians to northern California. Our knowledge of genetic structure within this central population is limited and it requires additional study. Compiling available abundance information, we estimated that in the recent past, Marbled Murrelets in Alaska numbered on the order of 1 million birds. We were unable to generate a similar estimate for historical population size in British Columbia. Using trend information from at-sea surveys spanning a wide geographic range in Alaska, murrelet numbers declined significantly at five of eight trend sites at annual rates of -5.4 to -12.7 percent since the early 1990s. Applying these rates of decline to the historical population estimate, the current murrelet population in Alaska is projected to be on the order of 270,000 birds. This represents an overall population decline of about 70 percent during the past 25 years. In British Columbia, available trend data indicate that murrelet populations there have experienced similar declines. We updated a recent (2002) population estimate for British Columbia, concluding that there are now between 54,000 and 92,000 murrelets in British Columbia. The rates of decline we observed are within, but at the high end of, a range of rates expected by chance. Given that declines were estimated for sites over essentially the entire northern range of the species, there is cause for concern about the species' status. In their marine habitats, Marbled Murrelets overlap with salmon (*Oncorhynchus* sp.) gillnetting operations in British Columbia and in Alaska (especially in Prince William Sound and Southeast Alaska), and annual bycatch mortality is likely in the low thousands per year, although bycatch rates are difficult to measure. The species' inshore distribution coincides with high levels of vessel traffic and makes them especially vulnerable to both chronic oil pollution and to catastrophic spills (e.g., the 1989 *Exxon Valdez* oil spill [EVOS] in south-central Alaska, which is estimated to have killed 12,000 to 15,000 murrelets). In their forested nesting habitats, Marbled Murrelets have lost about 15 percent of their suitable nesting habitat in Southeast Alaska, and 33 to 49 percent in British Columbia, from industrial-scale logging within the past half century. Increased predation also may be a threat to murrelet populations, related to fragmentation and edge effects from logging and development, and recent population increases

---

[1] U.S. Geological Survey.

[2] U.S. Fish and Wildlife Service.

[3] Department of Biology, University of Victoria, Victoria, British Columbia, Canada.

[4] Queen's University. Kingston, Ontario, Canada.

[5] Alaska Pacific University, Anchorage, AK.

observed for some important murrelet predators, including Bald Eagles (*Haliaeetus leucocephalus*), Common Ravens (*Corvus corax*), and Steller's Jays (*Cyanocitta stelleri*). Nesting habitat losses cannot explain the declines observed in areas where industrial logging has not occurred on a large scale (e.g., Prince William Sound) or at all (Glacier Bay). The apparent change in population size and rates of decline reported for the Marbled Murrelet are large, and we therefore considered alternative explanations and precedents for changes of similar magnitude in other marine wildlife populations in the Northeastern Pacific Ocean. The declines are likely real, and related to combined and cumulative effects from climate-related changes in the marine ecosystem (most likely the 1977 regime shift) and human activities (logging, gillnet bycatch, oil pollution). Much uncertainty about the decline could be alleviated by continuing to repeat boat surveys in Prince William Sound and lower Cook Inlet, and by repeating the boat survey of Southeast Alaska that was conducted in 1994. This survey used a statistically sound design and covered the region that has been and likely remains the center of the species' abundance. Important questions remain to be addressed about methods for measuring population status and change, adult mortality (major sources, density dependence, seasonal concordance), and the movements of wintering populations.

Introduction

The Marbled Murrelet is a member of the Auk family of diving seabirds. Like other members of this family, it feeds on schooling fishes in coastal waters, defers breeding until several years of age, and has a long life span. A successful breeding pair fledges only one chick per year. This species breeds from central California to the Aleutian Islands of Alaska, and is found in greatest abundance between Vancouver Island, British Columbia, and the Alexander Archipelago in Southeast Alaska. In contrast to other members of its family such as puffins (*Fratercula* sp.), the Marbled Murrelet does not breed on cliffs or in burrows on predator-free offshore islands. Rather, camouflaged adults nest on mossy-limbed branches of large conifers such as coast redwood (*Sequoia sempervirens*), western hemlock (*Tsuga heterophylla*), Douglas fir (*Pseudotsuga menziesii*), and Sitka spruce (*Picea sitchensis*), usually in mainland old-growth stands located within 60 km of marine waters. Some murrelets nest on the ground at higher altitudes, on mossy cliff ledges in British Columbia, and on treeless islands of Alaska, laying eggs on bare talus slopes in mountainous terrain.

Marbled Murrelet populations are believed to be threatened by logging of old-growth nesting habitat, oil pollution, and bycatch in fishing gear (Nelson, 1997), and also are influenced by natural changes in marine ecosystems (Becker and Beissinger, 2005). Current populations in Washington, Oregon, and California are small (tens of thousands) relative to the combined historical population of British Columbia and Alaska (hundreds of thousands). Owing to small population size, threats, and negative population trends, the U.S. Fish and Wildlife Service (USFWS) listed the Washington, Oregon, and California population of Marbled Murrelet as threatened under the ESA in 1993. In British Columbia, the murrelet was listed as threatened by the Canadian Federal government in 1990 because of loss of breeding habitat and declining populations, and that status was renewed in 2000. The status of populations in Alaska and British Columbia has been less clear and is the subject of this review. The USFWS did not list the Alaska murrelet population when it listed the Washington, Oregon, and California murrelet population because, in relation, Alaska had a large murrelet population and there was no information on murrelet population trends.

In 2003, the USFWS initiated a 5-year review of the status of the murrelet population in Washington, Oregon, and California. This work was conducted by EDAW, Inc., with the assistance of Hamer Environmental, L.P., and consisted of a review of available scientific information plus a regulatory review (McShane and others, 2004). Based on the EDAW, Inc., report, the USFWS concluded that the population of Marbled Murrelets in Washington, Oregon, and California did not satisfy the criteria for designation as a Distinct Population Segment (DPS) under the USFWS's 1996 DPS policy. The original listing determination for the Marbled Murrelet was made prior to the USFWS's 1996 DPS policy. That policy states that DPS designations made prior to the 1996 policy would be reviewed as a part of any 5-year review. In September 2004, the USFWS announced its intention to pursue delisting the murrelet in Washington, Oregon, and California.

Based on its analysis that the Washington, Oregon, and California murrelet population did not qualify as a DPS, the USFWS decided to conduct a status review of the species throughout its range. The questions of whether the population in Washington, Oregon, and California constitutes a significant portion of the species' population throughout its entire range, or whether the species as a whole is at risk of extinction, must be addressed before any action is made to change the status of the murrelet as a Threatened Species under the ESA. Delisting or reclassifying the Marbled Murrelet under the ESA will require a separate rulemaking, involving public notice and comment. In September 2006, the USFWS removed 94 percent of previously designated Critical Habitat in Washington, Oregon, and California from that protective status provided under the ESA (U.S. Fish and Wildlife Service, 2006).

Objectives and Focus of This Status Review

In March 2006, we were asked by the USFWS to review the status of the Marbled Murrelet in Alaska and British Columbia using existing information available from published papers, finalized agency reports, and pertinent archived datasets. We were asked to address the following specific topics:

1. Conservation status of the species;
2. Population ecology and characteristics of the species;
3. Habitat characteristics and trends;
4. Range and distribution;
5. Population status and trends, including information on genetic diversity;
6. Threats to populations; and
7. Ongoing conservation efforts.

Under the category of population ecology, we were asked to include descriptions of populations that may qualify as DPSs under the ESA, and to address any geographic, genetic, or other barriers relative to the Discreteness Test within the ESA DPS Policy.

Background – Previous Studies of Marbled Murrelets in Alaska and British Columbia

Prior to this report, the most recent compilation of information on Marbled Murrelets in Alaska was the U.S. Forest Service (USFS) status assessment, “Ecology and Conservation of the Marbled Murrelet” (Ralph and others, 1995a). That volume included several chapters on Marbled Murrelets in Alaska, including chapters on population status (Piatt and Naslund, 1995), inland habitat use (Kuletz and others, 1995c), inland activity patterns (Naslund and O’Donnell, 1995), food habits (Burkett, 1995), and threats to populations (Carter and Kuletz, 1995; Carter and others, 1995; Fry, 1995). That volume also contained assessments of marine and inland habitat use by Marbled Murrelets in British Columbia (Burger, 1995a, 1995b). At that time, we knew far more about the ecology of murrelets in Alaska than British Columbia because a large effort to study murrelets was initiated in Prince William Sound after the 1989 *Exxon Valdez* oil spill (EVOS) (e.g., Kuletz, 1996; and dozens of reports and publications associated with this work; see Piatt, 2005). Little research continued in Alaska after direct support for Marbled Murrelet research by the EVOS Trustee Council (EVOSTC) ended in 1995, except for work on population genetics (Friesen and Piatt, 2003) and their marine ecology (Kuletz, 2005). Murrelets also were surveyed by the USFWS, the U.S. Geological Survey (USGS), and the U.S. National Park Service (USNPS) in various at-sea survey programs (e.g., Irons and others, 2000; Stephensen and Andres, 2001; Robards and others, 2003; Lindell, 2005). Recent investigations by the Alaska Department of Fish and Game (ADFG) have resulted in new insights on vessel disturbance (Agness, 2006) and foraging behavior (M. Kirchoff, Alaska Department of Fish and Game, unpub. data, 2006) in Southeast Alaska. Research was initiated in the Tongass National Forest during the early 1990s (e.g., Brown and others, 1999; Smith and Harke, 2001), but because the bird was not listed as Threatened in Alaska at the time of listing of populations in Washington, Oregon, and California (1993), and with apparently abundant populations in Alaska, no conservation strategy was developed for murrelets in the Tongass (DeGange, 1996). We found a few reports of U.S. Forest Service (USFS) work on murrelets (Piatt, 2005), but much data resides at the district level, largely unanalyzed.

In contrast to Alaska, little was known about the biology of Marbled Murrelets in British Columbia prior to the 1995 Conservation Assessment (Ralph and others, 1995a), but much has been learned since that time. Early research was summarized by Rodway (1990), Rodway and others (1992), and Burger (1995a, 1995b). The first Canadian Marbled Murrelet Recovery Strategy (Kaiser and others, 1994) was primarily an analysis of research needs and data gaps. Following the listing as Threatened by the Canadian Federal government, and as Red-Listed by the provincial government, research and monitoring activities increased greatly in British Columbia in the 1990s. This included notable contributions from the Centre for Wildlife Ecology at Simon Fraser University, the Canadian Wildlife Service (CWS), the University of Victoria, the British Columbia ministries of Environment and Forests, Parks Canada, and several non-governmental organizations (NGOs). The British Columbia forest industry initiated large inventory and monitoring programs in many of the coastal forests. Much of the research in British Columbia followed methods developed in Washington, Oregon, and California, or Alaska (e.g., audio-visual surveys, at-sea transects, forest vegetation analysis), but there also has been pioneering work on radio-telemetry, demographics, movements at-sea, using radar for landscape-level habitat analyses and population monitoring, interpretation of aerial photography, and low-level helicopter assessments of forest habitat. Following a review by Hull (1999b), the murrelet’s Threatened Status in Canada was confirmed in 2000, as noted above. This was followed by a Conservation Assessment in 2001–03 comprising a biological review (Burger, 2002), management guidelines published by the Canadian Marbled Murrelet Recovery Team (CMMRT; Bertram and others, 2003), and a risk model (Steventon and others, 2003). Information from British Columbia also was included in the McShane and others (2004) review. To meet the requirements of Canada’s 2002 Species at Risk Act (SARA), a new Canadian Marbled Murrelet Recovery Strategy has been completed and is under review, and Recovery Action Plans are being developed.

In summary, most of what is known about the terrestrial ecology and breeding biology of murrelets in Alaska and British Columbia is derived from work started in the early 1990s. Much of that work has been reported or published. We reviewed those findings in this document, and synthesized it with more recent knowledge from studies in Washington, Oregon, and California. We reconsidered historical diet information in light of extensive new data from the 1990s that has never been published. We conducted a new analysis of genetic information, including samples from birds in Washington and Oregon, and information from additional markers. Most data on murrelet population abundance and trends have not been compiled or published since 1995 in Alaska or since 1999 in British Columbia. We compiled, verified, and analyzed several relevant datasets, to develop new and current population estimates for Alaska and British Columbia, and we examined trends in those populations. We created the first explicit models of murrelet population dynamics in Alaska. We reviewed knowledge of the marine ecology of the species, and compiled information on threats in the marine environment. We also compiled information on forest habitat use and trends in forest habitat for the major forested areas occupied by murrelets. We reviewed ongoing conservation efforts. We conclude the report with discussion that focuses on two topics: (1) factors relevant to designation of DPSs for the Marbled Murrelet; and (2) factors that could explain the widespread population declines we observed.

We refer to many place names in Alaska and British Columbia throughout the document, as we cite the various studies on murrelets and their habitats. To aid the reader, we provide a general locator map in figure 1.

Conservation Status of Taxon

Rangewide

There are two primary NGOs that evaluate the global status of animal populations by using a number of scientific criteria: the World Conservation Union (IUCN) and NatureServe (Gardenfors and others, 1999). For the last four decades, the IUCN, through its Species Survival Commission, has been assessing the conservation status of species and subspecies on a global scale to highlight taxa threatened with extinction. The IUCN “Red Data Book” was produced to provide scientists with objective, scientifically based information on the current status of globally threatened biodiversity. The IUCN “Red List of Threatened Species” provides taxonomic, conservation status, and distribution information on taxa that have been evaluated globally using the IUCN “Red List Categories and Criteria” (World Conservation Union, 2001, 2004). The evaluations are designed to determine the relative risk of extinction. Those taxa facing a higher risk of global extinction are listed as Critically Endangered, Endangered, and Vulnerable.

The Marbled Murrelet was listed as Vulnerable in 2000 and the status changed to Endangered in 2004. The species was last assessed in 2005 and is still considered Endangered (World Conservation Union, 2004; BirdLife International, 2005). This species was still considered abundant, but was treated as Endangered because its population was estimated to have undergone a very rapid reduction, greater than 50 percent in the last three generations (36 years), owing to a variety of threats. The assessment states that the decline was likely to continue and therefore the population was considered to be facing a very high risk of extinction in the wild. Some of the major threats listed for the population included habitat loss from timber harvest, accidental mortality from fisheries bycatch, and water pollution (oil spills).

NatureServe is a non-profit conservation NGO that provides scientific information to help guide conservation actions. NatureServe and its network of natural heritage programs provide information concerning rare and endangered species, and threatened ecosystems. NatureServe uses alphanumeric codes to rank the vulnerability of species it evaluates. The global status of the Marbled Murrelet was listed as G3G4 in January 2001 (NatureServe, 2006). A G3G4 rank indicates that there was roughly an equal chance of G3 or G4 rank and that other ranks were much less likely. A G3 rank means the population was considered vulnerable and at a moderate risk of extinction due to a restricted range, relatively few populations, recent and widespread declines, or other factors. The G4 rank means the population was considered secure, uncommon but not rare, but there were some cause for long-term concern due to population declines or other factors. Threats listed for the population included habitat loss due to logging, oil spills, and gillnet fisheries (NatureServe, 2006).

Canada

National

In Canada, the Marbled Murrelet is protected under the Migratory Birds Convention Act, which affords protection to the bird itself and active nest sites, but nesting and foraging habitats are not otherwise protected by this act. The species was first listed as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in 1990, following a review by Rodway (1990). This status was confirmed by COSEWIC in 2000, following a review by Hull (1999b). The first Recovery Strategy was completed in 1994 (Kaiser and others, 1994) and focused primarily on identifying knowledge gaps for research. Loss of nesting habitat in forests was identified as the primary threat in Canada, and oil spills and gillnets were identified as significant secondary threats (Rodway, 1990; Hull, 1999; Bertram and others, 2003).

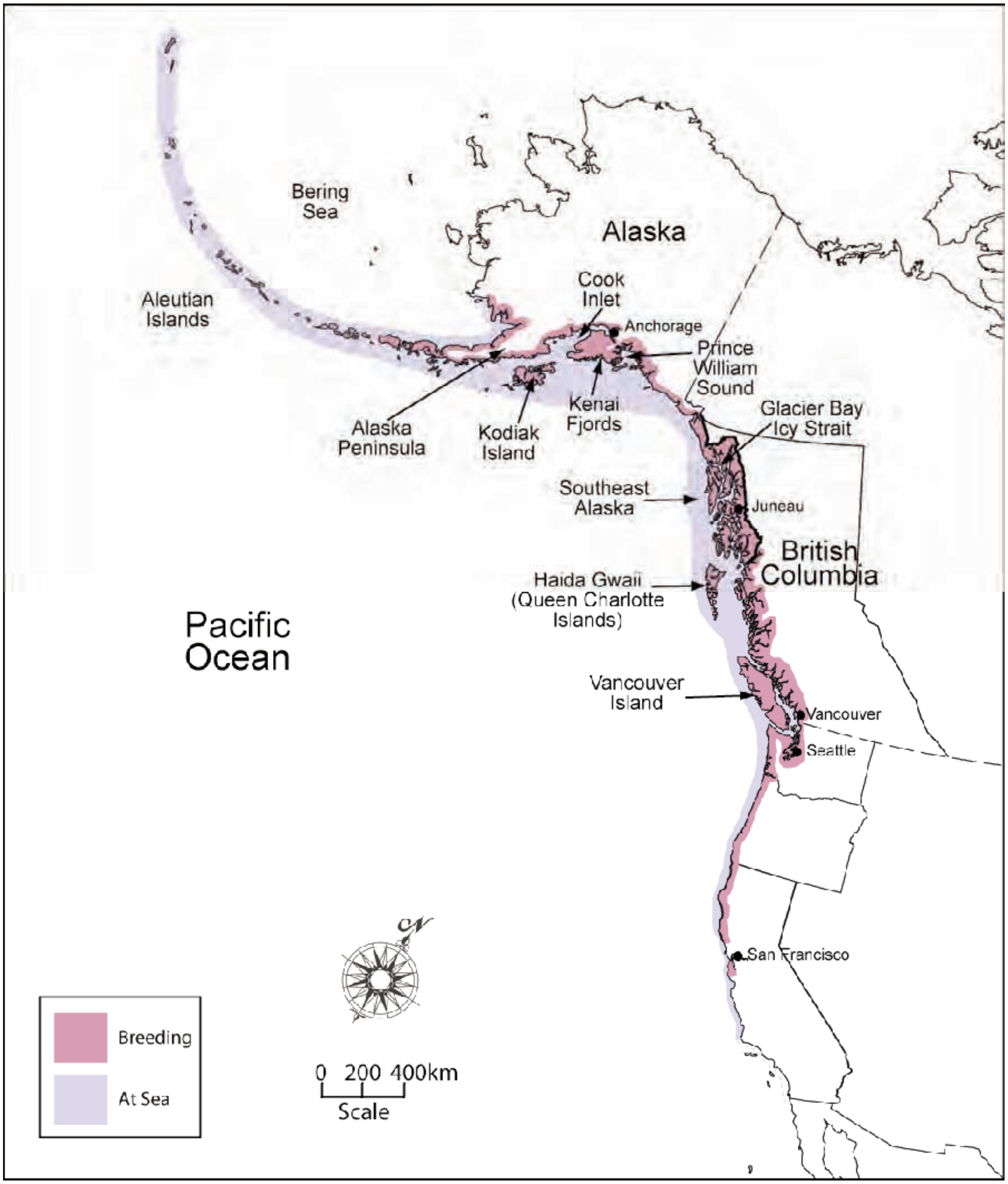


Figure 1. Distribution of Marbled Murrelets.

SARA came into effect in June 2003 and applies to all Federal lands in Canada, all wildlife species listed as being at-risk, and their critical habitat. The Marbled Murrelet was included on Schedule 1, the official list of wildlife species at-risk, because it was listed as Threatened by COSEWIC. Once listed, the measures to protect and recover a listed wildlife species are implemented. Under SARA, the Canadian Federal government has to approve a Marbled Murrelet Recovery Strategy by 2007, which will identify critical habitat and define the species' "residence," which are the two key elements afforded to habitat protection in this act.

The Recovery Strategy has been drafted, largely based on the guidelines published by the CMMRT (Bertram and others, 2003), but the Recovery Strategy is still under review by the Canadian and British Columbia governments. Under SARA, the Recovery Strategy has to identify one or more

Recovery Action plans that will provide the details and timing of recovery implementation. The CMMRT has decided to draft three Recovery Action plans: (1) Population Status and Trend Monitoring; (2) Nesting Habitat Retention; and (3) Marine and Mortality Issues. By November 2006, the Nesting Habitat Retention Action Plan had been drafted and was under review by the Canadian and British Columbia governments. The other two Recovery Action plans have yet to be drafted and are not anticipated to be completed within the next year. Details of the Recovery Strategy, associated Recovery Action plans, and their implementation schedules are not available.

In Canada, the Marbled Murrelet also is protected by the Canada National Parks Act (2000), where the species occurs in Gwaii Haanas, Pacific Rim, and Gulf Islands national park reserves.

Provincial

Marbled Murrelet is on the British Columbia Red List (i.e., a species legally designated or being considered for legal designation as Endangered or Threatened), and is one of the Identified Wildlife species within the British Columbia Forest and Range Practices Act (FRPA). The FRPA contains a number of provisions that contribute to managing Marbled Murrelet nesting habitat. FRPA Section 5 requires forest stewardship plans to be consistent with objectives set by the provincial government for a range of values including wildlife, biodiversity, soils, visual quality, water, and fish, all of which may contribute in part to managing Marbled Murrelet nesting habitat. FRPA Section 7 further defines the amount, distribution, and attributes of areas for the survival of species at-risk and regionally important wildlife. Notices under FRPA Section 7 are established for each forest district by the British Columbia Minister of Environment, and include objectives for Marbled Murrelet habitat. In practice, protection of Marbled Murrelet nesting habitat under FRPA is applied through the Identified Wildlife Management Strategy (IWMS). This establishes measures for selected species and plant communities that have been designated under the Forest Practices Code as Identified Wildlife.

Based on recommendations from the CMMRT (Bertram and others, 2003), IWMS measures for the maintenance of nesting habitat for Marbled Murrelets were adopted in 2004 (Identified Wildlife Management Strategy [British Columbia], 2004). The IWMS measures are the principal regulations governing maintenance of murrelet nesting habitat within forests designated as timber lands in British Columbia and provide fine-filter management of habitat. Identified Wildlife are managed through the establishment of wildlife habitat areas (WHAs), general wildlife measures, and wildlife habitat area objectives, or through other management practices, such as Old Growth Management Areas (OGMAs). Application of the IWMS is greatly hampered by the limit placed on its timber impacts by the Provincial Chief Forester: only 1 percent of mature forest, by area, of each forest district is allocated to the IWMS. As of November 2006, 124 Marbled Murrelet WHAs had been established, amounting to 18,400 ha[1], which amounts to about 2 percent of the habitat required to maintain 70 percent of the provincial population (Dechesne-Mansiere, 2004).

Much larger areas of habitat have been protected in parks under the 1996 British Columbia Parks Act, the 2000 Protected Areas of British Columbia Act, and the regional Land and Resources Management Plans (LRMPs). These include extensive tracts in Carmanah-Walbran Provincial and Strathcona parks, and recently protected areas proclaimed under the north and central coast LRMPs. Currently about 25-30 percent of estimated area of suitable nesting habitat in British Columbia falls within protected areas (T. Chatwin and M. Mather, British Columbia Ministry of Environment, unpub. data, 2006).

Other Designations in Canada

The species is ranked by NatureServe (2006) as N2 (Imperiled) within Canada, and as S2B (Imperiled – Breeding Population) and S4N (Apparently Secure – Non-Breeding Population) within British Columbia.

United States

National

In September 1992, the Washington, Oregon, and California population of Marbled Murrelets was listed as Threatened under the ESA of 1973, as amended (57 FR 45328). The listing decision was based on the determination that the Marbled Murrelet was Threatened from: (1) loss and modification of nesting habitat (older forests), primarily due to commercial timber harvesting; (2) mortality associated with gillnet fisheries off the Washington coast; and (3) mortality resulting from oil pollution. In 1996, the USFWS designated Critical Habitat in Washington, Oregon, and California. Critical Habitat included 32 Critical Habitat Units in Washington, Oregon, and California that were considered essential to the conservation of the species (U.S. Fish and Wildlife Service, 1996). Most of these Critical Habitat Units were located on Federal lands and almost entirely within Late-Successional Reserves. A recovery team was formed in 1993, with a recovery plan produced in 1997 (U.S. Fish and Wildlife Service, 1997). A primary objective of the Marbled Murrelet recovery plan was to stabilize the population at or near current levels by maintaining and/or increasing productivity, and removing and/or minimizing threats to survivorship (U.S. Fish and Wildlife Service, 1997).

---

[1] Available at http://www.env.gov.bc.ca/cgi-bin/apps/faw/wharesult.cgi?search=show_approved.

State-Level

On a State government-level, the species is considered Threatened in Washington and Oregon, and Endangered in California. At this time, the Marbled Murrelet in Alaska has no special status with the State of Alaska.

Within Alaska, there is an additional conservation status rating of Marbled Murrelets, which relates specifically to the species' recovery from the EVOS. As part of the Restoration Plan, the EVOSTC maintains a list of resources and services it considers to have been injured by the spill ("Injured Resources and Services List"), and they periodically update the list when new information becomes available to show which species or services they consider to be: (1) Recovered; (2) Not Recovering; (3) Recovering; or (4) Unknown. Based on the initial impact of the spill, which killed an estimated 7 to 12 percent of the murrelets in the spill area (Kuletz, 1996), the Marbled Murrelet was listed as an Injured Species. Recently, the recovery status of Marbled Murrelet was changed to Unknown (*Exxon Valdez* Oil Trustee Council, 2006) from the Recovering status on the 2002 List. The EVOSTC finds that breeding Marbled Murrelet populations in Prince William Sound (the main spill area) are in decline, but that the relation of the declines to the spill are unclear. They noted that there are no differences in population trends between populations in oiled and unoiled areas, and that other factors, such as climate and shifts in prey, are the most likely drivers of murrelet population dynamics (Integral Consulting, Inc., 2006).

Other Designations in the United States

The National Audubon Society developed a WatchList that identifies bird species that are facing population declines and/or threats such as habitat loss on their breeding and wintering grounds, or those species with limited geographic ranges (National Audubon Society Watchlist, 2002). The WatchList is an independent conservation status assessment of bird species that occur within the U.S. and some protectorates. Audubon has used two independent assessments published by BirdLife International (2005) and Partners In Flight (Panjabi and others, 2005) to place species in one of three conservation categories: Red, Yellow, or Green. The Marbled Murrelet was placed in the Red category, which represents species considered to be declining rapidly, having very small populations or limited ranges, and facing major conservation threats.

The National Audubon Society Watchlist (2002) states that Marbled Murrelets face three major threats. The greatest threat was considered to be logging of old-growth nesting habitat along the Pacific Coast. Because of its habit of feeding close to shore, this species also was considered to be highly vulnerable to oil spills. In addition, the WatchList states that large numbers of murrelets also are killed in Alaska on an annual basis as the result of gillnet fishing mortality.

Population Ecology and Characteristics of Murrelets in Alaska and British Columbia

In this section, we review the literature on the general biology and population ecology of Marbled Murrelets, focusing where possible on information derived from studies in Alaska and British Columbia. We provide a general description of the species, and review taxonomy, geographic distribution, migration and seasonal movements, and molt. We summarize feeding ecology, describing what is known about diets, spatial and temporal variability in diets, and foraging behavior and habitats. We turn then to a detailed description of breeding biology and natural mortality factors.

Taxonomy

Marbled Murrelets belong to the family Alcidae (Auks), within the order Charadriiformes (Strauch, 1985). Phylogenetic relations within the Alcidae have been described using both genetic and morphological evidence (Strauch, 1985; Moum and others, 1994; Pitocchelli and others, 1995; Friesen and others, 1996a). There are now three recognized species within the genus *Brachyramphus*: the Marbled, Long-Billed (*B. perdix*), and Kittlitz's (*B. brevirostris*) murrelets. The Marbled Murrelet breeds only in western North America, from California north to Alaska (wintering rarely to Baja, California and in only one recorded instance, wintering in northeastern Russia); the Long-Billed Murrelet breeds only in eastern Russia (wintering south to Japan, Korea, and China, with vagrants occurring widely in North America and rarely to Europe); and the Kittliz's Murrelet breeds only in Alaska and eastern Russia, rarely wintering south to California and Northern Japan (Sealy and others, 1982; Brazil, 1991; Nelson, 1997; Gaston and Jones, 1998; Day and others, 1999; Burger, 2002; Nelson and others, 2002).

There has been an interesting classification history of the Long-Billed and Marbled Murrelet. Although originally considered separate species in the 18th and 19th centuries, with the Long-Billed Murrelet known as the "Partridge Murrelet," the American Ornithologists' Union (American Ornithologists' Union, 1957) later declared them conspecifics. They remained as two subspecies until the mid-1990s, when molecular studies showed them to be distinctly different and probably genetically isolated for 5 to 6 million years (Friesen and others, 1996a, 1996b). These studies prompted recognition as separate species again in 1997 (American Ornithologists' Union, 1997) and this status remains today.

General Description

The Marbled Murrelet is a fairly small alcid. Body length is 23-25 cm, wing length 122-149 mm, and adults typically weigh 188-269 g (Nelson, 1997; McShane and others, 2004). There is no pronounced difference in size between sexes (i.e., adults are sexually monomorphic in size). Marbled Murrelets are similar in appearance and size to Kittlitz's and Long-Billed Murrelets. Compared to Kittlitz's Murrelets, Marbled Murrelets have a longer bill and darker plumage. They are much lighter in color with a shorter bill than the Long-Billed Murrelet (Friesen and others, 1996b).

Marbled Murrelets have a small black bill, dark brown eyes, and legs and toes that range from pink to dark gray with black webbing in between (Carter and Stein, 1995; Nelson, 1997). Adults are sexually monomorphic. The species has distinctly different Basic (winter), Alternate (breeding), and Juvenal plumages (Carter and Stein, 1995). Breeding (Alternate plumaged) birds are dark brownish-black above, with rusty margins on the back feathers (Carter and Stein, 1995). The underparts and sides are lighter and mottled brown. Rectrices (tail feathers) and upperwing-coverts are dark brown. Underwing-coverts and axillaries are gray-brown, and undertail coverts are white (Nelson, 1997). This cryptic speckled-brown plumage is almost certainly an adaptation for their solitary nesting habits, and need for camouflage against both mammalian and aerial predators when at nest sites. In contrast, winter-plumaged (Basic) birds have gray margins on their back-feathers and predominantly white scapulars. The underparts of wintering birds are pale, usually white, although brown / gray flecking may still be present on the flanks and sides. Wintering birds have white sides of the head, a nearly complete white collar, and white on the scapulars (Carter and Stein, 1995; Nelson, 1997).

Juvenal plumage is very similar to adult winter plumage, but the underparts are speckled with thin blackish-brown spots, and the gray margins are less visible. The white collar and scapular-patch of juveniles also are less distinct than in winter adults. Individuals that have recently fledged are darker overall, and it takes 2 weeks to 2 months for the juveniles to become lighter, the dark neck-band to disappear, and the dark brown flecking on the feather margins to become replaced by gray. During this stage, it is difficult to distinguish juveniles from winter-plumaged adults (Carter and Stein, 1995; Nelson, 1997). The single chick has thick yellow to grayish-yellow down that is spotted with black and brown on its upperparts, and gray on its underparts. It remains in this downy state until just prior to fledging (Binford and others, 1975; Gaston and Jones, 1998).

There is considerable diversity in nesting habitat and degree of coloniality among the Alcids (Gaston and Jones, 1998). For example, whereas Common Murres (*Uria aalge*) usually breed at high density in exposed habitat such as cliff-ledges or low-lying flat islands, the Marbled Murrelet typically nests solitarily in older trees, on the open ground, on cliffs, and, rarely, in deciduous trees (Day and others, 1983; DeGange, 1996; Bradley and Cooke, 2001). From British Columbia to California, nesting occurs primarily in old-growth forest. In southern Alaska, breeding habitats are varied but are primarily trees in forested areas of that coastline. On the Alaska Peninsula and in the Aleutian Islands, however, all nesting is on the ground because trees are absent. Their secretive behavior and dispersed nest sites have made Marbled Murrelets hard to study, and most of our current understanding stems from work conducted since the 1990s when there was an explosion of studies related to the economic significance of their old-growth nesting habitat (Carter and Morrison, 1992; Ralph and others, 1995a; Nelson, 1997; Gaston and Jones, 1998).

All alcids pursue their prey beneath the water using wing-propelled diving, but, unlike penguins (family Spheniseiformes), they have retained their ability to fly. The shape of their wing and body structure reflect this compromise, with wing area reduced to decrease underwater drag, breast muscles well-developed for underwater "flight," and wing-loading (ratio of body mass to wing area) consequently high. To overcome this constraint, alcids have a characteristic rapid, flapping aerial flight. Although their wings are longer, narrower, and more pointed than other alcids (Nelson, 1997), Marbled Murrelets have high wing-loading, and use high flight speeds to maintain lift and stay airborne (Nelson, 1997; Burger, 2002). In their radar study of murrelets on the Olympic Peninsula (Washington), Cooper and others (2001) calculated a mean flight speed of 92.2 ± 19.1 km/hr ($n = 311$; range = 56-153 km/hr). The Marbled Murrelet is one of the most vocal alcids at sea, with four general types of vocalization: a piercing 'keer-like call;' a 'whistle-like call;' a 'groan-like call;' and short 'chip' calls (Nelson, 1997; Gaston and Jones, 1998).

Geographic Distribution

North Pacific

Marbled Murrelets are distributed along the Pacific coast of North America, with birds breeding from central California through Oregon, Washington, British Columbia, southern Alaska, westward through the Aleutian Island chain, with presumed breeding as far north as Bristol Bay (Nelson, 1997; Gaston and Jones, 1998; Burger, 2002; fig. 1). Historically, most of the murrelet population was located in British Columbia (8 percent) and Southeast Alaska (71 percent; McShane and others, 2004). Current population estimates suggest a much lower proportion for Southeast Alaska (about 42 percent) and a higher proportion for British Columbia (about 19 percent; see section, "Population Status and Trends"). The wintering range encompasses the breeding range but also extends into southern California, and rarely to Baja California, Mexico (Nelson, 1997; McShane and others, 2004).

British Columbia

Marbled Murrelets appear to breed throughout coastal British Columbia, although in varying densities (Burger, 1995b, 2002b). High densities of murrelets occur at-sea during the breeding season on the west coast of Vancouver Island, in Desolation Sound on the southern mainland, in some of the inlets along the central and northern mainland coast, and on Haida Gwaii (Queen Charlotte Islands; Burger, 2002). Breeding populations are greatly reduced in the Georgia Depression (east coast of Vancouver Island and southern mainland) due to reductions in nesting habitat associated with urbanization, agriculture, and forestry (Burger, 2002). The long fjords that characterize the British Columbia mainland do not appear to be used by many murrelets, with higher concentrations found in nearshore waters at the mouths of inlets that are more exposed to the open sea.

The winter range in British Columbia is poorly known. There is certainly some seasonal migration within the province, and between British Columbia and Washington, but the extent of movements is unclear, with variable numbers of murrelets found in nearshore waters near the breeding grounds all year (Rodway and others, 1992; Carter and Stein, 1995; Burger, 1995b, 2002b; Beauchamp and others, 1999). Year-round counts in Barkley Sound, southwest Vancouver Island show consistently low numbers (less than 10 percent of summer mean) from late July through March. Numbers in more sheltered waters in the Strait of Georgia and surrounding inlets show increases in winter (Burger, 1995b, 2002b). Murrelets do not overwinter in the open ocean off British Columbia in significant numbers (Morgan and others, 1991; Burger and others, 2004b). The Strait of Georgia appears to be an important wintering ground (G. Kaiser, Canadian Wildlife Service, unpub. data, 2006), and might include murrelets from Alaska, although this has not been proven.

Alaska

Marbled Murrelets breed on the Aleutian Islands, from the Near (Attu), Andreanof (Adak, Atka, Kagalasta), and Fox (Unalaska) island groups east to the Alaska Peninsula, Cook Inlet, Kodiak, the Kenai Peninsula, and Prince William Sound, and south through the Alexander Archipelago in Southeast Alaska (Nelson, 1997). Limited breeding is presumed to occur as far north as northern Bristol Bay. Despite that broad range, breeding areas are largely concentrated in three important areas: the Kodiak Archipelago, Prince William Sound, and the Alexander Archipelago (Piatt and Ford, 1993). There are a few spring and summer records of birds observed north and west of the Alaska Peninsula – Bristol Bay, and Pribilof, St. Lawrence, Diomede, and Idlidlya (northern coast of Chukotski Peninsula, Russia) islands (Bédard, 1966; Bartonek and Gibson, 1972; Sealy and others, 1982). The wintering range is poorly known (see section, "Migration and Seasonal Movements"). Many birds appear to remain near breeding sites throughout the year, whereas others move offshore or to other inshore protected waters. Wintering areas include the Kodiak Archipelago, Cook Inlet, Prince William Sound, and the Alexander Archipelago, and out to 300 km in the Gulf of Alaska (Piatt and Naslund, 1995). It is a casual winter visitor to the Pribilof Islands (Hanna, 1920; Kessel and Gibson, 1978).

Feeding Ecology

Food Habits

The diets of Marbled Murrelets have been previously summarized by Sanger (1983), Carter (1984), Burkett (1995), DeGange (1996), Nelson (1997), and McShane and others (2004). Major differences in diet between summer and winter have been recorded, with birds preying primarily on small schooling fish such as Pacific sand lance (*Ammodytes hexapterus*), northern anchovies (*Engraulis mordax*), Pacific herring (*Clupea harengus*), capelin (*Mallotus villosus*), and osmerids during the summer season. Invertebrates (e.g., euphausiids and mysids) become more common in their diets during the winter and spring (Munro and Clemens, 1931; Sanger, 1987; Vermeer, 1992; Burkett, 1995; Nelson, 1997). Seasonal changes in diet may reflect both prey availability and preference (DeGange, 1996). Marbled Murrelets in some areas also forage to some degree on salmon smolt (*Oncorhynchus* spp.) in freshwater lakes during the summer. Freshwater foraging most likely occurs in British Columbia and Southeast Alaska, where there are large coastal lakes with relatively large numbers of small fish near nesting habitat (Carter and Sealy, 1986; Hobson, 1990; McShane and others, 2004).

In addition to seasonal variation in prey choice, there also are striking differences between adult and chick diets (Sealy, 1975; Carter, 1984; Carter and Sealy, 1987; Mahon and others, 1992; Burkett, 1995; Jones, 2001; Kuletz, 2005). Chicks typically are fed single large subadult or adult fish (typically larger sand lance, immature herring, and occasionally salmon smolt) that have higher energy value than juvenile and larval age classes of fish (Robards and others, 1999c). For example, Marbled Murrelets in Prince William Sound selected larger fish of higher energy content (81-135 mm, 1+ age class) for their chicks, whereas they fed themselves on large numbers of smaller (< 80 mm, 0+ age class) prey items (Kuletz, 2005). This pattern also was found for murrelets in Barkley Sound, British Columbia (Carter, 1984; Carter and Sealy, 1987, 1990). This foraging behavior is consistent with optimal foraging theory (McArthur and Pianka, 1966) and is observed in many other fish-eating alcids (e.g., Wilson and others, 2005). Chicks may require high-value prey for growth and development, and it is more beneficial for parents to deliver fewer, high-quality meals to their offspring because of the transport costs associated with provisioning in central place foragers (Orians and Pearson, 1979). In addition, Marbled Murrelets face a significant risk of predation when delivering food to their offspring (Marks and Naslund, 1994; Nelson, 1997; Kuletz, 2005), so it is to their advantage to minimize the number of trips to feed young. Despite predation risk, however, some adults will make multiple feeding trips in one morning to feed the chick (Carter and Sealy, 1986; Nelson, 1997).

Seasonal and age-related sources of variability must be taken into account when comparing Marbled Murrelet dietary studies. Prey destined for the chick versus parental consumption usually can be distinguished based on the fish-carrying behavior of individuals (Carter and Sealy, 1990). Parents feed themselves early in the day before flying to other areas to find food specifically for their chick (Carter and Sealy, 1990). Large prey items destined for the chick are usually caught at dawn, dusk, and possibly at night, when they are more abundant and easily caught near the surface of the water (Carter and Sealy, 1990; Kuletz, 2005). Most trips to the nest to feed chicks occur in the early morning, mainly pre-dawn, but as much as 1 to 2 hours after sunrise. Parents sitting in nearshore waters with prey in the bill during the evening hours may either wait until early morning or occasionally may make an evening trip to provision their chick (Carter and Sealy, 1987; Bradley and others, 2002; Speckman and others, 2004; Kuletz, 2005). In contrast, adults rarely hold prey for themselves at the surface of the water, and mostly ingest their prey under water (Mahon and others, 1992; Kuletz, 2005). Sightings of adults holding prey for themselves are therefore brief and sample sizes minimal.

Most studies on chick diet have focused on field observations of prey held by parents on the water prior to delivery to the nest (Carter, 1984; Kuletz, 2005), although some prey have been viewed on video cameras at nests. Studies of adult diet have used a variety of methods including: (1) analysis of stomach contents from collected birds (e.g., Sealy, 1975; Carter, 1984); (2) stable isotope analysis (e.g., Hobson, 1990); and (3) sampling of fish at foraging sites (e.g., Ostrand and others, 2004; Henkel and Harvey, 2006). There are inherent biases and problems associated with all three methods. Observation and species identification of fish-holding individuals at-sea are likely to be biased towards larger prey items that protrude farther from the bill. Stomach analysis often involves empty stomachs and digested prey remains, especially when birds are collected later in the day. Larval fish and soft-bodied invertebrate species may not be detected because of rapid digestion. Stable-isotope analysis enables a time-integrated estimate of assimilated food, and can provide a powerful, non-lethal tool to assess and compare the proportion of prey taken from different trophic levels (Hobson and others, 1994). This method is most useful when used in unison with other conventional methods that allow for species and age class determinations of prey. Finally, the interpretation of co-occurrence of fish schools and foraging murrelets involves assumptions about actual prey selection. Given these important sources of variation, we include details of season (winter vs. summer) and age class of murrelet (adult vs. chick) in reviewing the Alaska diet studies shown in table 1.

Alaska Diet

There have been a number of systematic and opportunistic studies on murrelet diet in Alaska (table 1), and these studies are described in detail in appendix A. The adult diet of Marbled Murrelets in Alaska is highly diverse (appendix A). The important prey species include Pacific herring, Pacific sand lance, pollock, and cod (Gadidae). Although sample sizes are minimal and murrelets in many areas have not been sampled at all, there is growing evidence for spatial, temporal, and age-related differences in diet. Similar to conclusions made in other summaries (e.g., Burkett, 1995), Alaska studies demonstrate differences in Marbled Murrelet diet between winter and summer months, with birds feeding more on invertebrates during the winter and fish during the summer (e.g., Krasnow and Sanger, 1982). Differences between the diet of adults and chicks also were found, with chicks having lower prey diversity and larger, more high quality prey items than adults (e.g., Carter, 1984; Kuletz, 2005).

Spatial Variability

Probably the most comprehensive spatial comparison of Marbled Murrelet diet in Alaska comes from collections of birds in the early to mid-1990s (Piatt and Anderson, 1996; J. Piatt, U.S. Geological Survey, unpub. data, 2006; table 2). Pollock, cod, and sand lance generally were the most important prey taken by murrelets collected across a wide geographic range. Despite this generalization, there also were geographic differences in diet. For example, myctophid fishes were an important component of the diet of birds from Icy Strait (Southeast Alaska) in the 1990s (J. Piatt, U.S. Geological Survey, unpub. data, 2006), presumably because of their abundance in this region (Abookire and others, 2002; J. Piatt, U.S. Geological Survey, unpub. data, 2006). Marbled Murrelet diet also differs on a more local scale. For example, Krasnow and Sanger (1982) found that adult Marbled Murrelets were eating very different prey in two areas of the Kodiak Archipelago. In Izhut Bay at Afognak Island, birds were feeding primarily on capelin, while birds in northern Sitkalidak Strait at Kodiak Island (about 120 km to the south), were feeding mostly on *Thysanoessa inermis*. Similarly, Kuletz (2005) found that Prince William Sound murrelets were feeding their chicks primarily on sand lance near Naked Island, whereas birds near Jackpot Bay (about 50 km away) fed their chicks mostly herring (appendix A). These studies highlight the breadth, flexibility, and generalist nature of adult murrelets’ diet, and the influence that local prey availability has on diet.

Table 1. Studies of Marbled Murrelet diet in Alaska.

[Details of each study are provided in Appendix A. **Abbreviations:** vis. obs., visual observation]

Study	Study year(s)	Location	Month	Murrelet age class	Sample size	Method
Sangster and others (1978)	1977	Prince William Sound	May to Sept.	Adult	8	Stomach
Oakley and Kuletz (1979)	1978	Prince William Sound	May to Aug.	Adult	14	Stomach
Krasnow and Sanger (1982)	1976–1977	Chiniak Bay, Kodiak	Dec. to Apr.	Adult	18	Stomach
Krasnow and Sanger (1982)	1978	Chiniak Bay, Kodiak	February	Adult	16	Stomach
Krasnow and Sanger (1982)	1978	Izhut Bay, Kodiak	Apr. to Aug.	Adult	25	Stomach
Krasnow and Sanger (1982)	1978	North Sitkalidak Strait, Kodiak	May to Aug.	Adult	17	Stomach
Sanger (1983)	1969–1978					Overview
Sanger (1987)	1977–1978	Katchemak Bay	Jan. to Apr.	Adult	18	Stomach
Day and Nigro (2000)	1996–1998	Prince William Sound	May to Aug.	Adult/nestling	40	vis. obs.
Kuletz and Labunski (U.S. Fish and Wildlife Service, unpub. data, 2006)	2004–2006	Katchemak Bay	June to Aug.	Adult	57	vis. obs.
Kuletz and Labunski (U.S. Fish and Wildlife Service, unpub. data, 2005)	2005	Katchemak Bay	August	Chick	16	vis. obs.
Kuletz (2005)	1997–1999	Naked, Prince William Sound	June to Aug.	Chick	62	vis. obs.
Kuletz (2005)	1997–2000	Jackpot, Prince William Sound	June to Aug.	Chick	310	vis. obs.
Piatt (U.S. Geological Survey, unpub. data, 2006)	1989–1996	Central-West Aleutians	June to Sept.	Adult	19	Stomach
Piatt (U.S. Geological Survey, unpub. data, 2006)	1989–1997	East Aleutians	June to Sept.	Adult	23	Stomach
Piatt (U.S. Geological Survey, unpub. data, 2006)	1989–1998	Alaska Peninsula	June to Sept.	Adult	52	Stomach
Piatt (U.S. Geological Survey, unpub. data, 2006)	1989–1999	Cook/Kodiak	June to Sept.	Adult	58	Stomach
Piatt (U.S. Geological Survey, unpub. data, 2006)	1989–2000	Prince William Sound	June to Sept.	Adult	43	Stomach
Piatt (U.S. Geological Survey, unpub. data, 2006)	1989–2001	Southeast Alaska	June to Sept.	Adult	35	Stomach
Newman and others (2006)	2005	Port Snettisham, SE Alaska	June	Chick	4	Dipnet during prey school

Temporal Variability

Seasonal and spatial variability in Marbled Murrelet diets complicates our ability to detect dietary change over time—ideally, diets should be compared from the same sites and during the same times of year. For example, Krasnow and Sanger (1982) were able to show inter-annual variability in the diet of Marbled Murrelets on Kodiak Island. In winter 1976 –77, diet was dominated by capelin, and smaller amounts of euphausiids and smelts, whereas the diet of winter 1978 was dominated by mysids (Krasnow and Sanger, 1982; appendix A). Changes in Marbled Murrelet diet among years and across broad regions in Alaska are thought to reflect the ‘regime shift’ that occurred in the North Pacific Ocean during the late 1970s (Anderson and Piatt, 1999; see section, “Marine Habitat: Characteristics and Threats”). For example, there was a near absence of capelin in the diet of Marbled Murrelets collected along the Alaska Peninsula and around Kodiak in the early 1990s (J. Piatt, U.S. Geological Survey, unpub. data, 2006; table 2). In contrast, capelin were a common component of diets during the summer for murrelets collected along the Alaska Peninsula and around Kodiak in the 1970s–1980s (Piatt and Anderson, 1996; appendix A). Similarly, there is evidence that changes in the Prince William Sound marine ecosystem in the 1980s negatively affected fish-eating birds (DeGange, 1996; Kuletz and others, 1997). Marbled Murrelets ate mostly sand lance during the late 1970s, whereas they started to feed almost entirely on lipid-poor gadids from 1989 to 1991, with capelin disappearing as a dietary item (DeGange, 1996; Kuletz and others, 1997; table 3).

British Columbia Diet

In British Columbia, murrelets have a diverse diet, but small schooling fish and large pelagic crustaceans (euphausiids, mysids, and amphipods) are the main prey items (see summaries by Sealy, 1975; Carter, 1984; Vermeer and others, 1987; Burkett, 1995; Nelson, 1997; Day and Nigro, 2000). The most common fish are Pacific sand lance, northern anchovy, immature Pacific herring, capelin, and smelt (*Hypomesus* sp.). Squid (*Loligo* spp.), immature salmon, and eulachon (*Strongylura exilis*) also are taken in some areas.

In British Columbia, the most common prey species is sand lance (Burkett, 1995). In many areas, the distribution, abundance, and movements of murrelets seem closely linked to those of sand lance, especially during the murrelet’s breeding season (Sealy, 1975; Carter; 1984; Mahon and others, 1992; Haynes and others, 2004). Little is known about

Table 2. Diet of Marbled Murrelet in Alaska.

[From Piatt and Anderson 1996; J. Piatt, U.S. Geological Survey, unpub. data, 2006. **Percent:** Percent number examined and number empty are calculated using the total number of birds examined. Percent frequency of occurrence, number of individuals, and estimated wet weight are calculated using the number of birds containing prey items. **Invertebrates:** Includes copepods and squid. **Other:** Includes sculpin (Cottidae), flatfish (Pleuronectidae), and unidentified fish; **Abbreviations:** g, gram]

	Central-Western Aleutians		Eastern Aleutians		Alaska Peninsula		Cook/ Kodiak		Prince William Sound		Southeast Alaska		Total	
	n	Percent	*n*	Percent	*n*	Percent	*n*	Percent	*n*	Percent	*n*	Percent	*n*	Percent
Number examined	19	8	23	10	52	23	58	25	43	19	35	15	230	100
Number empty	0	0	11	5	22	10	2	1	15	7	5	2	55	24
Frequency of Occurrence														
Invertebrates	0	0	2	17	0	0	2	4	0	0	1	3	5	3
Capelin (*Mallotus villosus*)	0	0	0	0	0	0	10	18	0	0	2	7	12	7
Lanternfishes (Myctophidae)	0	0	0	0	0	0	0	0	0	0	17	57	17	10
Pollock and cod (Gadidae)	7	37	8	67	13	43	6	11	24	86	2	7	60	34
Sand lance (*Ammodytes hexapterus*)	11	58	2	17	9	30	31	55	2	7	7	23	62	35
Other	1	5	0	0	8	27	7	13	2	7	1	3	19	11
Numbers of Individuals														
Invertebrates	0	0	30	44	0	0	2	1	0	0	1	1	33	4
Capelin (*Mallotus villosus*)	0	0	0	0	0	0	22	14	0	0	2	1	24	3
Lanternfishes (Myctophidae)	0	0	0	0	0	0	0	0	0	0	174	88	174	23
Pollock and cod (Gadidae)	25	31	35	51	90	70	20	13	122	96	5	3	297	39
Sand lance (*Ammodytes hexapterus*)	54	68	3	4	14	11	92	60	3	2	15	8	181	24
Other	1	1	0	0	25	19	17	11	2	2	1	1	46	6
Estimated Wet Weight (g)														
Invertebrates	0	0	<1	3	0	0	4	1	0	0	2	<1	7	<1
Capelin (*Mallotus villosus*)	0	0	0	0	0	0	43	10	0	0	4	<1	47	3
Lanternfishes (Myctophidae)	0	0	0	0	0	0	0	0	0	0	406	87	406	28
Pollock and cod (Gadidae)	31	28	18	64	175	83	15	4	194	87	3	<1	435	30
Sand lance (*Ammodytes hexapterus*)	80	72	9	33	25	12	354	83	30	13	50	11	548	37
Other	<1	<1	0	0	11	5	9	2	<1	<1	<1	<1	20	1

Table 3. Percent frequency of occurrence of three primary prey types in adult seabird diets in Prince William Sound in 1977–79, and Marbled Murrelet diet in Prince William Sound and Kachemak Bay in 1989–91.

[From Kuletz and others, 1997. Prey type: Other prey types or unidentified items not included]

Prey type	1977–79				1989–91		
	Prince William Sound				Prince William Sound		Kachemak Bay
	Pigeon guillemot	Marbled Murrelet	Blacklegged Kittiwake	Tufted Puffin	Common Mure	Marbled Murrelet	Marbled Murrelet
	n = 40	*n* = 27	*n* = 10	*n* = 8	*n* = 8	*n* = 27	*n* = 13
Ammodytes hexapterus	20	41	40	0	50	7	92
Osmeridae and Clupeidae	0	11	40	100	0	0	0
Gadidae	18	15	10	13	75	89	15

the distribution, densities, diurnal and seasonal movements, or, in fact, any aspect of the biology of this important feed fish within British Columbia (Haynes, 2006). Robards and others (1999c) have compiled a comprehensive annotated bibliography on Pacific sand lance. Some aspects of its biology can be inferred from general reviews (Field, 1988; Robards and others, 1999b) and work done elsewhere in the North Pacific (Robards and others, 1999a, 1999b, 1999c). Immature herring, and to a lesser extent, salmon smolts and immature rockfish (Scorpaenidae) are important alternative prey in British Columbia. Hay and others (1989, 1992) and Gillespie and Westrheim (1997) review data on forage fish important to seabirds in British Columbia, and Grosse and Hay (1988) and Hay and McCarter (1997) review herring biology.

Foraging Behavior

Diving Behavior

As discussed above, Marbled Murrelets are wing-propelled pursuit-divers that forage both during the day and at night (Carter and Sealy, 1986; Gaston and Jones, 1998). Little is known about the diving depths of Marbled Murrelets because their dispersed, tree-nesting habit makes it difficult to deploy and retrieve the time-depth-recorder devices used successfully with other alcids (e.g., Falk and others, 2002). Given their mass, Marbled Murrelets should be able to dive to depths of about 47 m (Mathews and Burger, 1998). Despite this ability, there is evidence that suggests that Marbled Murrelets usually make shallower dives. Carter and Sealy (1984) examined accidental gillnet mortalities, and concluded that most Marbled Murrelets were caught within 3-5 m from the surface, and Mathews and Burger (1998) observed a bird at a depth of 13.7 m near Vancouver Island. The deepest gillnet mortality record is 27 m off the California coast (Carter and Erickson, 1992).

Groups of two birds often forage together, vocalizing at the surface and diving simultaneously (Nelson, 1997). Dives are short (mean = 20-44 s; range 2-115; *n* = 6-119 dives; Thoresen, 1989; Carter and Sealy, 1990; Strachan and others, 1995; summarized in Nelson, 1997). The mean surface time between dives is 26.9 s ± 53.8 SD (*n* = 181 dives of 20 individuals; K. Kuletz, unpub. data; summarized in Nelson, 1997). Juveniles generally have shorter dives than adults (K. Kuletz, unpub. data; summarized in Nelson, 1997).

Foraging Strategy

Marbled Murrelets most often forage in pairs, although single birds are more common in the winter and birds tend to aggregate more in the summer (Sealy, 1974; Carter and Sealy, 1990; Strachan and others, 1995; Kuletz, 2005). Kuletz (2005) found that most birds in Prince William Sound (1997–99) occurred as singles or pairs (*n* = 11,280 birds; 22 percent = singles, 53 percent = pairs). Mean group size ranged among years from 2.11 (± 0.07) to 1.75 (± 0.03). Day and Nigro (2000) reported similar flock sizes of Marbled Murrelets feeding in Prince William Sound (mean = 1.7 ± 0.8; *n* = 4,636 birds).

Hatch-year (HY) birds generally forage alone (Kuletz and Marks, 1997; Kuletz, 2005). Subadults may feed alone during the spring and then join foraging adults in the summer (Sealy, 1975). Although chick-feeding Marbled Murrelets primarily forage as individuals, they are fairly flexible when self-feeding and in Prince William Sound, showed a tendency to forage in larger groups when prey availability was low (Kuletz, 2005). This suggests that there is a benefit to foraging in larger groups when foraging conditions are poor and food is harder to locate (Kuletz, 2005). Marbled Murrelets also may forage in large groups when prey are aggregated (see below; Kuletz, 2005). Marbled Murrelets often return to known feeding sites, perhaps encouraged by the presence of other birds or a reliable and predictable occurrence of prey (Carter and Sealy, 1990). Radio-tagging also has suggested that Marbled Murrelets exhibit fidelity to forage sites in Southeast Alaska (Quinlan and Hughes, 1992), British Columbia (Hull and others, 2001; Lougheed and others, 2002b; Bradley and others, 2004), and Prince William Sound (Kuletz, 2005).

Marbled Murrelets tend to aggregate where food is clumped, concentrated, or predictable, but within those aggregations murrelets tend to feed primarily in pairs or as singles. Murrelets are more aggregated in areas of protected water (Chilton and Sealy, 1987; Carter and Sealy, 1990; Mahon and others, 1992; Hunt, 1995; Strachan and others, 1995). They may avoid other individuals while foraging to reduce intra-specific competition.

Marbled Murrelets sometimes occur in mixed-species feeding flocks in Alaska and British Columbia (Chilton and Sealy, 1987; Carter and Sealy, 1990; Mahon and others, 1992; Hunt, 1995; Strachan and others, 1995; Day and Nigro, 2000). In Prince William Sound, murrelets composed an average of 17.3 percent (± 2.1) of all mixed-species flocks, ranging from 7 to 33 percent (Kuletz, 2005). Feeding flocks consisting only of murrelets were significantly smaller than mixed-species feeding flocks (Kuletz, 2005). In British Columbia, murrelets seem to avoid larger mixed-species flocks, especially those dominated by larger alcids and cormorants (Porter and Sealy, 1981, 1982), but will readily form mixed-flocks with gulls (Mahon and others, 1992).

There has been considerable work conducted in Alaska on mixed feeding flocks and the role Marbled Murrelets play in initiating these aggregations (Mansicalco and Ostrand, 1997; Ostrand, 1999; Day and Nigro, 2000). Ostrand (1999) studied feeding flocks in Prince William Sound, and concluded that all observed feeding flocks were initiated by pursuit-diving seabirds, and that 76.5 percent of the initiators were Marbled Murrelets. Murrelets therefore play an important role in increasing the foraging efficiency of Black-legged Kittiwakes (*Rissa tridactyla*) and Glaucous-winged Gulls (*Larus glaucescens*; Maniscalco and Ostrand, 1997), and may be an important component in the transfer of energy from the marine ecosystem to other avian predators (Ostrand, 1999). However, murrelets are vulnerable to kleptoparasitism by gulls (Maniscalco and Ostrand, 1997), and mixed-species feeding flocks that include larger, kleptoparasitic birds may be detrimental to murrelet foraging success (Maniscalco and Ostrand, 1997; Kuletz, 2005).

According to optimal foraging theory (McArthur and Pianka, 1966), central place foragers should travel long distances to forage if the probability of energy gain is high. Murrelets breeding in northern Southeast Alaska fly an average of 78 km to forage in Icy Strait (Whitworth and others, 2000), whereas birds breeding in Prince William Sound fly much shorter distances (mean = 16 km; Kuletz, 2005). Icy Strait is an area of upwelling, which concentrates prey and provides an important area of predictable prey availability for murrelets and other marine predators. It may therefore be more beneficial for birds breeding near Auke Bay (Southeast Alaska) to fly longer distances to Icy Strait for predictable prey than to forage locally on patchy and unpredictable prey (Whitworth and others, 2000). In contrast, Prince William Sound has relatively low productivity, low fish biomass, and small, dispersed fish schools (Ostrand and others, 1998; Haldorson and others, 1999), and it may be more beneficial for murrelets to be familiar with foraging grounds within a short distance of nesting areas versus flying longer distances in search of food (Kuletz, 2005).

Foraging Habitat

Marbled Murrelets are usually found within 5 km from shore, and in water less than 60 m deep (Sealy, 1975; Ainley and others, 1995a; Burger, 1995b; Strachan and others, 1995; Nelson, 1997; Day and Nigro, 2000). In general, birds occur closer to the shore in exposed coastal areas, and farther offshore in protected coastal areas (Nelson, 1997). A large scale modeling exercise using British Columbia data concluded that murrelet densities were highest near sandy substrates and estuaries, and lower near glaciers (Yen and others, 2004a). In Alaska, murrelets frequent glacial-fed waters, although finer scale habitat use in Prince William Sound fjords indicated that Marbled Murrelets were more prevalent in waters less than 200 m from shore than offshore, and preferred waters with no ice that were greater than 60ºC and salinity greater than 17 percent (Day and Nigro, 2000; Day and others, 2003). Compared to their congener, the Kittlitz’s Murrelet, Marbled Murrelets preferred clearer water, and avoided waters of high turbidity that limited visibility to less than 2 m (Day and others, 2003).

Physical and biological oceanographic processes that concentrate prey (such as upwellings and rip currents) have an important influence on the foraging distribution of Marbled Murrelets (Kaiser and others, 1991; Ainley and others, 1995b; Burger, 1995b, 2002b; Strong and others, 1995; Nelson, 1997; Day and Nigro, 2000; Kuletz, 2005). For example, although birds in Prince William Sound generally forage in water less than 30 m deep, birds breeding near deep water fjords feed on predictable concentrations of prey associated with glacial sills, sites of upwelling, and currents, rather than travel longer distances to shallower water (Kuletz, 2005). These bathymetric and oceanographic features may be especially important for Marbled Murrelets nesting near deep waters in Prince William Sound (Kuletz, 2005).

To examine the prey selection of Marbled Murrelets, Ostrand and others (2004) quantified the at-sea distribution of Marbled Murrelets in conjunction with hydroacoustic measurements of forage fish in Prince William Sound. Murrelets exhibited a highly flexible foraging strategy, responding to changes in food availability by switching their prey choices to maximize energy gain. For example, despite the higher abundance of low-lipid schooling fish during one year of the study, murrelets selected less abundant, higher value Pacific herring.

Migration and Seasonal Movements

Many studies have shown seasonal changes in the distribution of Marbled Murrelets. Studies in the northern part of their range have suggested that large proportions of birds move south from breeding areas, either from outer coastal to protected waters, or from breeding areas out to more open ocean (Sealy, 1974; Carter, 1984; Rodway and others, 1992; Burger, 1995b; Carter and Stein, 1995; Piatt and Naslund, 1995; Speich and Wahl, 1995; Kuletz, 1996). In California, most birds appear to be year-round residents near breeding areas (Naslund, 1993). The degree of residency and the distance of movements likely reflects the availability of suitable prey resources during the non-breeding season. There also is an increasing north to south trend of visiting nest sites during the non-breeding season through the species range (Carter and Sealy, 1986; Naslund, 1993; Beauchamp and others, 1999; Burger, 2002).

Patterns of movement in Alaska are largely unknown. Some birds may remain near their breeding sites, whereas other birds move south or offshore, or to unknown areas (Nelson, 1997). Wintering birds have been recorded as far as 300 km offshore in the Gulf of Alaska (Piatt and Naslund, 1995).

In British Columbia, migration from exposed coasts on Vancouver Island into more sheltered waters of Georgia Strait and Puget Sound has been inferred from at-sea counts (Rodway and others, 1992; Burger, 1995b, 2002b). Some birds remain all year along the outer coast, hence, the extent of movements is not known. Beauchamp and others (1999) obtained the only direct evidence to date of migration. An adult banded in Desolation Sound, southern British Columbia mainland, was recaptured where it wintered in the San Juan Islands, Washington, and recaptured again during the breeding season in Desolation Sound. Other marked murrelets from Desolation Sound, however, appeared to remain there after breeding (Beauchamp and others, 1999).

Most movements occur after the breeding season has ended (August and September), and again prior to the next breeding season (March-May; Bent, 1963; Burger, 1995b; Kuletz, 1996; Campbell and others, 1997). For example, no Marbled Murrelets are seen in Auke Bay, Southeast Alaska, from the middle of September through the end of October (G. van Vliet, Alaska Department of Fish and Game, oral commun., 2006), and numbers in Kachemak Bay in lower Cook Inlet increase during April, reach peak numbers in early May, and decrease again in August to a low in September (K. Kuletz, U.S. Fish and Wildlife Service, unpub. data, 2006). Some post-breeding movements occur prior to the flightless pre-basic molt, and may reflect the need for safe molting areas with minimal predation, low surf associated with storms, and reliable food resources (Carter and Stein, 1995). Other movements occur in autumn after the molt and may reflect shifts in prey availability and/or a need to winter in more protected waters.

In addition to larger scale movements before and after the breeding season, there is some evidence for changes in the foraging distribution of Marbled Murrelets during the breeding season. For example, summer changes in the foraging distribution of birds around Adak (Aleutian Islands) probably reflect shifting prey availability and the timing of candlefish (*Thaleichthys pacificus*), capelin, and Pacific sand lance spawning (Meehan, 1996).

Molt

The plumages and molts of the Marbled Murrelet have been described in detail by Carter and Stein (1995), and summarized by Nelson (1997) and Gaston and Jones (1998). The juvenile plumage is retained through the first winter, but the neck ring and speckling of their white underparts wears quickly. Within a month of fledging, juveniles and adults in winter plumage are hard to distinguish (Carter and Stein, 1995). Definitive Alternate (breeding) plumage is attained in an incomplete molt that takes place before the breeding season. The timing of initiation of the Pre-Alternate molt can occur as early as February (California) and as late as May (parts of Alaska). During this period, birds lose their contour feathers but retain their flight feathers. Birds undergo a complete Pre-Basic molt after breeding, when all flight feathers are dropped simultaneously and birds are flightless for about 1 to 2 months. The initiation of Pre-Basic molt can occur as early as June (California) and as late as October (Alaska). Adults retain their white Definitive Basic (winter) plumage until Pre-Alternate molt in February–May.

Breeding Biology

Reproductive Success

Marbled Murrelets, being solitary nesters with secretive breeding habits and remote, often inaccessible nest sites, present unique challenges to anyone attempting to measure reproductive success. The era of conventional observations of nest sites and breeding activities of this species dates only to 1974, when the first discovery of a nest containing a downy young murrelet was made in central California (Binford and others, 1975). Following listing of murrelets as Threatened in British Columbia, Washington, Oregon, and California, a large and systematic effort was mounted to locate and monitor nest sites of the species throughout its listed range and in Alaska. It was known from examination of collected females that murrelets had a characteristic clutch of one egg (Sealy, 1974), and no later information has altered that conclusion (DeSanto and Nelson, 1995). Upon losing their first clutch, however, some pairs are able to produce a replacement egg in the same season and may raise a chick successfully (McFarlane Tranquilla and others, 2003b; see more below).

By the mid-1990s, Nelson and Hamer (1995) were able to report at least fragmentary information on breeding activity and outcomes at 65 tree nests of murrelets observed from Alaska (n = 18) to California. Table 4 is a condensed version of their compilation with the addition of two ground nests observed in Alaska (Simons, 1980; Hirsch and others, 1981). The outcome (chick fledged or failed) was known for 11 of the 20 Alaska nests, and only 2 (18 percent) produced a fledgling. Outside of Alaska, 39 percent of 23 nesting attempts with known fate ended successfully, giving a range-wide estimate of mean nesting success of 32.4 percent (n = 34 nesting attempts). Subsequently, Manley (1999) studied 68 nesting attempts in British Columbia with ground observations and tree climbing, and reported a similar estimate of success of 0.33 percent. Those are low values in comparison to most other alcid species (Hudson, 1985; Gaston and Jones, 1998).

There is a tendency for the frequency of nest failure to increase from incubation to chick-rearing in Marbled Murrelets. Range-wide, hatching success was 67 percent (n = 20) and fledging success was 45 percent (n = 19) for nests with known outcomes (Nelson and Hamer, 1995; Nelson, 1997). Such estimates, which are obtained through direct observation of nests discovered in trees or on the ground, tend to be low (i.e., compare results from telemetry studies below). The most frequently reported cause of nest failure was depredation of the egg or chick by a known or presumed avian predator, but other observed outcomes included egg abandonment, chicks falling out of nests, and chicks dying in the nest before fledging (Nelson and Hamer, 1995). In Prince William Sound, murrelet productivity (as gauged by density of recently fledged juveniles at sea) has been studied

Table 4. Marbled Murrelet nesting success based on directly observed outcomes at nest sites in Alaska, British Columbia, Washington, Oregon, and California.

[Condensed from Nelson and Hamer, 1995. **Percent success:** Nest success calculated as percentage of nests fledging a chick of all nests with known outcome. **Source(s):** (1) Quinlan and Hughes (1990); (2) Naslund and others (1995); (3) Nelson and Hamer (1995); (4) Ford and Brown (1995), Ford (1995); (5) Simons (1980), Hirsch and others (1981)]

Location	Years	*n*	Outcome				
			Successful	Failed	Unknown	Percent Success (*n*)	Source(s)
Alaska							
Kelp Bay	1984	1	0	1	0	0 (1)	(1)
Naked Island	1991–92	10	0	7	3	0 (7)	(2)
Kodiak Island	1992	2	0	0	2	–	(2)
Afognak Island	1992	2	0	0	2	–	(2)
Chugach Island	1992	1	0	0	1	–	(3)
Prince of Wales Island	1992–93	2	0	1	1	[1]0 (1)	(4)
East Amatuli Island	1978–79	2	2	0	0	[1]100.0 (2)	(5)
Alaska total		20	2	9	9	18.2 (11)	
British Columbia	1990–93	9	1	0	8	100.0 (1)	(3)
Washington	1991–93	6	3	1	2	75.0 (4)	(3)
Oregon	1990–93	22	3	7	12	30.0 (10)	(3)
California	1989–93	10	2	6	2	25.0 (8)	(3)
Outside–Alaska total		46	9	14	24	39.1 (23)	(3)
All areas total		67	11	23	33	32.4 (34)	(3)

[1] One (failed) nest on Prince of Wales Island and two (successful) nests on East Amatuli Island were ground nests.

in relation to the abundance of prey such as herring and sand lance (Kuletz and others, 1995a; Kuletz and Kendall, 1998, 1999; Kuletz, 2005). The relationship appears to be complex, however, the density of juveniles at-sea generally declined over the course of Kuletz's study despite an increasing trend in fish school abundance, but the highest murrelet productivity occurred when local fish abundance was highest. Kuletz (2005) suggested the association may be non-linear, with a threshold level of local fish abundance required before a consistent and measureable response in murrelet productivity would occur.

Because of the difficulty in finding and monitoring adequate numbers of nests, other approaches have been devised to quantify the nesting success and productivity of Marbled Murrelets. A possible bias arises from sampling nests primarily in accessible locations (Naslund and others, 1995), and there also is the possibility that human observers influence nest outcomes by attracting predators (Naslund and others, 1995). Alternative methods for quantifying nesting outcomes include: (1) radio-telemetry, where the success or failure of nesting attempts is inferred from the behavior of radio-tagged individuals; and (2) counts of recently fledged juveniles at-sea. In the latter case, the value reported usually is a ratio of juveniles to adults counted concurrently on the water during the latter part of the breeding cycle (Andersen and Beissinger, 1995; Ralph and Long, 1995; Kuletz and Kendall, 1998; Lougheed, 1999; Lougheed and others, 2002a).

To date, the most extensive study employing radio-telemetry is work conducted at two locations in British Columbia (Bradley, 2002; Bradley and others, 2004; Zharikov and others, 2006). In a sample of 265 murrelets tagged before or during incubation in 1998–2001, nesting success (laying to fledging in 108 identified nests) was estimated at 48 percent in Desolation Sound (table 5). From a smaller effort in Clayoquot Sound (2000–02), Zharikov and others (2006) determined that 17 of 29 nests (58.6 percent) were successful to the "mid-rearing" stage (chicks surviving through day 20 post-hatch), a value slightly lower but not significantly different from the comparable measure of nesting success (65.7 percent survival to mid-chick stage) in Desolation Sound (Zharikov and others, 2006; table 6).

The strengths of the British Columbia telemetry study included large sample sizes, wide geographic and temporal scope (two study sites observed over several years), and the fact that nests were sampled without pre-selection (i.e., the capture of birds on the water ensured that nests were identified

Table 5. Estimated probability that breeding radio-marked Marbled Murrelets from Desolation Sound, British Columbia (1998–2001) reached successive stages of reproduction.

[From Bradley and others, 2004. *n* = 116]

Stage	Probability of success at each stage		Cumulative probability (Kaplan-Meier estimates)	
	Estimate	95-percent CI	Estimate	95-percent CI
Incubation (= hatching)	0.86	0.79–0.92	0.86	0.79–0.92
Mid-chick	0.81	0.73–0.88	0.69	0.61–0.77
Fledging	0.69	0.63–0.75	0.48	0.41–0.55

Table 6. Nest outcomes (through mid-chick-rearing stage) inferred from activity patterns of radio-marked murrelets in Desolation Sound and Clayoquot Sound, British Columbia, 1998–2002.

[Source of data: Zharikov and others, 2006]

Location	Years	*n*	Outcome	
			Successful (percent)	Failed
Desolation Sound	1998–2001	108	71 (65.7%)	37
Clayoquot Sound	2000–02	29	17 (58.6%)	12

independently of inland locations or accessibility). One weakness was the likelihood of missing an unknown number of early failures, because it was necessary to complete several days of successful radio-tracking to verify nesting behavior (Bradley and others, 2004).

The third approach to measuring murrelet productivity focuses on juvenile (HY) to after-hatching-year (AHY) ratios observed among birds on the water. The standard approach involves counting juveniles and adult-plumaged birds at a strategically chosen time in the breeding season (generally mid-July to mid- or late August in Alaska), and expressing the presumed productivity of the local breeding population as a ratio of the two (HY:AHY). In Alaska, Andersen and Beissinger (1995) found low ratios on five surveys conducted in Auke Bay during July–August 1993. They recorded only 12 juveniles in total, against 940 AHY birds, for a mean ratio of 0.013 (or 0.016 if they restricted their analysis to nearshore transects, where all juveniles occurred). At a number of sites surveyed within Prince William Sound, HY:AHY ratios ranged from 0.02 to 0.08 in 4 years, averaging 0.043 (Kuletz, 2005; table 7). Both studies imply low breeding success. The low values are partly due to the later stage at which HY:AHY ratios are determined—the cohort of juveniles on the water has been reduced to an unknown extent by losses incurred during the act of fledging and by early post-fledging mortality. However, HY:AHY ratios also are subject to several important biases that are difficult to control (Ralph and Long, 1995; Burger, 2002; McShane and others, 2004). The counts of AHY individuals include unknown proportions of subadult nonbreeders. Moreover, juveniles cannot be reliably distinguished from AHY murrelets once the latter have started their pre-basic molt (Carter and Stein, 1995). In Prince William Sound, however, Kuletz and Kendall (1998) found that adults left the area in August, apparently before molting, which thus minimized this source of bias. Additional surveys in Prince William Sound (Kuletz, 2005) showed the same pattern of adult departure prior to pre-basic molt. In Alaska, fledglings typically stay closer to shore than do adults (Andersen and Beissinger, 1995; Kuletz and Kendall, 1998), and differential movements of juveniles and AHY birds into or out of surveyed areas is a known problem (see Post-Breeding Dispersal).

Variations and refinements have been proposed as improvements on the standard "concurrent" HY:AHY ratio. Kuletz and Kendall (1998) found that a "sequential" ratio of HY density in July–August and AHY density measured in June produced an index that was more consistent among survey sites than a concurrent ratio taken in July–August. They advised sequential ratios whenever feasible, but recognized that the method may not be available to all workers because of the added time and expense required to obtain the additional data. Sequential ratios in Prince William Sound ranged from 0.03 to 0.26 juveniles per adult, averaging 0.098 in 4 years (table 7). As an alternative to either type of ratio, a simple count of juveniles within a suitably defined area may provide a useful index of production that avoids the problem of AHY dispersal during surveys (Kuletz and Kendall, 1998; Kuletz, 2005; table 7).

In British Columbia, Lougheed and others (2002a) obtained a sequential ratio (à la Kuletz and Kendall, 1998) that also corrected for the turnover of juveniles and proportion of the fledging period covered by the surveys. The refinement required information on the dispersal of radio-tagged HY birds, so widespread adoption of their approach is unlikely. The "corrected" ratios for Desolation Sound averaged three times higher than simple concurrent ratios in 3 years, 1996–98 (0.131 vs. 0.042), but they still were lower than measures of productivity obtained from nest monitoring.

Juvenile murrelets may at times congregate in "nursery areas" (Kuletz and Piatt, 1999), a behavior that would lend itself to better monitoring of year-class strength if the locations

Table 7. Marbled Murrelet abundance and productivity at three sites in Prince William Sound, Alaska.

[Data from Kuletz (2005). Means (±SE) are shown for adult densities (birds/km^2) in June (incubation phase) and July 18–August 10 (early fledging period). Juvenile densities are shown for July 27–August 24 (when sites had reached 75th percentiles) and for the core surveys (five highest juvenile counts), Concurrent ratio: Early fledging period was used to minimize the effect of post-breeding adult dispersal. Sequential ratios: Mean core juvenile density divided by the mean June adult density was used, providing one value per year]

Year	Site	June surveys		July 18–August 10				July 27–August 24		Core surveys (*n*=5)		Sequential ratio	
		n	Adult density	*n*	Adult density	Concurrent ratio	Mean ratio	*n*	Juvenile density	Juvenile density	Mean	Site/year	Mean
1995	Galena	3	5.87 (1.53)	5	10.69 (1.55)	0.02 (0.01)	0.04	5	0.23 (0.07)	0.23 (0.07)	0.98	0.04	0.08
	Naked	4	13.10 (3.63)	5	22.26 (2.37)	.06 (0.02)		6	1.47 (0.28)	1.67 (0.25)		0.13	
	Jackpot	4	16.58 (1.31)	5	18.71 (2.62)	.04 (0.01)		5	1.02 (0.17)	1.04 (0.16)		0.06	
1997	Galena	3	15.55 (7.60)	4	34.12 (12.4)	.04 (0.02)	0.04	6	0.64 (0.08)	0.68 (0.09)	0.96	0.04	0.03
	Naked	3	65.50 (15.32)	4	29.83 (7.02)	.05 (0.02)		6	1.38 (0.14)	1.51 (0.05)		0.02	
	Jackpot	3	33.05 (1.69)	5	12.71 (2.73)	.04 (0.02)		6	0.58 (0.18)	0.68 (0.19)		0.02	
1998	Galena	3	11.86 (2.92)	4	6.59 (2.09)	.02 (0.01)	0.03	5	0.19 (0.07)	0.19 (0.07)	0.65	0.02	0.03
	Naked	3	28.19 (3.84)	4	23.90 (3.02)	.06 (0.03)		6	1.23 (0.30)	1.37 (0.32)		0.05	
	Jackpot	3	17.65 (1.88)	4	21.10 (5.95)	.02 (0.01)		7	0.26 (0.06)	0.38 (0.05)		0.02	
1999	Naked	5	3.16 (1.04)	4	13.93 (1.08)	.08 (0.02)	0.06	6	1.07 (0.25)	1.42 (0.15)	0.95	0.45	0.26
	Jackpot	6	6.37 (1.12)	4	15.16 (2.76)	.04 (0.01)		7	.39 (0.09)	0.48 (0.11)		0.07	

and temporal use of such areas were adequately known. The only described example is from Kachemak Bay, where HY murrelets occurred at high densities on 2 of 10 transects (Kuletz and Piatt, 1999). Within the "nursery" itself, juveniles outnumbered AHY birds in a ratio of 1.3 to 1 (table 8). That is obviously an index of an altogether different kind than the standard HY:AHY ratios reported elsewhere. Nursery areas have not been identified at other locations in Alaska (Kuletz, 2005). In British Columbia, concurrent HY:AHY ratios from 0.2 to 0.4 occurred in some years off southwestern Vancouver Island (Bellefleur and others, 2005). Those are higher values than reported from anywhere else outside of Kachemak Bay, suggesting a possible, if less pronounced, "nursery" effect.

Of the several methods available to gauge the reproductive success of Marbled Murrelets, radio-telemetry seems to offer the best means of characterizing breeding success accurately and with reasonable efficiency. Such data are vital for demographic analyses, but much work remains to be done to refine the estimates, especially in Alaska. HY:AHY ratios will continue to be important as indices of productivity because they are relatively easy and inexpensive. In some situations, it may be possible to calibrate the information from at-sea surveys against other, more direct measures of nesting success, but a substantial commitment of resources will be required.

Table 8. Number of adult and juvenile Marbled Murrelets counted on survey routes in Kachemak Bay, Alaska, August 1996.

[From Kuletz and Piatt (1999). Survey segments i and j were perceived as "nursery area" for juvenile murrelets]

Location/segment	Date	Number of murrelets		Ratio
		Adults	Juveniles	
Inner Bay				
Segment a	13	72	0	0
Segment b	24	83	1	0.012
Segment c	13	19	0	0
Segment d	24	12	1	0.083
Inner Bay total		186	2	0.011
Outer Bay				
Segment e	13	37	1	0.027
Segment f	7	43	2	0.047
Segment g	7	7	3	0.429
Segment h	12	3	0	0
Segment i	12	7	23	3.286
Segment j	23	34	30	0.882
Outer Bay total		131	59	0.450
Total		317	61	0.192

Timing of Breeding

Marbled Murrelets have an asynchronous and protracted breeding season (Lougheed and others, 2002b). At a given nest, incubation lasts from 28 to 30 days and chick fledging occurs from 27 to 40 days after hatching (Hirsch and others, 1981; Nelson, 1997). Hamer and Nelson (1995) assumed modal values of 30 days for incubation and 28 days for chick age-at-departure in back-calculating or projecting the timing of events in the nesting cycle from observations of laying, hatching, nestling development, or fledglings at-sea. Their compilation of observed and calculated events for 86 nesting attempts from Alaska to California reveals a breeding period (first laying to last fledging) of about 106 days in Alaska—mid-May through late August or early September (fig. 2). Hatching begins around June 15 and the earliest juveniles arrive on the water in mid-July. A latitudinal cline is evident, with Alaska murrelets having a shorter and later breeding season than do populations to the south. Hamer and Nelson (1995) estimated that the overall breeding season averages 64 days fewer in Alaska than in California.

Few data on the breeding phenology of murrelets in Alaska have emerged since the summary depicted in figure 2 was prepared by Hamer and Nelson (1995). During at-sea surveys in Prince William Sound, Kuletz and Kendall (1998) noted a peak in fish-holding (i.e., chick-provisioning) adults on July 26, which agrees closely with the median date for chick-rearing in figure 2. The peak of fledging appeared to occur during the first or second week of August in 4 years (Kuletz, 2005), suggesting the median date is a week or two later in Prince William Sound than is depicted in figure 2. Newly fledged birds were seen as early as July 4 in Southeast

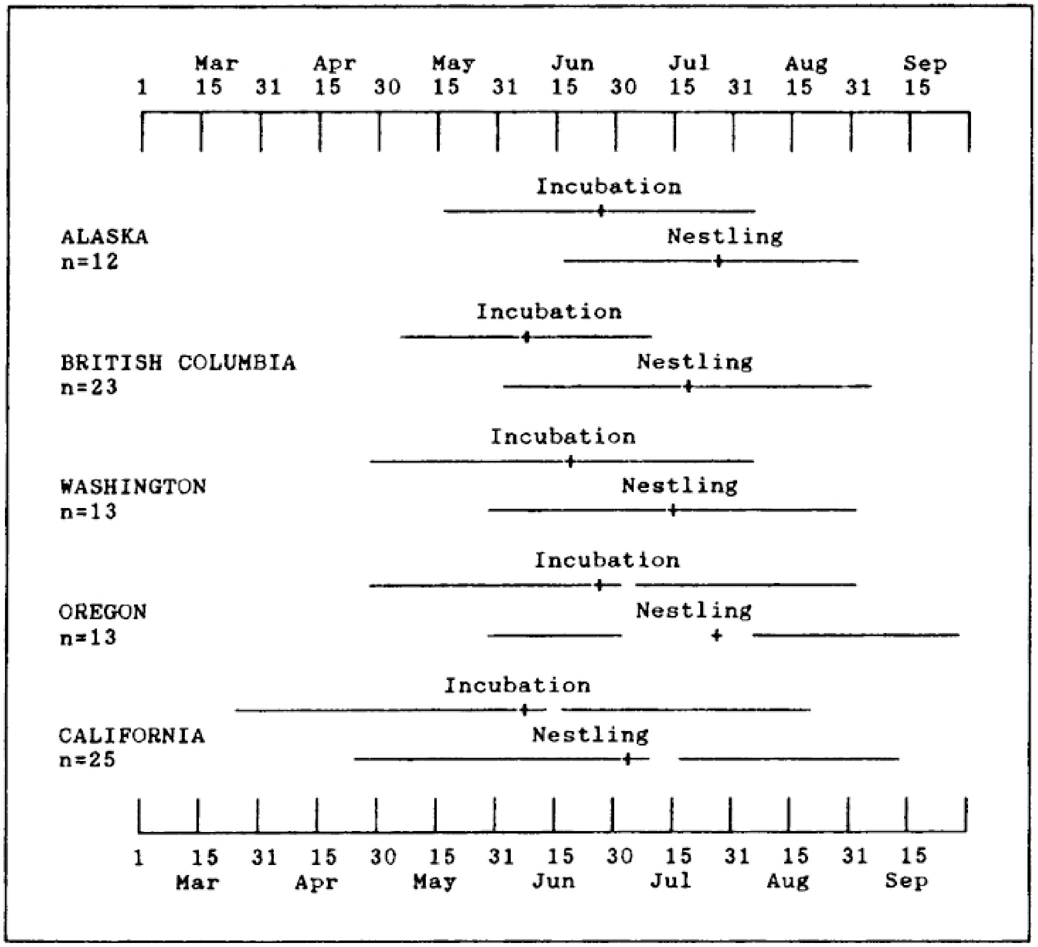


Figure 2. Breeding phenology of Marbled Murrelets from Alaska to California showing estimated onset, median dates, and endpoints of the incubation and nestling periods (from Hamer and Nelson, 1995).

Alaska (Doerr and Walsh, 1994) and in Kachemak Bay (K. Kuletz, U.S. Fish and Wildlife Service, unpub. data, 2004–06). Speckman and others (2000) inferred breeding phenology from the timing and behavior of adults and juveniles on the water in Auke Bay and Fritz Cove near Juneau. Their summary (fig. 3) corroborates in general the conclusions of Hamer and Nelson (1995; fig. 2), although it suggests that breeding commences in the first week of May in some locations or seasons in Alaska. Speckman and others (2000) estimated that breeding began about 19 days earlier in 1993 than in 1992, indicating that considerable interannual variation in nesting phenology can be expected. In Prince William Sound, the date when 50 percent of the season's juveniles were counted generally varied consistently among three sites (45–90 km apart) by as much as 1 to 2 weeks, suggesting local environmental influences on phenology (Kuletz, 2005). Elsewhere, McFarlane Tranquilla and others (2003c, 2005) reported annual variation of about 10 days in the onset of nesting by murrelets in Desolation Sound. The same study found that nesting began about 1 month earlier in Desolation Sound, a mainland site, than in Clayoquot Sound on the west coast of Vancouver Island (McFarlane Tranquilla and others, 2005). Thus, although the breeding phenology of murrelets at the northern end of their range has been documented in general, additional work in Alaska may discover interannual and among-site variation beyond what is currently known.

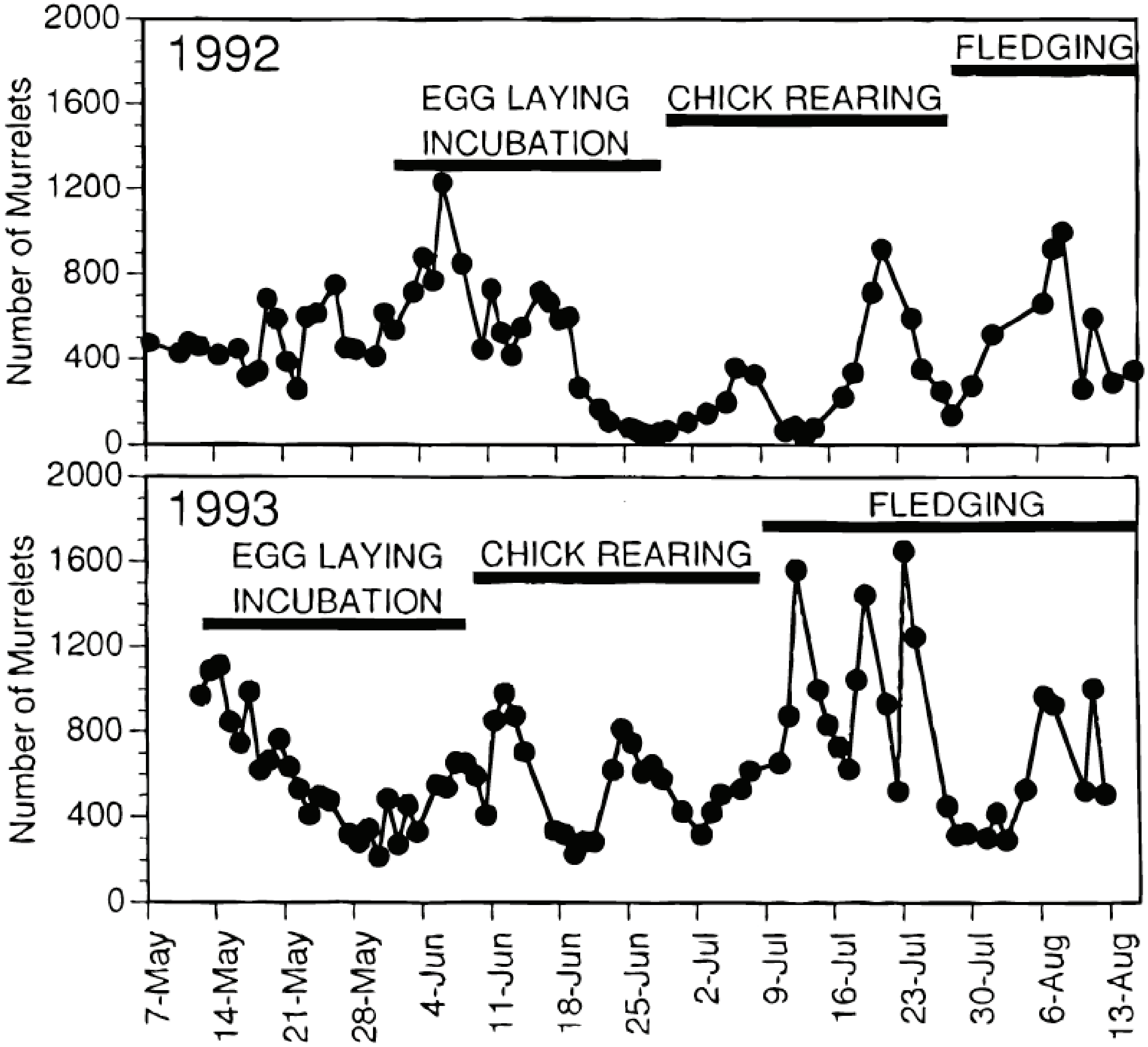


Figure 3. Breeding phenology of Marbled Murrelets in Southeast Alaska deduced from observations of fish-holding adults and chicks at-sea (from Speckman and others, 2000).

Post-Breeding Dispersal

Marbled Murrelets are common to abundant throughout the year over most of their range in Alaska (Mendenhall, 1992; DeGange, 1996). However, major shifts in seasonal distribution occur, primarily from the northernmost portions of the breeding range to wintering areas farther south. In Prince William Sound, numbers declined nearly 80 percent between summer and the nonbreeding period (Klosiewski and Laing, 1994; Agler and others, 1999), and a marked exodus in winter also is reported for Glacier Bay (DeGange, 1996). Piatt and Ford (1993) suggested that many murrelets from Prince William Sound winter in the Kodiak Archipelago or along the Alaska Peninsula, where numbers increase in the nonbreeding period (Forsell and Gould, 1981; Zwiefelhofer and Forsell, 1989; Piatt and Naslund, 1995). Murrelets favor sheltered waters such as bays and fjords in winter, but some seaward movement also occurs, as individuals are seen as much as 300 km offshore in the Gulf of Alaska (Piatt and Naslund, 1995).

Kuletz and Marks (1997) tracked the movements of a radio-tagged juvenile murrelet for 2 weeks after it departed its nest in Prince William Sound (Port Nellie Juan). The bird initially moved about 12 km from the nest site, then remained in a confined (12 km^2) area of nearshore waters for the duration of the study. During surveys at several additional sites in Prince William Sound, Kuletz and Kendall (1998) determined that recently fledged murrelets remained in nearshore waters for several weeks, whereas the post-breeding adult population rapidly vacated the area during the same period. A similar pattern may occur in Southeast Alaska, where radio-tagged adults from the Port Snettisham area moved as much as 200 km north and 160 km south in the early postbreeding dispersal period, July–August (Newman and others, 2006). Age-specific timing of dispersal may vary by location, because a different pattern—rapid juvenile dispersal and adult residency near the breeding sites through late summer—was reported for Desolation Sound, British Columbia (Lougheed, 1999). However, the apparent difference in juvenile behavior was likely due in part to a difference in scale between the relatively large survey areas in Alaska and the smaller, fjord area examined in British Columbia (Kuletz, 2005).

Site Fidelity and Natal Dispersal

Nest sites of Marbled Murrelets often go unused in consecutive years, possibly as a way of reducing the likelihood of detection by predators (Divoky and Horton, 1995). Consistent use of the same or nearby nest trees is well-documented, however, which suggests a high degree of fidelity to a given locality by nesting murrelets in different years (Naslund and others, 1995; Nelson, 1997; Manley, 1999). On Naked Island (Prince William Sound), Naslund and others (1995) found no indication that five nest sites located in 1991 were reused the following year, although observations of murrelets using the same trees for landing or nesting in both years confirmed the pattern of repeated activity in a given vicinity. Because adult murrelets have not been banded at the nest, it remains an assumption that reuse of the same trees involves one or both of the same individuals.

There are too few data—and none from Alaska—to say anything definitive about natal dispersal in Marbled Murrelets. In the long-term study in Desolation Sound, only 2 of 106 murrelets banded as nestlings were recaptured in subsequent years, suggesting that most young murrelets emigrated to other areas to breed (Lank and others, 2003). Divoky and Horton (1995) reasoned that natal dispersal may be high in Marbled Murrelets considering the overlap between their wintering and breeding areas, the distances that individuals are known to move in winter, and the fact that murrelet nesting is dispersed over a wide band of forest habitat extending at least 60 km inland from the coast.

Overwinter Occupation of Nesting Habitat

Marbled Murrelets may be unique among alcids in Alaska in that at least some individuals visit their nesting habitats during most months of the year. The behavior is best documented for Southeast Alaska (Doerr and Walsh, 1994; DeGange, 1996; Brown and others, 1999), but also has been observed in Chiniak Bay, Kodiak Island (Dick, 1979). From December 1992 through November 1996, Brown and others (1999) conducted dawn surveys at 2-week intervals at four sites within the Alexander Archipelago. Excluding a 2 month hiatus in September and October, when no birds occurred inland, and another period of reduced activity in April, murrelets were detected on 90 percent of surveys conducted throughout the year. The two periods of relative inactivity corresponded to the murrelets' complete Pre-Basic molt in the autumn and their Pre-Alternate molt in the spring (Carter and Stein, 1995). The number of detections per survey was lower by one-half or more in winter as compared to peak numbers in July and August, but forest visitation was fairly consistent during all nonbreeding months that were unconstrained by molt. The patterns observed in Alaska closely parallel those reported by Naslund (1993), who studied the year-round attendance of murrelets in old-growth forests of central California. Naslund (1993) suggested that winter occupation of nesting habitat may be important for retention of nest sites and pair bonds.

Natural Mortality

Disease

Information on the kinds and incidence of diseases experienced by Marbled Murrelets is lacking, both in Alaska and elsewhere in the species' range. Newman and others (1997) analyzed the blood of 11 murrelets collected in the Shumagin Islands, and reported reference ranges for standard parameters of hematology and plasma biochemistry in presumed healthy individuals. That information may prove useful for the future detection and characterization of disease in this species.

Predation

Current knowledge of predator effects on Marbled Murrelets in Alaska is briefly summarized below. Readers should refer to the section, "Nesting Habitat: Characteristics Threats and Trends," for more information on predator-prey interactions involving Marbled Murrelets.

Predation on adult murrelets, eggs, and nestlings is well-documented outside of Alaska (Nelson and Hamer, 1995; Nelson, 1997; Burger, 2002; Burger and others, 2004c; McShane and others, 2004). Known or suspected avian predators on adults include Bald Eagles, Peregrine Falcons (*Falco peregrinus*), Northern Goshawks (*Accipiter gentilis*), Sharp-shinned Hawks (*A. striatus*), and Common Ravens. Common Ravens, Steller's Jays, Northwestern Crows (*C. caurinus*), Sharp-shinned Hawks, and Great Horned Owls (*Bubo virginianus*) are likely nest predators that occur commonly within the Alaska breeding range of Marbled Murrelets. Nest predation by mammals is unconfirmed but strongly suspected. Potential mammalian predators in Alaska include forest mustelids (marten, *Martes americana*, and fisher, *M. pennanti*), red squirrels (*Tamiasciurus hudsonicus*), mice (*Peromyscus* spp.), and raccoons (*Procyon lotor*; Nelson, 1997; Raphael and others, 2002b; Bradley and Marzluff, 2003).

Direct or indirect observations of murrelet depredation in Alaska are few. Marks and Naslund (1994) witnessed one incident of a female Sharp-shinned Hawk killing an adult murrelet at or near its nest site on Storey Island in Prince William Sound. Based on damaged eggshells remaining in failed nests, Naslund and others (1995) believed Steller's Jays were likely predators at several nests on nearby Naked Island.

Burger (2002b) summarized unpublished data supplied by the State of Alaska (S. Lewis, Alaska Department of Fish and Game, 2001–01) on the occurrence of Marbled Murrelets in the prey remains of Northern Goshawks in Southeast Alaska. Murrelets composed 2.8 percent of the material collected at goshawk nests (10 of 361 prey remains) and 3.1 percent of prey items identified in pellets (12 of 382). Murrelets were only 0.8 percent of all prey deliveries (11 of 1,451) at goshawk nests, but were brought at least once to 6 of 10 nests observed. Iverson and others (1996) reported as much as 20 percent frequency of occurrence of alcids (mostly Marbled Murrelets) in goshawk nests in the Tongass National Forest as a whole. Ralph and others (1995b), citing a personal communication from Jeff Hughes (Alaska Department of Fish and Game), noted that murrelet wings were the most common prey remains found at Peregrine Falcon nests in coastal Alaska.

Nelson and Hamer (1995) proposed that murrelets become more vulnerable to predators as a result of habitat fragmentation and the creation of forest "edge" habitat through clear-cutting. They suggest this as an explanation for lower nesting success in sites located closer to forest edges. Follow-up work by Burger and others (2004c) on Vancouver Island found that predation risk at Marbled Murrelet nests was higher near clearcuts and roads than in interior forests, and higher in fragmented landscapes than in relatively intact old-growth forests. In contrast, however, Zharikov and others (2006) concluded that murrelets bred as successfully in forests fragmented by logging as they did in undisturbed habitats.

Population Genetics

In this section, we briefly review the literature on population genetic variation in Marbled Murrelets, and present new information that includes analysis of birds from locations in Washington and Oregon. The result of this new analysis is a more complete picture of the population genetics of the species.

Background

Several studies of genetic variation have been published for Marbled Murrelets. Pitocchelli and others (1995) analyzed restriction fragment length polymorphisms in mitochondrial DNA (mtDNA) from murrelets collected from tree- versus ground-nesting ecoregions in Alaska; they found no evidence of differentiation between the two types. Subsequently, Friesen and others (1996b) compared variation in the mitochondrial cytochrome *b* gene and 39 allozyme loci from 43 birds sampled between the western Aleutian Islands and Oregon. They reported evidence for low but significant population genetic structure, but could not determine how the populations differed. Based on variation in nine nuclear introns in 120 birds from the western Aleutian Islands to southern British Columbia, Congdon and others (2000) found that murrelets from mainland Alaska and British Columbia are similar, but differ from those in the western and central Aleutian Islands. Most recently, Friesen and others (2005) surveyed variation in four introns and three microsatellite loci from murrelets from Alaska, British Columbia and California. They reported significant differentiation of birds from peripheral sites, i.e., California and the Aleutian Islands, but little genetic structuring in the central area. Friesen and others (2005) also analyzed variation in a 547 base pair (bp) fragment of the mitochondrial control region, and found significant population genetic structure as well as weak phylogeographic structure (i.e., geographical segregation of related genotypes). Both Congdon and others (2000) and Friesen and others (2005) found evidence for a genetic cline, and Friesen and others (2005) argued for the recognition of three to five genetic management units. However, these studies were limited in the number of either sites (Congdon and others, 2000) or loci (Friesen and others, 2005) that were sampled.

New Analyses Using Samples from Washington and Oregon and Multiple Loci

A definitive analysis of population genetic structure in Marbled Murrelets requires a range-wide sampling of birds and analysis of multiple genetic loci. With this objective in mind, we recently completed an analysis of variation in 9 nuclear introns and 15 microsatellites for 282 murrelets sampled from throughout the species' range, i.e. the western Aleutian Islands to central California (Friesen and others, Queens University, unpub. data, 2006). Here we incorporate previously published intron data for murrelets from Alaska, British Columbia, and California (Congdon and others, 2000; Friesen and others, 2005) with new data on intron variation for murrelets from California, Oregon, Washington, and Unalaska Island, and new microsatellite data for all samples. Combining results from mtDNA, rapidly evolving microsatellites, and more slowly evolving introns permits analysis of recent as well as more ancient population parameters. We apply both traditional and state-of-the-art methods of data interpretation to estimate the extent of genetic differentiation and gene flow among birds from multiple sampling sites. This study constitutes the most comprehensive genetic analysis of Marbled Murrelets to date, and provides a robust picture of global genetic structuring of the species.

Methods

Sampling

The present data set includes DNA samples from 282 birds collected between 1989 and 2005 (fig. 4). Sampling for Alaska, British Columbia, and California was described in detail previously (Congdon and others, 2000; Friesen and others, 2005). Briefly, solid tissue was sampled from murrelets collected (under USFWS permit) for dietary analysis in Alaska between 1989 and 1995. Breeding status was determined after collection from total external evidence (plumage [adult vs. subadult or juvenile] and brood patch [usually but not always partially or fully developed during breeding season]), and internal evidence (Bursa of Fabricus present or absent, development of gonads, evidence for recent passing of egg [expanded oviduct], or presence of egg). All but four specimens used for genetic analyses were determined to be breeders. For British Columbia and California, blood samples were collected from birds caught for banding and/or telemetry between 1996 and 2004. Recently, we obtained samples from 33 birds from Washington and 18 birds from Oregon. These samples comprised blood or solid tissue collected either from individuals netted at-sea at night or from carcasses on beaches between 1990 and 2005. All these samples were from adults with brood patches and/or were collected during the breeding season (May through August).

DNA Preparation

DNA was prepared using standard proteinase k/phenol/chloroform extraction (Sambrook and others, 1989) or DNeasy kits® (Qiagen, Mississauga, Ontario). For the former method, approximately 20 mg solid tissue or the equivalent of 5 µL of whole blood was incubated for 4 hr at 65ºC in 500 mL of buffer containing 100 mM Tris pH 8.0, 100 mM NaCl, 10 mM EDTA, 0.1 percent SDS, and 0.2 mg proteinase k. Tissue digests were then extracted twice with equal volumes of Tris-saturated phenol (pH 8.0) and once with chloroform/isoamyl alcohol (24:1). DNA extracts were diluted 10-fold with distilled water before use. DNeasy preparations were done according to the manufacturer's instructions.

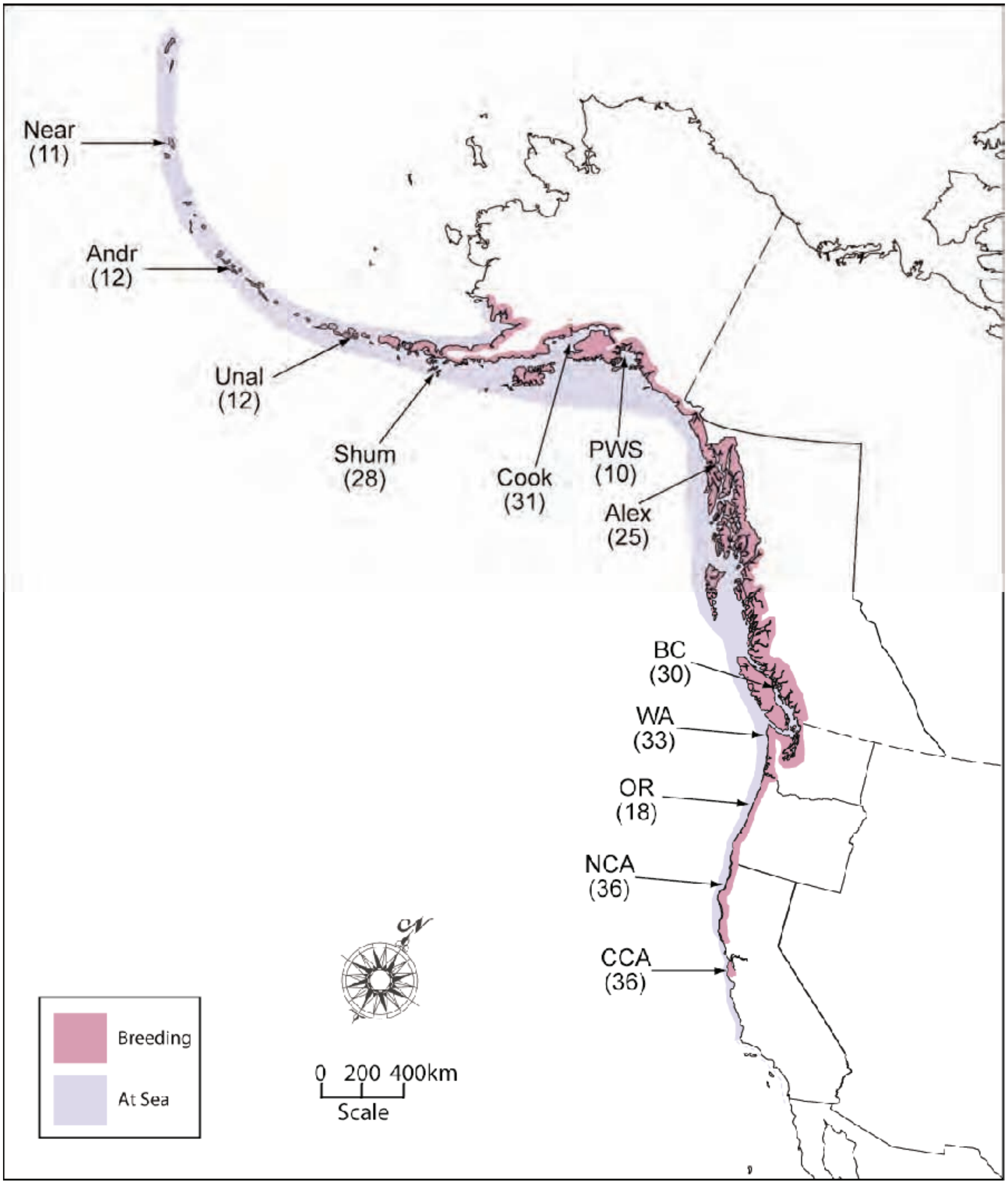


Figure 4. Approximate breeding distribution (shaded coastal areas), and origins and numbers of Marbled Murrelets sampled for genetic analyses.

Introns

Variation in introns was assessed using analysis of single-stranded conformational polymorphisms (SSCPs) and direct sequencing (Friesen and others, 1997, 1999, 2005; Congdon and others, 2000; table 9). Polymerase chain reaction (PCR) amplifications were done in 15 µL volumes containing 10 mM Tris pH 8.4, 50 mM KCl, 1.5 mM $MgCl_{2,}$ 0.01 percent gelatin, 0.06 mg/mL bovine serum albumin, 0.2 mM dNTPs, 1 µCi ^{33}P-α-dATP, 0.4 µM each primer, and 0.5 units *Taq* DNA polymerase (Qiagen). Products were subjected to electrophoresis through 0.5 percent MDE® (J.T. Baker) nondenaturing acrylamide gels at 4ºC. Tentative genotypes were assigned, and samples were ordered by genotype and rerun to confirm scoring. Representative individuals that were homozygous for common alleles, individuals with unique alleles, and individuals with ambiguous genotypes were re-amplified without ^{33}P-α-dATP, and PCR products were sequenced either manually with Thermosequenase® kits (GE Healthcare, Montreal, Quebec) according to the manufacturer’s suggested protocol, or using an automated platform (3730XL DNA Analyzer®, Applied Biosystems) operated by Genome Quebec (McGill University, Montreal, Quebec). *Tropomyosin* did not amplify reliably, and so was excluded from all analyses. Introns also did not amplify reliably for samples from Unalaska Island due to sample degradation; this site was therefore excluded from population-level analyses involving introns. Note that sample sizes for the Andreanof Island also are low for introns.

Hayashi (1991) reported that analysis of SSCPs detects about 99 percent of sequence variation for DNA fragments about 100–300 bp in length and about 89 percent of variation for fragments 300–450 bp in length. Previously, we reported that analysis of SSCPs missed one bp substitution in one of ten Marbled Murrelets screened for a about 500 bp fragment of cytochrome *b* (Friesen and others, 1996b). To determine the level of undetected variation in the present study, we compared genotype scores from direct sequencing with genotype scores from SSCPs for 37 birds representing ten genotypes for *OD*. (Note that *OD* is the largest intron analyzed.) Only one new allele was found among 74 screened. Whereas, this level of undetected variation may lead to slight underestimates of effective population size (that we deliberately did not generate in the present study), it should have minimal effect on indices of population differentiation.

Microsatellites

Microsatellite loci were amplified using PCR buffers and cycle profiles given in Ibarguchi and others (2000) and annealing temperatures from Rew and others (2006; table 9). Briefly, reactions were conducted in 10–15 µL reaction volumes under standard conditions after one PCR primer was end-labeled with ^{33}P-γ-dATP. PCR products were subjected to electrophoresis through 6 percent denaturing polyacrylamide gels and visualized on X-ray film. Allele sizes were determined using sequencing ladders as standards. This ‘manual’ approach tends to be more repeatable and accurate than capillary-based automated methods because it is not affected by differences in running conditions (e.g., gel density) between capillaries. ‘Stuttering’ was minor. A subset of 26 samples from central California also was analyzed at the University of California on an automated sequencer using Rew and others (2006) protocols; genotype scores were identical to those obtained manually. Variability for *Bma14b29* did not fit the usual pattern for a microsatellite: only three alleles were found (one of which occurred only in homozygous form in a single individual), and alleles did not differ by 2 bp as expected for a dinucleotide repeat. This locus was therefore eliminated from further analyses.

Table 9. Genetic loci, PCR primer sequences, and annealing temperatures employed in Marbled Murrelet population genetic analysis.

Locus	Primer Sequences	Annealing temperature
	Introns	
Ald[1]	F: 5’-ATCATCAAAGAAAAAGGCATGGTGGTGGG-3’ R: 5’-AGCACCATCTTTCTTGTACTGGGCACAGCG-3’	59ºC
Enolase[1]	F: 5’-CCAGGCACCCCAGTCTACCTGGTCAAA-3’ R: 5’-TGGACTTCAAATCCCCCGATGATCCCAGC-3’	60ºC
Gpd[1]	F: 5’-CATCAAGTCCACAACACGGTTGCTGTA-3’ R: 5’-ACCTTTAATGCGGGTGCTGGCATTGC-3’	65ºC
LDH[2]	F: 5’-GGAAGACAAACTAAAAGGAGAAATGATGGA-3’ R: 5’-TTCCTCTGAAGCAGGTTGAGACGACTCTC-3’	57ºC
Lamin[1]	F: 5’-CTGCCGCCCGTTGTCGATCTCCACCAG-3’ R: 5’-CCAAGAAGCAGCTGCAGGATGAGATGC-3’	70ºC
MPP[2]	F: 5’-TTGCAGATGGAGAGCAGGTTGGAGCC-3’ R: 5’-TACATCTACTTTAACACCTGGACCACCTG-3’	65ºC
OD[2]	F: 5’-GACTCCAAAGCAGTTTGTCGTCTCAGTGT-3’ R: 5’-TCTTCAGAGCCAGGGAAGCCACCACCAAT-3’	72ºC
RP40[2]	F: 5’-GCTTTCTCAGCAGCAGCCTGCTC-3’ R: 5’GGGCCTGATGTGGTGGATGCTGGC-3’	65ºC
Tropomyosin[2]	F: 5’-CGGTCAGCCTCTTCAGCAATGTGCTT-3’ R: 5’-GAGTTGGATCGGGCTCAGGAGCG-3’	72ºC
	Microsatellites	
Cco5-21[3]	F: 5’-TCAAGATGATGAAGACCCTAAT-3’ R: 5’-AGAGTTGCACAGGTTAAATACC-3’	52ºC
Bma10-18[3]	F: 5’-GGTAGGAGCGGAGTAGGAGG-3’ R: 5’-GCAAAATAAGGGTGAAGGCA-3’	60ºC
Ulo14b29[4]	F: 5’-GTATTATGTTCCGGAAAACTGT-3’ R: 5’-TACCCCTATATACAAACCCAAG-3’	57ºC
Bma301[5]	F: 5’-AGATCTATCCCTTGGCTGGA-3’ R: 5’-TATCTGCCAAAATCTGCTGAA-3’	59ºC
Bma356[5]	F: 5’-GTCCACTGAGTTTAGCAGCAA-3’ R: 5’-TGCAGCTCACTATACCAAGGA-3’	58ºC
Bma365[5]	F: 5’-GCTTTATCTGTGGCAACACTG-3’ R: 5’-GCTGTAGGGAGGATATGATGC-3’	62ºC
Bma368[5]	F: 5’-AATCACCAAGGATAAAGGATGATA-3’ R: 5’-AGGGGACCTGCCCATATATTA-3’	62ºC
Bma371[5]	F: 5’-GTCCCCTTTCTAACAGGCACT-3’ R: 5’-GTAAAGGTGGGGGAGCATATT-3’	62ºC
Bma433[5]	F: 5’-TCAGAAGATCCTTCTCCCTCA-3’ R: 5’-CCAAAGGCCAAAGAATGATTA-3’	59ºC
Bma439[5]	F: 5’-GAGGGGAGGGTGTATCTTTTC-3’ R: 5’-ATGTCACTCTGGTGGAGAACC-3’	62ºC
Bma443[5]	F: 5’-TGCCAGGCCATCTACTTTAAT-3’ R: 5’-GCTTATCTTTCCCTCCATCCT-3’	59ºC
Bma453[5]	F: 5’-TCCTCCACATGTTTTGCAGTA-3’ R: 5’-CAGGAGCACCATGTATGTTTG-3’	59ºC
Bma523[5]	F: 5’-TGAATCCAGTGGAACAAAACA-3’ R: 5’-AATGAACTAATGAGGGCGATG-3’	59ºC
Bma553[5]	F: 5’-TTGTGAGAGGGTCACTTATCAAAT-3’ R: 5’-CATCTCTCTTTCAGAAGAGCAGTC-3’	59ºC
Bma555[5]	F: 5’-GACAGAATATAAATGGAGACATGG-3’ R: 5’-AGGCAGAGATGAGAAGGCTAA-3’	59ºC

[1] Friesen and others, 1997.

[2] Friesen and others, 1999.

[3] Friesen and others, Queens University, unpub. data, 2005–06.

[4] Ibarguchi and others, 2000.

[5] Rew and others, 2006.

Population Genetic Structure

Genotype frequencies were tested for deviations from Hardy-Weinberg expectations and for evidence of inbreeding (significantly negative F_{IS} estimates) within sampling sites by randomization (10,000 replications) using ARLEQUIN (version 3.1; Schneider and others, 2000) and FSTAT (version 2.9.3.2; Goudet, 1995), respectively. Multilocus genotypes also were tested for linkage disequilibrium within sampling sites using ARLEQUIN with 10,000 permutations of the data.

For introns, global (species-wide) and pairwise estimates of population differentiation were indexed using Φ_{ST}, an analog of Wright's F_{ST} that incorporates sequence differences among alleles. Wright's F_{ST} (assuming an infinite alleles model of sequence evolution) also was used because: (1) no currently available program can incorporate sequence variation for multiple loci into an analysis of molecular variance; (2) most intron alleles differ by only one or two substitutions (see Results); and (3) pairwise estimates of Φ_{ST} were similar to pairwise estimates of F_{ST} for individual introns (see Results). Whereas an analogue of Wright's F_{ST} that incorporates stepwise mutations has been developed for microsatellites (R_{ST}; Slatkin, 1995), F_{ST} was used to index population differentiation for murrelets because the latter index is preferable when the number of samples and/or loci is moderate to small, as in the present study (Gaggiotti and others, 1999). All estimates were tested for significance by randomization (10,000 replications).

To test for isolation by distance, the shortest geographic distance between sampling sites was estimated using either the most common sampling site (e.g., Dutch Harbor for Unalaska Island) or the mid-point of mutliple sampling sites (e.g., the mid-point of Kachemak Bay and Shuyak Island for Cook Inlet). The correlation between genetic distance (Wright's linearized F_{ST}) and the natural logarithm of geographic distance was assessed using Mantel's tests as implemented in ARLEQUIN with 1,000 randomizations of the data.

To help determine the nature of population genetic structure in Marbled Murrelets, genetic variation was analyzed using the program STRUCTURE, which uses a Bayesian approach to find the grouping of individuals that minimizes deviations from Hardy-Weinberg and linkage equilibrium (Pritchard and others, 2000). The program was run under the admixture model with correlated allele frequencies, a burn-in of 5,000 iterations, and 50,000 replications after the burn-in. (These numbers were first determined to be sufficient for likelihood values to stabilize.) Sampling location was not used as *a priori* information. Each value of *k* (number of populations) between 1 and 12 was run six times, and significance was calculated from the posterior probabilities following the protocols suggested by Pritchard and Wen (2003) and Evanno and others (2005). Note that this program makes no assumptions about the mutation model of the markers, so data for introns and microsatellites were pooled.

Contemporary Gene Flow

Estimation of gene flow from F_{ST} or its analogues is not valid for this species because: (1) populations may not have attained equilibrium between migration and genetic drift following recession of the Pleistocene glaciers; (2) gene flow may not be symmetrical and may not follow an *n*-island model; (3) effective population sizes may not be equal and stable; and (4) mutation rates are high for several molecular markers (especially the microsatellites; Hedrick, 1999). Use of the program MIGRATE (Beerli and Felsenstein, 1999) also is not valid because populations may not be in migration/drift equilibrium. We attempted to estimate contemporary migration rates using a maximum likelihood based Bayesian approach (specifically, using the program BAYESASS; Wilson and Rannala, 2005), but reliable results could not be obtained, probably because of high gene flow within the central part of the species' range (see Results). We therefore used probabilities of assignment from STRUCTURE as a first approximation of contemporary gene flow.

Results

Genetic Variability

All loci were variable, with the number of alleles per locus ranging from 5 (*Ald*) to 35 (*Bma453*; table 10). Most intron alleles differed by only one or two substitutions (Congdon and others, 2000; Friesen and others, Queens University, unpub. data, 2006). Significant heterozygote deficiencies were found for *Ald* in British Columbia, Washington, and northern California samples (table 10), suggesting the possible existence of a null (non-amplifying) allele. Further analyses were therefore conducted both with and without this locus; results are reported without *Ald*, but do not differ qualitatively if *Ald* was included. Otherwise, only two heterozygote deficiencies were found (table 10).

Table 10. Sample sizes (*N*), allele frequencies, allelic richness estimates (A_R, corrected for the minimum per-locus sample size), observed and expected heterozygosities (H_0 and H_E, respectively) and Wright's inbreeding coefficients (F_{IS}) for 23 loci within 12 populations of Marbled Murrelets.

[Heterozygosity estimates in bold indicate significant deviations from Hardy-Weinberg expectations. Inbreeding coefficients in bold are significantly less than zero. Blank cells indicate allele not found. Population abbreviations as in figure 4]

Locus/allele	Near	Andr	Unal	Shum	Cook	PWS	Alex	BC	WA	OR	NCA	CCA
Ald												
N	10	10	3	24	25	10	21	28	31	8	34	29
2				0.042								
3				0.042	0.040	0.100	0.024	0.143	0.145		0.059	0.086
4	1.000	1.000	1.000	0.917	0.960	0.900	0.881	0.821	0.855	1.000	0.912	0.914
5											0.029	
6							0.095	0.036				
A_R	1.000	1.000	na	1.754	1.363	1.763	1.917	2.144	1.819	1.000	1.753	1.626
H_O	na	na	na	0.167	0.000	0.000	0.143	**0.000**	**0.033**	na	**0.059**	0.172
H_E	na	na	na	0.160	0.078	0.189	0.220	**0.309**	**0.252**	na	**0.167**	0.160
F_{IS}	NA	NA	na	**-0.045**	1.000	1.000	0.355	1.000	0.874	NA	0.651	**-0.077**
Enol												
N	10	8	3	20	26	10	24	29	33	15	36	36
1	0.100	0.375	0.167	0.150	0.192	0.200	0.083	0.103	0.106	0.067	0.028	0.069
2	0.600	0.500	0.167	0.425	0.288	0.150	0.313	0.328	0.318	0.133	0.389	0.528
3	0.300	0.125	0.667	0.400	0.519	0.650	0.583	0.569	0.545	0.800	0.556	0.361
4											0.028	0.014
6				0.025								
7									0.015			0.014
8												0.014
9							0.021		0.015			
A_R	2.758	2.875	nc	3.092	2.885	2.851	2.815	2.685	2.990	2.386	2.516	2.946
H_O	0.500	0.625	0.667	0.550	0.462	0.600	0.458	0.620	0.606	0.400	0.528	0.444
H_E	0.568	0.633	0.600	0.653	0.622	0.542	0.566	0.568	0.599	0.349	0.546	0.594
F_{IS}	0.126	0.014	**-0.143**	0.161	0.262	-0.113	0.194	-0.094	-0.013	**-0.151**	0.034	0.254
Gpd												
N	11	9	3	24	25	10	21	30	26	7	36	31
1									0.019			
2				0.021	0.020		0.048	0.083				
3	0.364			0.438	0.360	0.350	0.357	0.517	0.404	0.214	0.403	0.468
4	0.045	0.111	0.500	0.042	0.080	0.200	0.119	0.017	0.115		0.028	0.016
6	0.136	0.556	0.500	0.354	0.340	0.450	0.381	0.183	0.346	0.500	0.444	0.371
6	0.227	0.111		0.042	0.060		0.071	0.067	0.058	0.143	0.069	0.032
7				0.021	0.020			0.017				
8	0.136	0.111		0.042	0.040		0.024	0.050	0.058	0.143	0.014	0.032
9	0.045	0.111			0.020						0.028	
10				0.042	0.040						0.014	0.081
11					0.020							
12								0.017				
13								0.017				
14								0.017				
15								0.017				
21	0.045											
A_R	5.046	4.268	nc	3.916	4.610	2.955	3.984	4.458	3.885	3.857	3.330	3.350
H_O	0.727	0.778	1.000	0.625	0.760	0.900	0.240	0.700	0.692	0.571	0.750	0.677
H_E	0.810	0.680	0.600	0.690	0.755	0.668	0.722	0.695	0.710	0.714	0.642	0.645
F_{IS}	0.106	-0.155	**-1.000**	0.096	-0.007	-0.373	0.280	-0.007	0.026	0.213	-0.170	-0.051

Table 10. Sample sizes (N), allele frequencies, allelic richness estimates (A_R, corrected for the minimum per-locus sample size), observed and expected heterozygosities (H_O and H_E, respectively) and Wright's inbreeding coefficients (F_{IS}) for 23 loci within 12 populations of Marbled Murrelets.—Continued

[Heterozygosity estimates in bold indicate significant deviations from Hardy-Weinberg expectations. Inbreeding coefficients in bold are significantly less than zero. Blank cells indicate allele not found. Population abbreviations as in figure 4]

Locus/allele	Near	Andr	Unal	Shum	Cook	PWS	Alex	BC	WA	OR	NCA	CCA
Ldh												
1	0.045			0.021	0.019		0.068		0.040		0.056	0.097
2	0.091	0.100		0.063	0.212	0.167	0.091	0.161	0.160	0.192	0.097	0.056
4	0.864	0.900	0.750	0.792	0.769	0.833	0.795	0.821	0.640	0.769	0.750	0.847
5				0.083			0.045	0.018				
6			0.250	0.021					0.080	0.038	0.028	
7				0.021					0.020		0.056	
8									0.020		0.014	
9									0.040			
A_R	2.169	2.000	nc	2.758	2.121	1.931	2.614	2.033	3.586	2.318	2.981	2.124
H_O	0.273	0.200	0.500	0.375	0.385	0.111	0.409	0.286	0.600	0.308	0.333	0.167
H_E	0.255	0.200	0.500	0.369	0.370	0.294	0.360	0.305	0.566	0.385	0.427	0.273
F_{IS}	**-0.071**	0.000	0.000	-0.017	-0.040	0.636	**-0.139**	0.063	-0.062	0.207	0.222	0.394
Lam												
N	10	8	3	24	25	10	24	27	33	6	36	36
1											0.042	
2						0.050		0.037				
3	0.850	0.500	0.833	0.792	0.900	0.700	0.750	0.759	0.758	0.917	0.764	0.694
4				0.083	0.040	0.100	0.021	0.037	0.045		0.069	0.097
6				0.021		0.100	0.083	0.056	0.045		0.042	
6	0.150	0.500	0.167	0.104	0.060	0.050	0.146	0.111	0.152	0.083	0.083	0.181
7												0.028
A_R	1.895	2.000		2.536	1.859	3.526	2.658	2.871	2.620	1.833	2.876	2.809
H_O	0.300	0.500	0.333	0.375	0.120	0.200	0.417	0.407	0.364	0.167	0.389	0.583
H_E	0.268	0.533	0.333	0.363	0.189	0.511	0.418	0.413	0.405	0.167	0.407	0.482
F_{IS}	**-0.125**	0.067	0.000	-0.035	0.368	0.621	0.002	0.014	0.104	**0.000**	0.045	-0.215
MPP												
N	8	5	0	22	24	10	20	27	32	10	36	36
1				0.023					0.031		0.042	
2	0.563	0.500		0.750	0.854	0.700	0.750	0.778	0.609	0.800	0.764	0.556
3		0.100		0.045	0.104	0.150	0.100	0.130	0.047	0.100	0.069	0.069
4	0.438	0.400		0.159	0.042	0.150	0.100	0.074	0.172		0.056	0.278
5				0.023			0.050	0.019	0.063		0.056	0.069
6										0.050	0.014	0.028
7									0.078	0.050		
A_R	2.000	3.000	na	2.721	2.084	2.789	2.843	2.540	3.654	2.763	2.958	3.306
H_O	0.625	0.600	na	0.318	0.208	0.600	0.400	0.407	0.531	0.400	0.389	0.583
H_E	0.525	0.644	na	0.419	0.263	0.489	0.426	0.379	0.595	0.383	0.409	0.712
F_{IS}	-0.207	0.077	na	0.244	0.212	**-0.241**	0.062	-0.075	0.109	**-0.108**	0.050	0.048
OD												
N	11	10	3	24	26	10	24	27	33	15	36	36
1	0.682	0.350	0.667	0.458	0.673	0.400	0.521	0.519	0.439	0.500	0.444	0.486
2		0.050		0.146	0.019	0.150	0.042	0.074	0.091	0.067	0.056	
3	0.227	0.050	0.167	0.167	0.192	0.150	0.292	0.222	0.167	0.233	0.208	0.264
4				0.063	0.038	0.200	0.042	0.037				
5	0.045	0.350		0.063	0.058		0.021	0.093	0.015	0.033	0.028	0.042
6	0.045	0.050		0.042		0.100	0.021	0.056				
8				0.063	0.019		0.021		0.076		0.056	
9									0.045		0.028	0.014
10												0.014
11												0.014
12		0.050							0.030		0.083	0.167

Table 10. Sample sizes (*N*), allele frequencies, allelic richness estimates (A_R, corrected for the minimum per-locus sample size), observed and expected heterozygosities (H_O and H_E, respectively) and Wright's inbreeding coefficients (F_{IS}) for 23 loci within 12 populations of Marbled Murrelets.—Continued

[Heterozygosity estimates in bold indicate significant deviations from Hardy-Weinberg expectations. Inbreeding coefficients in bold are significantly less than zero. Blank cells indicate allele not found. Population abbreviations as in figure 4]

Locus/allele	Near	Andr	Unal	Shum	Cook	PWS	Alex	BC	WA	OR	NCA	CCA
OD—Continued												
N	11	10	3	24	26	10	24	27	33	15	36	36
13											0.014	
14										0.033	0.014	
15							0.042		0.076	0.033	0.028	
16											0.028	
17										0.033	0.014	
18									0.030			
19									0.015			
21			0.167									
22										0.067		
23									0.015			
A_R	2.879	4.760	nc	4.612	3.123	4.509	3.735	3.971	5.060	4.422	4.897	3.605
H_O	0.636	0.900	0.667	0.708	0.538	0.800	0.625	0.667	0.758	0.600	0.750	0.667
H_E	0.502	0.774	0.600	0.743	0.514	0.784	0.651	0.676	0.766	0.706	0.753	0.673
F_{IS}	**-0.284**	-0.174	**-0.143**	0.048	-0.048	-0.021	0.040	0.014	0.012	0.154	0.004	0.010
RP40												
N	9	5	0	23	26	10	22	28	31	11	36	36
1		0.200		0.283	0.288	0.150	0.364	0.232	0.323	0.318	0.292	0.542
2	0.444	0.500		0.435	0.192	0.350	0.273	0.321	0.177	0.409	0.306	0.167
3	0.056			0.174	0.212	0.300	0.205	0.196	0.226	0.227	0.208	0.153
4	0.500	0.300			0.058		0.045	0.071	0.048			0.014
5				0.022	0.058	0.050		0.018	0.032		0.042	
6				0.022								
7				0.022	0.096	0.050	0.045	0.054	0.081		0.042	0.056
8				0.043	0.096	0.100	0.068	0.107	0.097	0.045	0.111	0.069
9									0.016			
A_R	2.556	3.000	na	3.903	5.121	4.651	4.257	4.741	4.950	3.419	4.326	3.825
H_O	0.667	0.600	na	0.696	0.731	0.900	0.818	0.679	0.806	0.636	0.806	0.583
H_E	0.582	0.689	na	0.713	0.826	0.789	0.760	0.799	0.807	0.710	0.773	0.656
F_{IS}	-0.157	0.143	na	0.025	0.117	-0.149	-0.078	0.153	0.001	0.108	-0.043	0.113
Cco5-21												
N	7	4	6	24	29	10	21	28	0	7	32	36
101				0.063	0.017		0.024	0.018			0.016	
105	0.357	0.625	0.083	0.292	0.276	0.200	0.214	0.143		0.214	0.250	0.167
107			0.083	0.021	0.034		0.024	0.018			0.031	
109	0.143	0.125	0.500	0.479	0.534	0.650	0.524	0.607		0.786	0.609	0.694
111					0.034			0.018				
113	0.071	0.125	0.250	0.042	0.034	0.050	0.119	0.054			0.078	0.042
117				0.021								
121	0.214	0.125	0.083	0.063	0.052	0.050	0.095	0.143			0.016	0.083
123	0.071											
125	0.143			0.021	0.017	0.050						0.014
A_R	4.755	4.000	3.982	3.615	3.355	3.098	3.521	3.273	na	1.945	2.900	2.719
H_O	0.571	0.750	0.500	0.750	0.552	0.600	0.571	0.607	na	0.429	0.594	0.444
H_E	0.835	0.643	0.727	0.689	0.642	0.558	0.671	0.597	na	0.363	0.567	0.488
F_{IS}	0.333	**-0.200**	0.333	-0.091	0.143	-0.080	0.152	-0.017	na	**-0.200**	-0.047	0.090
Bma10-18												
N	7	5	7	24	26	10	22	30	0	8	36	36
1		0.100		0.125	0.058	0.050	0.091				0.056	0.153
4					0.019			0.017		0.063		
5	0.143	0.100		0.042	0.077		0.068	0.033		0.125	0.111	0.139
6	0.071	0.100	0.214	0.167	0.231	0.300	0.205	0.217		0.125	0.306	0.264

Table 10. Sample sizes (*N*), allele frequencies, allelic richness estimates (A_R, corrected for the minimum per-locus sample size), observed and expected heterozygosities (H_O and H_E, respectively) and Wright's inbreeding coefficients (F_{IS}) for 23 loci within 12 populations of Marbled Murrelets.—Continued

[Heterozygosity estimates in bold indicate significant deviations from Hardy-Weinberg expectations. Inbreeding coefficients in bold are significantly less than zero. Blank cells indicate allele not found. Population abbreviations as in figure 4]

Locus/allele	Near	Andr	Unal	Shum	Cook	PWS	Alex	BC	WA	OR	NCA	CCA
Bma10-18—Continued												
N	7	5	7	24	26	10	22	30	0	8	36	36
7		0.200	0.143	0.063	0.135	0.200	0.045	0.100			0.042	0.069
8	0.286		0.071	0.104	0.077	0.200	0.205	0.217		0.125	0.139	0.028
9	0.071	0.100	0.214	0.208	0.173	0.050	0.136	0.083		0.313	0.125	
10	0.071	0.200	0.071	0.063	0.038		0.045	0.100		0.063	0.097	
11					0.038		0.023	0.050			0.056	0.056
12	0.143	0.100		0.021	0.000		0.045	0.017		0.063	0.028	0.014
13				0.083	0.058	0.050	0.023	0.067				0.028
14											0.014	0.028
15	0.143	0.100	0.214	0.104	0.038	0.100	0.091	0.017		0.125	0.028	0.208
16				0.021		0.050		0.017				
17	0.071							0.017				
18					0.038			0.033				
19			0.071		0.019							
20								0.017				
22												0.014
23							0.023					
A_R	5.776	6.756	5.385	5.615	5.671	5.024	5.599	5.566	na	5.554	5.157	4.953
H_O	1.000	0.800	1.000	0.760	0.846	0.900	0.909	0.967	na	0.625	0.861	0.722
H_E	0.901	0.956	0.890	0.900	0.891	0.853	0.889	0.883	na	0.883	0.852	0.845
F_{IS}	**-0.120**	0.179	**-0.135**	0.115	0.051	-0.059	-0.023	-0.096	na	0.307	-0.011	0.148
Bma301												
N	11	12	12	27	31	9	22	30	33	15	36	36
134									0.015			
136		0.042	0.042	0.185	0.097	0.111	0.068	0.133	0.076	0.067	0.153	0.139
140	0.227	0.250	0.042	0.185	0.274	0.389	0.182	0.333	0.227	0.267	0.361	0.194
144	0.136	0.042	0.208	0.259	0.274	0.111	0.250	0.100	0.197	0.233	0.181	0.139
148	0.545	0.542	0.542	0.278	0.242	0.278	0.409	0.317	0.288	0.300	0.250	0.222
152	0.091	0.083	0.125	0.093	0.081	0.111	0.068	0.067	0.197	0.100	0.056	0.306
156		0.042	0.042		0.016			0.050		0.033		
160					0.016		0.023					
A_R	3.922	4.898	4.971	4.797	5.142	4.980	4.849	5.123	4.960	5.232	4.562	4.836
H_O	0.636	0.750	0.500	0.667	0.742	0.889	0.727	0.700	0.818	0.867	0.611	0.722
H_E	0.654	0.659	0.670	0.793	0.787	0.778	0.744	0.767	0.794	0.795	0.759	0.792
F_{IS}	0.028	-0.145	0.263	0.162	0.059	-0.153	0.023	0.088	-0.031	-0.093	0.197	0.089
Bma356												
N	11	12	12	28	31	9	23	30	33	15	36	36
119				0.018			0.022		0.045		0.014	
123					0.048	0.056	0.022	0.017			0.014	
127					0.016	0.056		0.033	0.015			0.014
131				0.036				0.017	0.030			
135			0.042	0.018	0.065	0.111	0.043	0.033	0.015	0.033	0.014	
139	0.045	0.042		0.143	0.065		0.109	0.083	0.030	0.100	0.056	0.014
143	0.273	0.292	0.125	0.036	0.065	0.167	0.087	0.083	0.061	0.100	0.056	0.194
147	0.136	0.125	0.125	0.125	0.113		0.217	0.083	0.258	0.100	0.306	0.153
151	0.227	0.250	0.125	0.179	0.145	0.278	0.152	0.233	0.182	0.167	0.181	0.236
155	0.136	0.125	0.167	0.143	0.129	0.222	0.152	0.183	0.197	0.333	0.111	0.083
159	0.091	0.042	0.250	0.232	0.161	0.056	0.022	0.100	0.091	0.067	0.153	0.056
163			0.125	0.054	0.097	0.056	0.152	0.117	0.061	0.067	0.069	0.042
167		0.083	0.042		0.065		0.022	0.017	0.015	0.033	0.014	0.181
171	0.091	0.042			0.032						0.014	0.014

Table 10. Sample sizes (*N*), allele frequencies, allelic richness estimates (A_R, corrected for the minimum per-locus sample size), observed and expected heterozygosities (H_0 and H_E, respectively) and Wright's inbreeding coefficients (F_{IS}) for 23 loci within 12 populations of Marbled Murrelets.—Continued

[Heterozygosity estimates in bold indicate significant deviations from Hardy-Weinberg expectations. Inbreeding coefficients in bold are significantly less than zero. Blank cells indicate allele not found. Population abbreviations as in figure 4]

Locus/allele	Near	Andr	Unal	Shum	Cook	PWS	Alex	BC	WA	OR	NCA	CCA
Bma356—Continued												
N	11	12	12	28	31	9	23	30	33	15	36	36
175				0.018								0.014
A_R	6.571	6.843	7.216	7.269	8.709	7.549	7.578	7.865	7.297	7.365	6.928	6.757
H_O	1.000	0.833	0.833	0.893	1.000	0.778	0.956	0.967	0.848	0.933	0.889	0.833
H_E	0.857	0.844	0.880	0.867	0.909	0.869	0.879	0.879	0.855	0.848	0.838	0.850
F_{IS}	**-0.176**	0.013	0.056	-0.031	**-0.103**	0.111	-0.090	-0.102	0.007	-0.104	-0.062	0.020
Bma365												
N	11	12	12	28	29	9	23	30	33	14	36	36
196									0.015			
200	0.318	0.125	0.125	0.143	0.155	0.222	0.196	0.250	0.167	0.036	0.139	0.167
204	0.045	0.042		0.232	0.103	0.111	0.130	0.083	0.152	0.143	0.111	0.083
208	0.136	0.125	0.208	0.107	0.241	0.278	0.065	0.150	0.106	0.179	0.278	0.056
212		0.167	0.042	0.125	0.121	0.222	0.152	0.133	0.121	0.214	0.264	0.417
216	0.318	0.500	0.500	0.214	0.224	0.111	0.239	0.333	0.197	0.286	0.083	0.181
220	0.091		0.042	0.054	0.052		0.087		0.106	0.107	0.042	0.056
224				0.018	0.086		0.043	0.017	0.106		0.056	
228				0.054		0.056		0.017	0.030		0.028	0.042
232	0.045	0.042	0.042	0.036	0.017		0.087	0.017		0.036		
236			0.042									
240	0.045			0.018								
A_R	6.104	5.271	5.638	7.083	6.444	5.876	6.858	5.479	7.092	6.041	6.177	5.550
H_O	0.636	0.750	0.500	0.750	0.862	0.667	0.870	0.867	0.879	0.929	0.861	0.806
H_E	0.801	0.717	0.714	0.860	0.846	0.843	0.862	0.792	0.874	0.836	0.820	0.762
F_{IS}	0.213	-0.048	0.309	0.130	-0.019	0.220	-0.009	-0.097	-0.005	-0.116	-0.050	-0.058
Bma368												
N	11	12	9	25	30	9	23	30	33	15	35	36
158									0.015			
174				0.020	0.100			0.083	0.061	0.133	0.014	0.111
178			0.056		0.017	0.056		0.017	0.121	0.100	0.100	0.083
186									0.015			
190					0.017							
194	0.045		0.111	0.100	0.067	0.056	0.087	0.050	0.015	0.100	0.086	0.028
198	0.045		0.000	0.020	0.050	0.056	0.022	0.050	0.076	0.033	0.043	0.014
202			0.167	0.100	0.050	0.111	0.109	0.033	0.076	0.100	0.014	0.056
206					0.017		0.130	0.067	0.061	0.033	0.014	0.014
210				0.100	0.050		0.043	0.017	0.000	0.033	0.029	
214	0.045	0.042	0.056	0.060	0.083	0.056	0.022	0.050	0.030		0.014	0.014
218			0.056	0.040	0.033	0.056	0.022				0.014	
222			0.056	0.020	0.017	0.056	0.022	0.017	0.061		0.029	0.083
226	0.227	0.250	0.056	0.060	0.017	0.056	0.043	0.050	0.015	0.033	0.071	0.056
230	0.318	0.208	0.222	0.040	0.083		0.065	0.050			0.086	0.014
234	0.136	0.250		0.040	0.017	0.056	0.065	0.017	0.045	0.133	0.057	0.028
238	0.045	0.125	0.056	0.020			0.087	0.100	0.045		0.057	0.028
242	0.045	0.083		0.060	0.067	0.111		0.050	0.076	0.067	0.043	0.139
246		0.042		0.160	0.083	0.056	0.130	0.067	0.045	0.033	0.114	0.153
250			0.111	0.060	0.033	0.111	0.065	0.067	0.045	0.033	0.029	0.042
254	0.045		0.056	0.060	0.083	0.056	0.043	0.033	0.045	0.033	0.057	0.069
258	0.045			0.020	0.083	0.111	0.022	0.067	0.030	0.033	0.071	0.069
262				0.020	0.017		0.022	0.017	0.076	0.100	0.057	
266					0.017			0.083	0.030			
274									0.015			

Table 10. Sample sizes (*N*), allele frequencies, allelic richness estimates (A_R, corrected for the minimum per-locus sample size), observed and expected heterozygosities (H_O and H_E, respectively) and Wright's inbreeding coefficients (F_{IS}) for 23 loci within 12 populations of Marbled Murrelets.—Continued

[Heterozygosity estimates in bold indicate significant deviations from Hardy-Weinberg expectations. Inbreeding coefficients in bold are significantly less than zero. Blank cells indicate allele not found. Population abbreviations as in figure 4]

Locus/allele	Near	Andr	Unal	Shum	Cook	PWS	Alex	BC	WA	OR	NCA	CCA
Bma368—Continued												
N	11	12	9	25	30	9	23	30	33	15	35	36
278								0.017				
A_R	8.078	6.202	10.209	10.592	11.211	12.863	10.457	11.557	11.357	10.626	10.905	9.707
H_O	0.727	0.750	1.000	0.920	**0.867**	1.000	1.000	0.933	0.970	0.933	0.971	0.944
H_E	0.853	0.841	0.928	0.838	**0.950**	0.974	0.938	0.955	0.952	0.943	0.945	0.923
F_{IS}	0.153	0.112	**-0.083**	0.020	0.089	**-0.029**	**-0.068**	0.023	-0.019	0.010	-0.028	-0.023
Bma371												
N	11	12	11	28	30	9	23	30	33	15	36	36
224					0.017							
232					0.017							
234										0.033		
236				0.018	0.017					0.033		
240			0.045	0.018								
242					0.017				0.015			
246									0.015			0.042
248			0.045		0.017							
250					0.050			0.017	0.015		0.014	0.028
252					0.017							
254					0.033		0.065	0.050	0.045	0.033	0.042	0.042
258				0.018	0.083	0.111	0.043	0.033	0.061	0.100	0.042	0.014
262	0.045	0.042		0.071	0.083	0.056	0.130	0.150	0.045	0.100	0.250	0.097
264					0.017							
266	0.091	0.208	0.273	0.232	0.167	0.111	0.196	0.217	0.152	0.067	0.097	0.139
268										0.033		
270	0.318	0.458	0.455	0.250	0.233	0.222	0.283	0.183	0.273	0.400	0.236	0.250
274	0.136	0.125	0.045	0.232	0.117	0.222	0.174	0.250	0.242	0.167	0.194	0.167
278	0.273	0.042	0.091	0.107	0.083	0.167	0.109	0.067	0.061			0.028
282	0.091	0.125							0.015	0.033	0.069	0.111
286					0.017	0.056					0.014	0.056
290				0.018	0.017				0.030		0.028	
294			0.045	0.018		0.056		0.017	0.030		0.014	0.028
298	0.045			0.018								
386								0.017				
A_R	6.312	5.277	5.844	6.331	8.743	7.654	6.108	6.515	7.275	7.264	6.672	7.744
H_O	0.727	0.750	0.636	0.679	0.900	0.778	0.870	0.867	0.939	0.867	0.917	0.972
H_E	0.823	0.743	0.736	0.826	0.892	0.889	0.835	0.840	0.842	0.809	0.836	0.872
F_{IS}	0.121	-0.010	0.141	0.181	-0.009	0.132	-0.043	-0.033	-0.117	-0.074	-0.097	-0.117
Bma433												
N	9	12	11	26	24	8	22	30	33	14	35	36
137				0.019								
147				0.019						0.036		
149			0.045	0.058	0.250	0.063	0.159	0.117	0.121	0.036	0.071	0.194
153	0.222	0.250	0.318	0.077	0.104	0.188	0.227	0.117	0.106	0.107	0.343	0.292
157	0.056	0.167	0.227	0.212	0.271	0.063	0.136	0.233	0.258	0.250	0.243	0.097
159				0.038	0.021		0.045	0.050	0.015		0.014	0.014
161					0.063	0.063	0.023	0.033	0.030	0.036		0.014
163						0.063						
165	0.500	0.375	0.091	0.135	0.063		0.023	0.017	0.045		0.014	0.167
169	0.167		0.091	0.038	0.042	0.188	0.023	0.100	0.015	0.071	0.029	
171							0.023					
172									0.015			

Table 10. Sample sizes (*N*), allele frequencies, allelic richness estimates (A_R, corrected for the minimum per-locus sample size), observed and expected heterozygosities (H_0 and H_E, respectively) and Wright's inbreeding coefficients (F_{IS}) for 23 loci within 12 populations of Marbled Murrelets.—Continued

[Heterozygosity estimates in bold indicate significant deviations from Hardy-Weinberg expectations. Inbreeding coefficients in bold are significantly less than zero. Blank cells indicate allele not found. Population abbreviations as in figure 4]

Locus/allele	Near	Andr	Unal	Shum	Cook	PWS	Alex	BC	WA	OR	NCA	CCA
Bma433—Continued												
N	9	12	11	26	24	8	22	30	33	14	35	36
173			0.045	0.038	0.021		0.068	0.050	0.076	0.071	0.071	
175								0.017				
177			0.045	0.077	0.063			0.067	0.045	0.036	0.057	
181				0.019		0.125	0.045	0.033	0.045	0.071	0.071	0.014
185			0.045	0.038			0.068	0.033	0.091	0.036	0.014	0.139
189	0.056				0.021	0.063			0.030	0.179	0.029	0.042
191				0.038								
193				0.038		0.125	0.045	0.017	0.030		0.029	
197				0.019	0.042		0.045		0.030			
201				0.038				0.033		0.036		
205				0.038					0.015			
209		0.042	0.045					0.017				
213		0.125							0.015			
217				0.019						0.036		
221				0.019	0.021		0.023				0.014	
225							0.023	0.017				
229					0.021		0.023					
233						0.063						0.028
237		0.042						0.033				
241				0.019					0.015			
257								0.017				
277			0.045									
A_R	4.778	5.299	8.234	10.522	7.804	10.000	9.363	9.529	9.248	9.400	7.001	6.318
H_O	0.889	0.833	0.909	0.885	0.875	0.875	0.955	0.967	**0.879**	0.929	0.800	0.833
H_E	0.706	0.783	0.857	0.925	0.854	0.933	0.904	0.907	**0.896**	0.902	0.813	0.829
F_{IS}	-0.280	-0.068	-0.064	0.045	-0.025	0.067	-0.058	-0.067	0.020	-0.030	0.017	-0.005
Bma439												
N	11	12	11	26	31	9	23	30	33	15	35	36
252				0.038						0.067		
268					0.016							
276				0.019	0.016							
280		0.042		0.038	0.016	0.056	0.043	0.050			0.100	0.097
284				0.038	0.129	0.056		0.117	0.045	0.067	0.014	0.042
288	0.182	0.250	0.182	0.115	0.177	0.000	0.174	0.183	0.182	0.133	0.114	0.153
292	0.318	0.125	0.045	0.115	0.113	0.111	0.065	0.050	0.121	0.133	0.114	0.028
296	0.182	0.000	0.045	0.154	0.065		0.043	0.100	0.106	0.067	0.157	0.111
300	0.000	0.208	0.182	0.154	0.097	0.111	0.239	0.133	0.167	0.133	0.086	0.042
304	0.227	0.292	0.364	0.231	0.242	0.333	0.174	0.167	0.197	0.200	0.200	0.208
308	0.091	0.083	0.136	0.096	0.065	0.278	0.196	0.117	0.136	0.167	0.171	0.208
312			0.045		0.032	0.056	0.043	0.067	0.030		0.014	0.042
316					0.032			0.017	0.015	0.033	0.014	0.069
320											0.014	
324							0.022					
A_R	4.931	5.536	6.165	7.400	7.724	6.654	6.758	7.750	6.877	7.777	7.256	7.377
H_O	0.818	0.833	0.818	0.741	0.968	0.667	0.783	0.833	0.788	1.000	0.800	0.889
H_E	0.810	0.819	0.814	0.881	0.874	0.824	0.852	0.889	0.866	0.894	0.874	0.869
F_{IS}	-0.011	-0.019	-0.006	0.156	-0.109	0.200	0.083	0.063	0.091	**-0.123**	0.086	-0.023

Table 10. Sample sizes (N), allele frequencies, allelic richness estimates (A_R, corrected for the minimum per-locus sample size), observed and expected heterozygosities (H_O and H_E, respectively) and Wright's inbreeding coefficients (F_{IS}) for 23 loci within 12 populations of Marbled Murrelets.—Continued

[Heterozygosity estimates in bold indicate significant deviations from Hardy-Weinberg expectations. Inbreeding coefficients in bold are significantly less than zero. Blank cells indicate allele not found. Population abbreviations as in figure 4]

Locus/allele	Near	Andr	Unal	Shum	Cook	PWS	Alex	BC	WA	OR	NCA	CCA
Bma443												
N	11	12	11	28	30	9	23	30	33	13	35	36
146				0.036								
150							0.022					
154				0.018				0.017				
158		0.042	0.091	0.018	0.033	0.111		0.050	0.015	0.077	0.043	
162	0.182	0.208	0.045	0.107	0.150	0.111	0.022	0.033	0.076	0.115	0.214	0.153
166	0.273	0.083	0.227	0.214	0.100		0.174	0.233	0.106	0.115	0.100	0.014
170	0.318	0.083	0.091	0.179	0.117	0.111	0.152	0.083	0.212	0.192	0.143	0.528
174	0.136	0.125	0.273	0.125	0.133	0.111	0.152	0.267	0.136	0.115	0.100	0.014
178	0.091	0.125	0.091	0.196	0.167	0.167	0.174	0.183	0.242	0.154	0.100	0.069
182		0.125		0.089	0.183	0.111	0.109	0.100	0.121	0.192	0.171	0.097
186		0.208	0.136	0.018	0.083	0.167	0.174	0.033	0.045		0.043	0.083
190			0.045		0.033	0.111	0.022		0.045	0.038	0.071	0.042
194											0.014	
A_R	4.920	7.378	7.247	6.930	7.319	7.961	6.796	6.439	6.841	7.317	7.513	5.292
H_O	0.818	0.917	0.909	0.786	0.833	0.778	0.870	0.833	0.879	0.769	0.886	0.722
H_E	0.801	0.888	0.866	0.862	0.880	0.922	0.869	0.833	0.855	0.889	0.878	0.684
F_{IS}	-0.023	-0.034	-0.053	0.090	0.054	0.164	-0.001	-0.001	-0.029	0.140	-0.009	-0.056
Bma453												
N	11	12	11	28	31	9	23	30	33	14	35	36
216					0.016							
220				0.018							0.014	
224												0.014
228				0.054	0.016		0.087	0.050	0.015	0.036	0.043	
230							0.022			0.036		
232		0.042	0.045	0.054	0.081		0.065	0.017	0.061	0.071	0.071	
234					0.032	0.056						
236				0.071	0.065		0.043	0.150	0.030	0.107	0.029	0.014
238		0.042	0.045	0.036			0.022				0.014	
240	0.091			0.054	0.032	0.111	0.043	0.100	0.152	0.071	0.086	0.069
242			0.045	0.018	0.016					0.036		
244	0.045	0.083	0.091	0.054	0.097	0.167	0.130	0.017	0.091	0.143	0.057	0.333
246		0.083	0.045	0.036	0.016			0.017	0.030	0.036		
248	0.273	0.042	0.091	0.054	0.145	0.167	0.022	0.050	0.091	0.036	0.186	0.153
250				0.018			0.022	0.017			0.029	
252	0.182	0.292	0.227	0.089	0.048	0.111	0.109	0.100	0.076	0.071	0.143	0.069
254			0.091	0.036	0.016			0.033	0.061	0.071	0.029	
256	0.227	0.250	0.091	0.036	0.081	0.167	0.065	0.083	0.076	0.107	0.071	0.153
258				0.018	0.032		0.022	0.050	0.045	0.036		
260		0.125		0.125	0.145	0.056	0.065	0.083	0.030	0.036	0.057	0.042
262							0.087	0.017		0.036	0.057	
264	0.045			0.036	0.032		0.043		0.045		0.029	0.014
266			0.045	0.018			0.043	0.067	0.015			0.042
268				0.054	0.032	0.056		0.034	0.045	0.071	0.014	0.014
270					0.016		0.043	0.033	0.061		0.014	0.028
272			0.091	0.054	0.016		0.022		0.045		0.029	0.014
274			0.000	0.018	0.016			0.033	0.015			
276	0.045		0.045	0.018	0.016		0.022					
278				0.036		0.056	0.022					0.014
280		0.042	0.045		0.016			0.033			0.014	
282								0.017	0.015			
284	0.045					0.056					0.014	

Table 10. Sample sizes (*N*), allele frequencies, allelic richness estimates (A_R, corrected for the minimum per-locus sample size), observed and expected heterozygosities (H_0 and H_E, respectively) and Wright's inbreeding coefficients (F_{IS}) for 23 loci within 12 populations of Marbled Murrelets.—Continued

[Heterozygosity estimates in bold indicate significant deviations from Hardy-Weinberg expectations. Inbreeding coefficients in bold are significantly less than zero. Blank cells indicate allele not found. Population abbreviations as in figure 4]

Locus/allele	Near	Andr	Unal	Shum	Cook	PWS	Alex	BC	WA	OR	NCA	CCA
Bma453—Continued												
N	11	12	11	28	31	9	23	30	33	14	35	36
286												0.028
296					0.016							
A_R	7.569	7.436	10.766	11.965	10.724	9.431	11.376	10.761	10.712	11.540	10.118	7.554
H_O	0.818	0.750	0.909	0.929	0.903	0.778	0.913	0.867	0.970	1.000	0.914	0.917
H_E	0.861	0.851	0.935	0.958	0.936	0.928	0.951	0.941	0.940	0.955	0.924	0.838
F_{IS}	0.053	0.124	0.029	0.032	0.036	0.170	0.040	0.079	-0.032	**-0.049**	0.010	-0.095
Bma523												
N	11	12	11	27	30	9	23	30	33	14	35	36
100		0.042				0.111			0.030	0.036	0.071	
104					0.017			0.017	0.015	0.036	0.057	0.042
108	0.045			0.111	0.083	0.056	0.130	0.133	0.045	0.071	0.057	0.056
112	0.273	0.208	0.182	0.111	0.133	0.222	0.196	0.067	0.182	0.107	0.114	0.069
116	0.136	0.208	0.318	0.093	0.217	0.111	0.065	0.183	0.197	0.071	0.057	0.097
120	0.318	0.125	0.091	0.074	0.183	0.056	0.196	0.217	0.167	0.179	0.100	0.347
124	0.045	0.208	0.227	0.185	0.167	0.222	0.283	0.167	0.182	0.250	0.200	0.069
128		0.125	0.091	0.278	0.150	0.167	0.087	0.117	0.152	0.143	0.300	0.083
132	0.182	0.083	0.091	0.111	0.050	0.056	0.043	0.067	0.030	0.107	0.043	0.208
136								0.033				0.028
140				0.019								
144				0.019								
A_R	5.439	6.506	5.803	6.858	6.498	7.654	6.054	6.942	6.522	7.626	6.975	6.650
H_O	0.818	1.000	1.000	0.926	0.767	1.000	0.826	0.833	0.970	0.786	0.743	0.889
H_E	0.805	0.866	0.827	0.853	0.856	0.889	0.831	0.864	0.853	0.881	0.842	0.816
F_{IS}	-0.017	**-0.163**	**-0.222**	-0.088	0.106	**-0.134**	0.006	0.037	-0.139	0.112	0.120	-0.091
Bma553												
N	10	12	11	26	26	9	22	30	33	14	35	36
119												0.028
121	0.450	0.208	0.091	0.038	0.096			0.067	0.106	0.107	0.029	0.083
125	0.050	0.208	0.182	0.019	0.057	0.111	0.091	0.083	0.076		0.029	0.042
129		0.083	0.091	0.115	0.019	0.056		0.083	0.045	0.036	0.014	0.069
133				0.058	0.038			0.050	0.061	0.071	0.014	
137		0.083	0.182	0.115	0.096	0.056	0.159	0.067	0.152	0.107	0.157	0.097
141	0.350	0.333	0.273	0.288	0.346	0.389	0.273	0.317	0.273	0.214	0.214	0.139
145			0.091	0.192	0.288	0.278	0.091	0.183	0.152	0.286	0.314	0.375
149	0.050	0.083	0.091	0.135	0.038		0.205	0.150	0.061	0.179	0.200	0.153
153				0.038	0.019	0.056	0.182		0.061		0.029	
157						0.056			0.015			0.014
A_R	4.568	5.693	6.736	6.763	6.051	6.549	5.639	6.587	7.390	6.252	5.606	6.401
H_O	0.600	1.000	0.909	0.885	0.769	0.889	0.909	0.867	0.848	0.714	0.857	0.806
H_E	0.695	0.815	0.866	0.845	0.788	0.791	0.828	0.832	0.862	0.841	0.799	0.804
F_{IS}	0.143	**-0.239**	-0.053	-0.048	0.022	-0.133	-0.101	-0.042	0.016	0.156	-0.074	-0.002
Bma555												
N	11	12	10	28	30	9	23	30	33	15	36	36
114					0.017			0.033			0.014	
118		0.042	0.050	0.143	0.150	0.111	0.152	0.183	0.167	0.133	0.153	0.194
122				0.018				0.017			0.014	
134			0.150									
138		0.042	0.100	0.143	0.083	0.167	0.087	0.067	0.030	0.100	0.014	0.097
142	0.091		0.050	0.018	0.067	0.111	0.022	0.033	0.030			0.056
144								0.017				

Table 10. Sample sizes (N), allele frequencies, allelic richness estimates (A_R, corrected for the minimum per-locus sample size), observed and expected heterozygosities (H_O and H_E, respectively) and Wright's inbreeding coefficients (F_{IS}) for 23 loci within 12 populations of Marbled Murrelets.—Continued

[Heterozygosity estimates in bold indicate significant deviations from Hardy-Weinberg expectations. Inbreeding coefficients in bold are significantly less than zero. Blank cells indicate allele not found. Population abbreviations as in figure 4]

Locus/allele	Near	Andr	Unal	Shum	Cook	PWS	Alex	BC	WA	OR	NCA	CCA
Bma555—Continued												
N	11	12	10	28	30	9	23	30	33	15	36	36
146	0.364	0.542	0.150	0.071	0.100		0.109	0.017		0.033	0.056	0.042
150	0.227	0.250	0.000	0.036	0.050		0.043	0.050	0.091	0.100	0.014	
154							0.022	0.017		0.033	0.111	0.014
158	0.136	0.042	0.050	0.054	0.067		0.043	0.017	0.061	0.067	0.069	0.069
162	0.091	0.083	0.250	0.089	0.133	0.222	0.043	0.067	0.136	0.133	0.153	0.028
166			0.150	0.179	0.100	0.111	0.109	0.117	0.106	0.100	0.111	0.125
170	0.045			0.125	0.117	0.111	0.152	0.117	0.121	0.133	0.111	0.278
174	0.045			0.071	0.067	0.056	0.043	0.133	0.197	0.100	0.069	0.056
178				0.018	0.033	0.056	0.130	0.100	0.045	0.067	0.069	0.042
182			0.050	0.036		0.056	0.022	0.017	0.015		0.042	
186							0.022					
190					0.017							
AR	6.311	4.898	8.158	8.605	9.079	8.641	9.195	9.156	7.836	9.180	8.793	7.435
HO	0.818	0.417	1.000	0.929	0.967	1.000	0.957	0.900	0.879	1.000	0.889	0.861
HE	0.814	0.659	0.895	0.903	0.917	0.915	0.916	0.911	0.886	0.923	0.909	0.856
FIS	-0.006	0.379	**-0.125**	-0.029	-0.055	**-0.099**	-0.045	0.013	0.009	**-0.082**	0.022	-0.006
Mean AR for introns	2.538	2.863	na	3.162	2.896	3.122	3.103	3.180	3.571	2.750	3.205	2.949
Mean AR for microsatellites	5.717	5.857	6.882	7.453	7.462	7.424	7.154	7.324	7.784	7.366	6.897	6.378
Mean AR for all loci	4.561	4.768	6.882	5.893	5.802	5.860	5.681	5.818	6.099	5.687	5.555	5.131
Overall FIS	0.005	0.003	-0.033	0.071	0.051	0.036	0.025	0.020	0.014	0.041	0.008	0.006

Most sampling sites only had significant deviations from linkage equilibrium for 5 or fewer pairs of loci (of a possible 231 pairs; table 11a). However for Oregon, 31 pairs of loci showed significant deviations from linkage equilibrium, suggesting the possibility of nonrandom sampling and/or non-random mating at this site. After excluding samples from Oregon, only 3 pairs of loci (of a possible 231 pairs) showed evidence of linkage disequilibrium within 2 or more sites: (1) *Bma10-18* and *Cco5-21*; (2) *Bma365* and *Bma553*; and (3) *Bma433* and *Bma553* (table 11b). Subsequent analyses were therefore conducted both with and without *Bma10-18* and *Bma553* to reduce potential complications from linkage. Results are reported without these loci, but do not differ qualitatively if they are included.

With one exception (*Ald*, which was invariant in the three Aleutian Islands sites), all loci were variable in all sites. Allelic richness did not differ among sites for introns ($F_{11,76} = 0.48$, $P = 0.91$), microsatellites ($F_{11,154} = 1.49$, $P = 0.14$), or all loci combined ($F_{11,242} = 1.07$, $P = 0.39$; table 10). Several estimates of Wright's inbreeding coefficient (F_{IS}) were significantly less than zero after Bonferroni corrections (table 10). However, these low values tended to occur in sites with small sample sizes (e.g., Near and Unalaska islands), suggesting they represent a sampling artifact. Allelic richness, observed heterozygosity and F_{IS} did not differ significantly among sites (analyses of variance, all $P > 0.10$; table 10).

Population Genetic Structure

All sampling sites except the Andreanof Islands had private alleles at one or more nuclear loci (table 10). However, only one of these alleles occurred at a frequency higher than 0.10. No evidence was found for phylogeographic structuring of intron alleles (data not shown).

Table 11a. Number of pairs of loci (*N*) showing significant deviations from linkage equilibrium for each of 12 sampling sites.

Site	*N*	Site	*N*
Near	0	Alex	10
Andr	2	BC	3
Unal	3	WA	0
Shum	0	OR	31
Cook	6	NCA	0
PWS	2	CCA	0

Global estimates of Φ_{ST} or F_{ST} were low but significantly greater than zero for most loci, and averaged 0.022 over all loci (*SE* = 0.002; max = 0.047; table 12). Estimates of Φ_{ST} and F_{ST} were similar for each intron (table 12). In pairwise comparisons of sampling sites, estimates of Φ_{ST} or F_{ST} ranged as much as 0.109, and were significantly greater than 0 for most comparisons involving birds from the Near Islands and/or central California as well as for several comparisons involving birds from the Andreanof Islands and/or northern California (table 13).

Mantel's tests indicated a low but significant correlation between Wright's linearized F_{ST} and the natural logarithm of geographic distance both for all loci combined ($r = 0.45$, $P = 0.001$; fig. 5), and for introns and microsatellites separately ($r = 0.30$, $P = 0.015$; and $r = 0.28$, $P = 0.007$; respectively). Note however that almost all comparisons involving the Near Islands, Andreanof Islands and/or central California have positive values of Wright's linearized F_{ST} whereas few comparisons within the central area do, and that the correlation loses significance if any of the peripheral sites are removed. Thus, the correlation does not appear to be a simple effect of isolation by distance, but a result of differentiation of murrelets in the Near and Andreanof Islands and central California.

Results from STRUCTURE provided strong support for four genetic populations ($P < 0.0001$; table 14; fig. 6). Genetic Population 1 (represented by red on fig. 6) primarily comprised samples from the Near and Andreanof Islands; Genetic Population 4 (yellow on fig. 6) primarily comprised samples from central California. Individuals sampled between Unalaska Island and northern California were assigned with varying probabilities to two additional genetic populations (green and blue on fig. 6), which did not appear to be geographically segregated. To resolve these latter two populations, the analysis was re-run: (i) under the no-admixture model; (ii) with introns only; (iii) with microsatellites only; and (iv) without samples from the Near or Andreadnof Islands or central California (see Evanno and others, 2005). Introns alone did not resolve any population genetic structure, presumably because of low power (only seven loci). Microsatellites alone yielded results similar to the full data set (i.e., four genetic populations) but with lower probabilities of assignment. For the analysis involving samples from the central region only, the most probable value of *k* was 1 ($P < 0.0001$), suggesting that murrelets from Unalaska Island to northern California comprise a single genetic population.

Table 11b. Number of sampling sites with significant deviations from linkage equilibrium at a Bonferroni corrected a = 0.05 for pairwise comparisons of loci.

[Numbers below the diagonal include all populations; numbers above the diagonal exclude samples from Oregon. Blank cells = no populations exhibit linkage disequilibrium.]

	Ald	***Eno***	***Gpd***	***Ldh***	***Lam***	***MPP***	***OD***	***RP40***	***Cco 5-21***	***Bm 10-18***	***Bma 301***	***Bma 356***	***Bma 365***	***Bma 368***	***Bma 371***	***Bma 433***	***Bma 439***	***Bma 443***	***Bma 453***	***Bma 523***	***Bma 553***	***Bma 555***
Ald															1			1				
Enol															1							
Gpd																						
Ldh															1							
Lam			1												1							
MPP							1	1														
OD						1																1
RP40						1											1					
Cco5-21										3												
Bma10-18									4													
Bma301																					1	1
Bma356											1										1	
Bma365																	1				2	1
Bma368											1	1				1				1		
Bma371	1	1		1	1						1	1	1	1								
Bma433														1							2	
Bma439								1					1	1	1			1				1
Bma443	1	1												1		1	1		1			
Bma453													1			1		2				
Bma523													1	1		1		1	1			
Bma553											1	1	3			3	1	1	1	1		
Bma555							1				1		1		1	1	2				1	

Table 12. Locus-specific estimates of global Φ_{ST} (for introns) or F_{ST} (for introns and microsatellites) for Marbled Murrelets.

[ns, not significant]

Locus	Φ_{ST}	*P*	F_{ST}	*P*
Ald	0.018	ns	0.016	ns
Enol	0.045	<0.001	0.047	<0.0001
GPD	0.028	<0.001	0.021	<0.01
LDH	0.001	0.1	0.006	ns
Lam	0.021	<0.01	0.019	<0.05
MPP	0.041	<0.0001	0.036	<0.0001
OD	0.034	<0.0001	0.018	<0.01
RP40	0.043	<0.0001	0.033	<0.0001
Cco5-21			0.027	<0.01
Bma10-18			0.015	<0.01
Bma301			0.033	<0.0001
Bma356			0.004	ns
Bma365			0.030	<0.0001
Bma368			0.015	<0.0001
Bma371			0.010	<0.05
Bma433			0.033	<0.0001
Bma439			0.004	ns
Bma443			0.035	<0.0001
Bma453			0.017	<0.0001
Bma523			0.020	<0.0001
Bma553			0.025	<0.0001
Bma555			0.028	<0.0001
Mean	0.029		0.022	
SE	0.005		0.002	

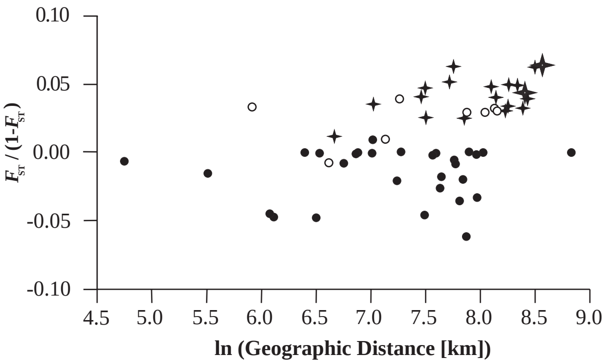


Figure 5. Correlation between Wright's linearized FST (=FST / [1 - FST]) and the natural logarithm of the shortest geographic distance between sampling sites (km) for Marbled Murrelets.

Crosses indicate comparisons involving the Near or Andreanof islands; open symbols indicate comparisons involving central California.

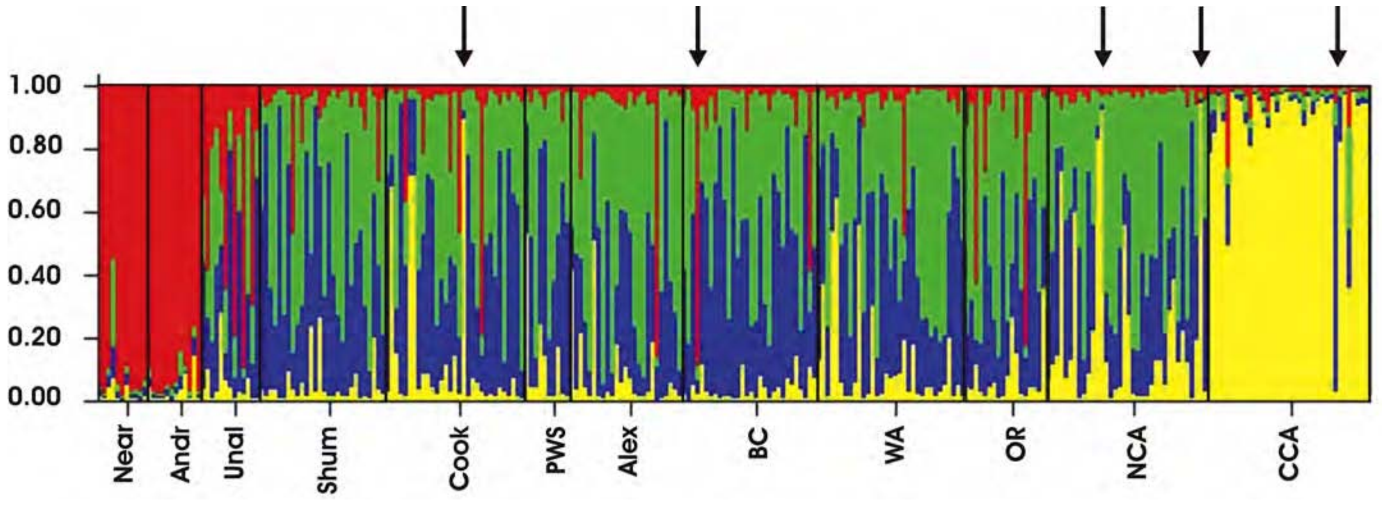


Figure 6. Probability of assignment of individual Marbled Murrelets (represented by vertical bars) to each of four genetic populations (represented by different colors).

Table 13a. Estimates of shortest geographic distance (km; above diagonal), and F_{ST} for all loci except *Ald*, *Bma10-18* and *Bma553* (below diagonal) for pairwise comparisons of sampling sites.

[Site abbreviations as in figure 4. Values in **bold** are significantly greater than 0. Negative values indicate that variation within sites is greater than variation among sites. ~, insufficient data. Samples from Unalaska were too degraded for introns to amplify reliably]

	Near	Andr	Unal	Shum	Cook	PWS	Alex	BC	WA	OR	NCA	CCA
Near		750	1,380	1,770	2,300	2,340	3,270	4,260	4,440	4,620	4,890	5,340
Andr	0.012		740	1,140	1,710	1,780	2,690	3,600	3,770	3,910	4,160	4,500
Unal	~	~		400	990	1,070	1,960	2,860	3,030	3,200	3,470	3,830
Shum	**0.045**	**0.036**	~		600	700	1,560	2,470	2,640	2,830	3,120	3,480
Cook	**0.049**	**0.030**	~	0.002		120	980	1,990	2,200	2,450	2,800	3,170
PWS	**0.059**	0.027	~	-0.002	-0.008		930	1,990	2,200	2,470	2,930	3,200
Alex	**0.047**	**0.027**	~	0.000	-0.001	0.000		1,140	1,370	1,730	2,140	2,520
BC	**0.048**	**0.039**	~	0.003	-0.001	-0.002	0.000		240	660	1,110	1,450
WA	**0.032**	**0.029**	~	-0.021	-0.028	-0.023	-0.021	-0.015		440	890	1,220
OR	**0.038**	**0.048**	~	-0.033	-0.036	-0.066	-0.049	-0.051	-0.051		440	800
NCA	**0.060**	**0.034**	~	0.004	0.001	-0.001	0.007	**0.013**	-0.009	-0.051		380
CCA	**0.060**	**0.043**	~	**0.031**	**0.029**	**0.029**	**0.028**	**0.039**	**0.011**	-0.017	**0.033**	

Table 13b. Estimates of Φ_{ST} for introns (below diagonal) and F_{ST} for microsatellites (above diagonal) for pairwise comparisons of sampling sites.

[~, insufficient data. Samples from Unalaska were too degraded for introns to amplify reliably]

	Near	Andr	Unal	Shum	Cook	PWS	Alex	BC	WA	OR	NCA	CCA
Near		0.001	0.026	**0.041**	**0.041**	**0.046**	**0.045**	**0.039**	0.008	**0.039**	**0.056**	**0.061**
Andr	0.053		0.005	**0.026**	**0.022**	0.021	**0.021**	**0.023**	**0.034**	**0.035**	**0.038**	**0.053**
Unal	~	~		-0.008	-0.009	0.002	-0.004	-0.016	-0.022	0.020	0.008	**0.029**
Shum	0.043	-0.017	~		-0.002	0.003	0.002	0.004	-0.058	-0.038	**0.012**	**0.038**
Cook	**0.067**	0.031	~	0.010		-0.007	0.005	-0.001	-0.062	-0.038	0.006	**0.030**
PWS	**0.084**	-0.004	~	0.001	0.009		0.007	-0.005	-0.078	-0.034	-0.001	0.018
Alex	**0.062**	0.021	~	-0.001	0.001	-0.005		-0.000	-0.061	-0.024	0.012	**0.032**
BC	**0.056**	0.036	~	0.003	0.010	0.002	-0.003		-0.063	-0.045	0.016	**0.041**
WA	**0.053**	-0.017	~	0.005	0.010	0.005	-0.004	0.003		-0.041	-0.051	-0.033
OR	0.060	**0.109**	~	-0.095	-0.089	-0.187	-0.116	-0.111	-0.101		-0.035	-0.017
NCA	**0.062**	-0.012	~	-0.002	0.007	0.002	-0.008	0.003	0.001	-0.122		**0.033**
CCA	0.052	-0.022	~	0.017	**0.042**	0.055	0.016	0.029	0.025	-0.041	0.023	

Table 14. Maximum value of ln Pr (X | *k*) from multiple runs of STRUCTURE for each value of *k* (number of populations) from one to twelve.

k	ln P(X|*k*)	P (*k*)
1	-21334	<0.0001
2	-21212	<0.0001
3	-21219	<0.0001
4	-20909	>0.9999
5	-21622	<0.0001
6	-21530	<0.0001
7	-22842	<0.0001
8	-21603	<0.0001
9	-23071	<0.0001
10	-21830	<0.0001
11	-22877	<0.0001
12	-22256	<0.0001

Contemporary Gene Flow

Individual murrelets from the Near and Andreanof Islands had a high probability of being assigned to Genetic Population 1 by STRUCTURE (mean $P = 0.97$, $SE = 0.021$); those from central California had a high probability of being assigned to Genetic Population 4 (mean $P = 0.93$, $SE = 0.036$; table 15; appendix L). At least one bird in central California (indicated by an arrow on fig. 6) had a high probability ($P > 0.90$) of being an immigrant from Genetic Population 2, and four individuals between Unalaska Island and northern California had high probabilities of being immigrants from Genetic Populations 1 or 4. Lower probabilities of assignment may result from difficulties by the program in assigning individuals due to errors around population-specific genotype frequencies and/or interbreeding between individuals from

Table 15. Proportion of birds from different sites that were assigned to each of four genetic populations by STRUCTURE.

[Population abbreviations as in figure 4]

Sampling site	Genetic population				
	1	2	3	4	Number of individuals
Near	0.957	0.017	0.025	0.001	11
Andr	0.986	0.005	0.003	0.005	12
Unal	0.37	0.337	0.262	0.031	13
Shum	0.028	0.472	0.485	0.014	28
Cook	0.067	0.403	0.406	0.124	31
PWS	0.008	0.434	0.437	0.121	10
Alex	0.052	0.312	0.583	0.052	25
BC	0.056	0.533	0.401	0.011	30
WA	0.02	0.469	0.414	0.098	33
OR	0.116	0.358	0.491	0.035	18
NCA	0.001	0.319	0.489	0.19	36
CCA	0.003	0.043	0.023	0.931	36

different genetic populations (i.e., second or third generation immigrants). Thus, assignment of individuals to specific populations when their probability of assignment to that population is less than 0.80 (a standard value for β in statistical tests) is tenuous.

Discussion

Genetic Viability

In theory, declining populations suffer increasing inbreeding, which may lead to inbreeding depression. They also lose genetic variation, which may compromise their ability to adapt and evolve. No strong evidence for either inbreeding or low genetic variation was found within any sampling site in the present study (table 10). Thus, inbreeding and loss of genetic variation do not appear to be a concern for Marbled Murrelets at this time.

Population Genetic Structure

Estimates of F_{ST} or Φ_{ST} both for all loci combined and for introns or microsatellites separately indicated that low but significant population genetic structure exists within Marbled Murrelets (tables 12, 13, 14, and 15). These results agree with findings of previous studies, which reported estimates of global F_{ST} or Φ_{ST} between 0.05 and 0.09 based on allozymes, mtDNA, introns and/or microsatellites (Friesen and others, 1996b, 2005; Congdon and others, 2000). Previous studies (Congdon and others, 2000; Friesen and others, 2005) as well as the present results (fig. 5) suggested that genetic variation changes clinally in this species. However, the present results indicate that variation does not change gradually but may instead represent a step cline. Specifically, several lines of evidence indicate that murrelets in the central and western Aleutian Islands (Near and Andreanof islands) and central California differ significantly from those in central parts of the species' range:

1. Pairwise estimates of F_{ST} or Φ_{ST} were significant for most comparisons involving the Near and Andreanof islands and central California, with estimates ranging as high as 0.109 (table 13). This finding was consistent across loci, and is supported by results of previous studies (Friesen and others, 1996b, 2005; Congdon and others, 2000);

2. Although Mantel's tests indicated isolation by distance, significance was lost when peripheral sites were eliminated from the analysis; and

3. STRUCTURE placed samples into four genetic populations, with most samples from the Near and Andreanof islands, and central California being placed in distinct genetic populations (fig. 6).

As in previous studies (Friesen and others, 1996b, 2005, Congdon and others, 2000), no evidence was found for differentiation among sampling sites between the Alaska Peninsula and British Columbia (table 13). Although the sample size for Unalaska Island was low, results of the present study suggest that murrelets from the eastern Aleutian Islands (Unalaska Island), Washington and Oregon also do not differ genetically from mainland Alaska and British Columbia birds in that: (1) birds from these areas generally did not differ from birds from the central region in pairwise comparisons of sites (table 13); and (2) most samples from these sites were assigned to Genetic Populations 2 or 3 by STRUCTURE.

Previously, Friesen and others (2005) suggested that: (1) birds from the Near and Andreanof islands may differ genetically from each other; and (2) birds from northern California may differ both from those in central California and from those in British Columbia north. However, they argued that these possibilities require further investigation. Results of the present study did not consistently separate samples from the Near versus Andreanof islands, or those from northern California versus central regions (table 13; fig. 6).

Congdon and others (2000) argued that genetic differences between Marbled Murrelets from the Aleutian Islands versus mainland Alaska and British Columbia are a result of historical fragmentation, probably by Pleistocene glaciers. Although population genetic structure has been attributed to Pleistocene glaciers in several species in this region (Harlin-Cognato and others, 2006), more recent results for Marbled Murrelets do not support this interpretation. Specifically, the Aleutian samples lack private nuclear alleles at high frequency (Friesen and others, 2005, and present results), and there is no evidence of historical fragmentation from mtDNA data (e.g., deep branches in the gene tree; Friesen and others, 2005). Population genetic structure in this species may instead be a product of genetic drift and selection in situ following recession of the glaciers. Resolution of this problem will require additional analyses (e.g., nested clade analysis, Templeton, 1998).

Contemporary Gene Flow

Molecular assignments indicated that gene flow among Marbled Murrelets in Near / Andreanof islands versus central part of the range versus central California is very low. Specifically: (1) most birds in the Near or Andreanof islands and central California had very high probabilities of assignment to Genetic Populations 1 or 4, respectively (table 15; appendix L); (2) none of 23 birds from the Near or Andreanof islands had even a modest probability (> 0.70) of assignment to a population other than Genetic Population 1; and (3) only 1 of 36 birds from central California had even a modest probability of originating from a population other than Genetic Population 4. Nonetheless, these regions are not completely isolated genetically: one bird sampled between Unalaska Island and northern California had a high probability (> 0.90) of assignment to Genetic Population 1, and three birds sampled in this region had a high probability (> 0.90) of assignment to Genetic Population 4 (fig. 6). Although some of these assignments may represent Type II Errors, they suggest that gene flow does occur among the regions. In contrast, Genetic Populations 2 and 3 did not correspond with any geographic region, few birds sampled between Unalaska Island and northern California could be assigned with confidence to any genetic population, and analysis only of samples from Unalaska to northern California using STRUCTURE indicated a single genetic population. Thus, gene flow appears to occur among sites within the central region.

Note that these results do not contradict recent telemetry studies and population modeling studies which indicate potentially high dispersal between central California and other sites (Peery and others, 2006b). First, dispersal does not necessarily result in gene flow (e.g., movements could represent seasonal dispersal or prospecting juveniles). Second, although migration rates could not be estimated with the present data, STRUCTURE identified several potential migrants both into and out of central California, which is compatible with telemetry studies and population modeling. Other migrants may exist but not be identified with high confidence using molecular assignments. Third, migration may be naturally sporadic (i.e., periods of little or no gene flow may be interspersed with occasional periods of gene flow). Finally, gene flow requires time to homogenize populations (Birky and others, 1989); thus, if populations were historically isolated but are now exchanging migrants (e.g., due to anthropogenic disturbance), they will display both population genetic differences and gene flow for a length of time that depends on the initial level of differentiation, the effective population sizes and the migration rates.

Genetic Units of the Marbled Murrelet

Marbled Murrelets appear to comprise three genetic units: (1) western and central Aleutian Islands; (2) eastern Aleutian Islands to northern California; and (3) central California. These units were first identified by Congdon and others (2000) and Friesen and others (2005), and have been upheld by analyses of additional samples and loci. They are supported by both traditional (e.g., Wright's F_{ST}) and state-of-the-art analyses (e.g., coalescent theory), and three types of molecular markers (mtDNA, introns, and microsatellites). Loss of any of these populations would result in loss of a portion of the species' genetic resources and/or local adaptations, and may compromise its long-term viability. Due to their generally small size, relative isolation, and often marginal habitat, peripheral populations are expected to be more vulnerable to extinction (reviewed in Lessica and Allendorf, 1995; Vucetich and Waite, 2003). Our analyses confirm that murrelets in the western and central Aleutian Islands, and central California are genetically distinct, peripheral populations.

Population Status and Trend

Methods Used to Survey Murrelets

Marbled Murrelets are difficult to census compared to a variety of related seabird species such as Common Murres or Tufted Puffins (*F. cirrhata*), which conveniently gather in densely populated breeding colonies, where they may be counted in whole or on a selected sample survey of plots. On land, murrelets disperse over vast areas of old-growth forest habitat to nest, and they fly to and from nest sites before dawn. It is possible to monitor audio-visual detections of Marbled Murrelets during these flights, and relate the frequency of those detections to habitat (Ralph and others, 1995b) or obtain relative indices of abundance within and between years (Naslund, 1993), but detections are highly variable and their use for estimating population abundance is limited. In recent years, radar technology has greatly improved the ability of investigators to count and monitor murrelet numbers in forest habitat (Burger, 2001b), and is becoming a standard tool for this purpose (Burger and others, 2004a). When positioned at the mouth of a watershed, radar provides a relatively consistent count of murrelets entering the watershed, and counts can then be applied to analyze landscape-level associations between murrelets and habitat (Burger, 2001b; Raphael and others, 2002b; Bigger and others, 2006). Although radar counts are now routinely used to estimate sizes of populations in British Columbia (see below), there has been only one pilot study on using radar for this purpose in Alaska (Cooper, 1993).

The most common source of information on the distribution and abundance of murrelets in Alaska is derived from surveys at-sea. When they are not attending nest sites, murrelets are found at-sea where they forage on small schooling fish (see section, “Feeding Ecology”). In general, abundance at-sea is often not well-correlated with numbers nesting in adjacent terrestrial breeding habitat (Marks and others, 1995; Speckman, 1996; Whitworth and others, 2000), but on a landscape- or regional-scale, murrelets are most abundant in waters within foraging range of old-growth forests (Hull and others, 2001; Meyer and others, 2002; Miller and others, 2002). Therefore, broad-scale surveys for murrelets at-sea can provide good information on regional population trend, status, and distribution. This has been shown especially well for the semi-enclosed marine waters of Prince William Sound (Agler and others, 1998; Lance and others, 2001), where murrelet populations have been repeatedly estimated from counts on sample surveys since 1989, counts show relatively low variation from one year to the next (trends notwithstanding), and spatial variability within a year is low (CVs of 20–40 percent are not unusual).

In Alaska, surveys for marine birds generally employ strip-transect methods, whereby all birds observed within a fixed-width strip (e.g., 200–300 m) around a moving vessel are recorded (Gould and Forsell, 1989; Klosiewski and Laing, 1994). In Washington, Oregon, and California, murrelets are now usually counted using line-transect methods without fixed widths, and the distance to every bird also is recorded so that detection functions may be calculated to adjust for conservative negative bias (under estimate) due to the drop-off in visibility of birds with distance (Bentivoglio and others, 2002). This method has not been adopted in Alaska yet, in part because of concerns about comparability with historical data and because it might be difficult to collect line-distance data on the large number of murrelets and other species typically found in Alaska during summer. In any case, small boat surveys in Alaska generally employ 200-m strip widths (Agler and others, 1998), i.e., 100 m to either side of the vessel. There is a small conservative bias in strip-transect methods (Klosiewski and Laing, 1994), where most murrelets (and other species) observed out to the full 100 m are counted. The bias is likely to be consistent over time (Evans Mack and others, 2002), but contributes to conservative, underestimates of the population size (see below).

Sources of Error Associated with Boat-Based Surveys

Several sources of error are associated with using boat-based survey data to estimate populations (Gould and Forsell, 1989; Agler and others, 1998; McShane and others, 2004). In general, these sources of error tend to be consistently present among studies and years, and tend to cancel out when making inferences about trend using data that are collected in a similar way each year. With respect to estimating population size, however, these sources of error tend to bias the estimate either high or low, and include:

1. Strip-transects tend to underestimate densities for small seabirds like murrelets because the visibility of birds drops off with distance from the transect line (see above). It appears likely, however, that under a range of typical viewing conditions, observation teams of 2 or more people see 80–95 percent of all murrelets within 100 m (Evans Mack and others, 2002). Detection rates may be higher in the more protected waters of Prince William Sound and Southeast Alaska.

2. Counting of all flying birds on strip (and line) transects tends to overestimate actual densities because of the continuous flux of incoming birds (Gould and Forsell, 1989) leading to overestimates of actual density by 25–40 percent for fast-flying birds (Spear and others, 1992). McShane and others (2004) thought this might not be a serious problem in Washington, Oregon, and California because <2.5 percent of murrelets were thought to fly during observations on transect (citing Strong and others, 1995). In contrast, we have found that 20 to 40 percent of murrelets may be observed flying on marine bird surveys in some areas of Alaska (J. Piatt, U.S. Geological Survey, unpub. data, 1999–2005). In Southeast Alaska, for example, 31 percent of all birds were flying on surveys conducted in Icy Strait by Lindell (2005). Similarly, 28.3 percent of all murrelets observed by Agler and others (1998) during 6 weeks of sampling throughout Southeast Alaska were flying. Agler and others (1998) addressed this uncertainty by estimating the abundance of murrelets with counts of flying birds excluded (reducing the

population estimate by about 200,000 birds). However, that approach overcompensates for this source of error. Preliminary analysis of experimental surveys (G. Drew, U.S. Geological Survey, unpub. data, 1999–2993) where continuous counts of flying birds in Glacier Bay were compared with periodic scan counts that compensate for flux (Gould and Forsell, 1989) suggests that counts of flying murrelets should be reduced by about 60 percent to compensate for flux. This is similar to the ratio for medium-sized alcids calculated by Gaston and others (1987). Using this ratio, it appears that Agler and others (1998) would have overestimated murrelet abundance in Southeast Alaska by 13 percent, or by about 92,000 birds.

3. Other factors that may bias counts are inter-observer variability, poor viewing or sea conditions, double-counting of birds that move ahead of the vessel, and missing of birds diving underwater. In general, these are well-recognized problems (Agler and others, 1998; Evans Mack and others, 2002) that may be minimized with thorough training of observers and a commitment to survey only under specific conditions (e.g., Agler and others, 1998). It is possible to assess errors arising from these factors on an experimental basis (e.g., Evans Mack and others, 2002), but more difficult to assign error retroactively to any given survey.

4. The total number of murrelets on the water in any given location varies throughout summer (DeGange, 1996; Speckman and others, 2000; Kuletz, 2005). The number of birds found on the water must be a fraction of the total population during incubation when one member of each pair remains at the nest site during day (Kuletz, 1996). Ironically, we should probably survey murrelets during incubation to assess population trends because numbers at-sea are less variable at this time (Speckman and others, 2000), but clearly that is a bad time to survey for population size because one-half the active breeders should be attending nest sites. Numbers on the water increase after incubation (May–June) and by as much as 20 to 40 percent during late July and early August (Kuletz and Kendall, 1998; Speckman and others, 2000; Lindell, 2005).

5. Changes in the environment can have large effects on local and even regional populations. At small scales, bird numbers are significantly affected by tide and time of day (Speckman and others, 2000). In theory, this variability is balanced out by sampling at all times of day and over periods of weeks (Agler and others, 1998). At larger scales, evidence suggests that regional abundance may vary with water temperatures, for example during El Niño-Southern Oscillation (ENSO) events, leading to unusual fluctuations in abundance (Burger, 2002; Kuletz, 2005). Care must be taken interpreting trends or population estimates that include such anomalous years (Burger, 2002).

The assumption that all murrelets within the strip-transect are counted will tend to underestimate ‘actual’ population size by perhaps 15 to 20 percent, while inclusion of counts of flying birds tends to overestimate abundance by perhaps 13 percent [see (1) and (2) above]. In most cases, we restricted analysis to surveys conducted before July 15 so that some fraction of the populations probably would still be attending nest sites [see (4) above]. In general, these analysis methods are expected to yield conservative under-estimates of the ‘actual’ population sizes. The effects of other sources of error [see (3) and (5) above] contribute to variance (SEs) and potential biases of the estimates, but these are well-recognized problems (Agler and others, 1998; Mack and others, 2002) that we assume were reasonably dealt with through training of observers and a commitment to survey only under specific conditions (e.g., Agler and others, 1998). The potential large scale effects of water temperature and regime shifts are discussed below and in conclusions.

Alaska Population

Alaska Population Estimates

Marbled Murrelets range widely in Alaska (see section, “Geographic Distribution”). From the border with British Columbia in Southeast Alaska to Attu Island in the western Aleutians, there are only a few gaps in distribution (e.g., island passes in the Aleutians). However, the majority of murrelets are concentrated during the breeding season in just three main areas: Southeast Alaska (the Alexander Archipelago), Prince William Sound, and in the area of lower Cook Inlet – Kodiak Archipelago (Piatt, 1994; Piatt and Naslund, 1995; Agler and others, 1998). Historical estimates from these three areas (table 16) are believed to account for about 95 percent of the total Alaska population. In these areas, Marbled Murrelets ovelap in distribution with Kittlitz’s Murrelets. Whenever possible, murrelets were identified to species on population surveys, but a significant proportion were recorded as unidentified *Brachyramphus* murrelet. Identification of murrelets in the field can be difficult, even for experienced observers, and the fraction of birds that were categorized as unidentified *Brachyramphus* sometimes exceeded 50 percent

Table 16. *Brachyramphus* murrelet population estimates for areas in Alaska that have been surveyed systematically.

[Historic population estimates are made from the earliest reliable survey data for each area and provide an estimate of the historic maximum size of the murrelet population. Few population-scale surveys have been repeated. Using data from eight trend sites within or near these areas, we can project what the population would be if populations followed the observed linear trends to 1999 and leveled off after a weak regime shift, or if they continued to follow linear trends to summer 2006. In these scenarios, areas with no trend data are assumed to remain constant. Data sets used to estimate trends always include more than just the population-scale survey data presented in this table and so differ in apparent percent change over time (see text for detail)]

Area	Historic population survey estimate				Most recent population survey estimate					Projected population in 1999			Projected population in 2006		
	Year	N	LCL	UCL	Year	N	LCL	UCL	Percent change[1]	Trend[2]	N	Percent change[3]	Trend[4]	N	Percent change[5]
Southeast Alaska	1994	687,061	485,899	888,223	---					-19.2	236,620	-66	-12.2	144,188	-79
(Glacier Bay)[6]	1991	75,486	59,721	92,627	2003	16,178	12,851	20,070	-79%	---	---	---	---	---	---
(Icy Strait)[6]	1993	44,993	30,032	61,804	2003	15,880	8,966	23,654	-65%	---	---	---	---	---	---
Yakutat	2000	8,344	3,740	12,948	---					n/a	8,344	---	-5.4	5,980	---
Outer Coast[7]	~2003	16,785	8,689	24,881	---						16,785	---	-5.4	13,442	-20
Prince William Sound	1989	107,354	88,145	126,563	2005	43,061	34,498	51,624	-60%	-5.5	60,973	-43	-6.7	33,745	-69
GOA (to 300 km)[8,9]	~1984	9,820	2,455	17,185	---					-5.5	4,203	-57	-6.7	3,240	-67
Kenai Fjords[10]	2002	9,554	2,315	22,164	2006	5,264	3,776	7,338	-45%	n/a	9,554	---	n/a	5,264	---
Cook Inlet	1993	58,227	42,169	74,285	1996	29,127	21,076	40,255	-50%	-3.7	46,438	-20	-3.7	35,666	-39
Kodiak Archipelago[8]	~1984	23,722	12,067	35,377	---					-3.7	13,475	-43	-3.7	10,349	-56
Alaska Peninsula	2003	7,389	2,098	17,708	---					n/a	7,389	---	n.d	7,389	---
Unalaska Island	2005	7,486	5,936	9,439	---					n/a	7,486	---	n.d.	7,486	---
Atka Island	2004	724	353	1,485	---					n/a	724	---	n.d.	724	---
Adak Island	2006	1,674	1,015	2,333	---					n/a	1,674	---	n.d.	1,674	---
Attu Island	2000	75	19	131	---					n/a	75	---	n.d.	75	---
Bering Sea[8,9]	~1984	1,960	490	3,430	---					n/a	1,960	---	n.d.	1,960	---
TOTAL[11]		**940,175**	**655,390**	**1,236,152**							**415,700**	**-56**		**271,182**	**-71**

[1] Percent change calculated between historic population estimate and most recent estimate.

[2] Trend calculated from date of earliest trend survey (see "Trends" table) to 1999 only.

[3] Percent change calculated between the population size estimated from historic surveys and population size projected for 1999 from trend data.

[4] Trend calculated from data of earliest trend survey to most recent trend survey (up to 2003–06, see "Trends" table).

[5] Percent change calculated between the population size estimate from historic surveys and population size projected for 2006 from trend data.

[6] Glacier Bay and Icy Strait are subareas of Southeast Alaska, and murrelet populations are subsets of the above total estimated from a region-wide survey in 1994.

[7] Estimated from ship-based surveys conducted in 2002–04, with 2003 as mid-point (M. Kissling, U.S. Fish and Wildlife Service, unpub. report, 2006).

[8] Estimated from ship surveys conducted in 1975–93, with 1984 as mid-point (Piatt and Ford, 1993).

[9] Confidence limits approximated as ±75 percent.

[10] Trend estimated from coastal survey initiated in 1976. First population survey of all habitats in 2002.

[11] Total does not include estimates from Glacier Bay or Icy Strait because these are included in the overall Southeast Area estimate.

of all birds observed. For purposes of analyses and discussion here, all Marbled, Kittlitz's and Unidentified murrelets were combined as *Brachyramphus* murrelets. Because usually only a fraction of these were Kittlitz's Murrelets in glaciated regions (as much as about 10 percent in Prince William Sound and about 15 percent in Glacier Bay), overall trends discussed here can be attributed mostly to the Marbled Murrelet. Its should be noted, however, that Kittlitz's murrelet also appears to be declining rapidly throughout its range, and so contributes to the overall declines in *Brachyramphus* murrelet reported here (Kuletz and others, 2003b). All murrelets recorded on surveys in British Columbia were Marbled Murrelets, as were virtually all murrelets observed south of Icy Strait in Southeast Alaska.

Isleib and Kessel (1973) provided the first published estimate of Marbled Murrelet abundance in Alaska, suggesting that the northern Gulf of Alaska population might be "several hundred thousands, probably millions." This was conjectural, but based on first-hand observations of large numbers of murrelets in Prince William Sound and elsewhere. Analysis of the earliest of all quantitative surveys for murrelets in Alaska indicated a population of 304,000 murrelets in Prince William Sound during summer 1972 (Klosiewski and Laing, 1994). A 1989 survey indicated a population estimate of 107,300 birds (table 16; Klosiewski and Laing, 1994). Piatt and Ford (1993) estimated Marbled Murrelet populations in Alaska at about 160,000 based on greater than 18,000 km of ship-based surveys in offshore marine waters of Alaska. However, the ship-based surveys poorly sampled the inside waters of Prince William Sound and Southeast Alaska, and so must be considered minimum estimates (Agler and others, 1998). Piatt and Naslund (1995) revised that estimate upwards to 280,000 after considering other survey results from Prince William Sound and lower Cook Inlet. With the addition of subsequent detailed surveys of Southeast Alaska, the estimate for murrelet populations in the three areas of concentration (Southeast Alaska, Prince William Sound, and lower Cook Inlet) increased to about 859,000 (± approx. 203,000) birds (Agler and others, 1998). Independent surveys of local concentrations of murrelets in subareas of Southeast Alaska (Glacier Bay and Icy Strait) corroborate the high abundance of murrelets in this region (Robards and others, 2003; Lindell, 2005).

Some areas remain poorly surveyed, and we still rely on the earlier ship-based surveys (Piatt and Ford, 1993) to estimate population sizes for the Kodiak Archipelago, open waters of the Gulf of Alaska, and coastal and shelf waters of the southeastern Bering Sea (table 16). However, other areas of Alaska have been surveyed more recently (table 16) using small boat-based survey methods similar to those used in Prince William Sound. Moving north from the inside waters of Southeast Alaska, Stephensen and Andres (2001) estimated that about 8,300 *Brachyramphus* murrelets resided in waters of Yakutat and adjacent bays, while Kissling and others (U.S. Fish and Wildlife Service, 2006) estimated that about 17,000 murrelets used outer coast waters from Cross Sound to Icy Bay along the outer coast. Prince William Sound has been surveyed eight more times since 1989, the year that surveys were initiated to assess damages from the EVOS (McKnight and others, 2006). Owing to the long time span between the first (1972) and second (1989) surveys of Prince William Sound, and uncertainty about what the population may have been doing in the intervening 17 years, the latter estimate of about 107,000 murrelets is often used for comparison with other studies and for examination of trend (Agler and others, 1998; Kuletz, 2005; see appendixes F-K). All remaining areas, including Kenai Fjords (Van Pelt and Piatt, 2003), the Alaska Peninsula (Van Pelt and Piatt, 2005), and Unalaska (Romano and others, 2005a), Atka (Romano and others, 2005b), Adak (J.F. Piatt, U.S. Geological Survey, unpub. data, 2006), and Attu (Piatt and others, 2005) islands, have been surveyed in the 2000s as part of an ongoing effort to fill in gaps in our knowledge about the distribution and abundance of *Brachyramphus* murrelets in Alaska.

Adding together all the earliest possible population estimates from different areas of Alaska, and acknowledging that dates of census vary widely, mostly from 1989 to 2006, we can estimate that the total Alaska population was once in the order of 940,000 birds, with an approximate 95 percent CI of 655,000–1,236,000 birds (table 16). If we used the earliest estimate of Prince William Sound populations from 1972, the estimate would include almost 200,000 more birds, but because it used a slightly different design and was only a single survey, it would be more conservative to use data after 1989. Despite an intensive effort to survey many new areas, this current estimate represents only a modest increase (9 percent) over the previous estimate of 859,000 *Brachyramphus* murrelets by Agler and others (1998). This underscores the importance of the three primary areas of Southeast Alaska, Prince William Sound, and lower Cook Inlet for murrelet populations in Alaska. It is unlikely that any significant new populations will be found in Alaska (at least from the numerical perspective).

Alaska Population Trends

We can examine population trends in two ways: (1) by direct comparison of recent population-level surveys with historical surveys; and, (2) by using trend site data to estimate change within surrounding areas and over uniform periods of time.

We have repetitive population survey data from only 5 of 16 areas in Alaska (table 16). Three areas (Glacier Bay, Icy Strait, Prince William Sound) have been surveyed multiple times over many years (see table 17), and two areas (Kenai Fjords and Cook Inlet) were surveyed only twice, with only a few-year interval between surveys. Historical and recent population estimates for Glacier Bay, Icy Strait and Prince William Sound are provided in appendixes H, G, and J, respectively. Estimates from Kenai Fjords are from Van Pelt and Piatt (2003), and updated with data collected in 2006 (M. Romano, U.S. Fish and Wildlife Service, unpub. data, 2006). Estimates from Cook Inlet are from Agler and others (1998) and a reanalysis of 1996 data collected (Piatt, 2002) and compared over the same spatial scale (S. Speckman, U.S. Fish and Wildlife Service, unpub. data, 2006).

When we compare historical survey data with the most recent survey data in each area, it appears that murrelets have declined by 45–79 percent in these areas. As one might expect, the magnitude of change is larger where the interval between first and last surveys is greatest— and perhaps more trustworthy. For example, while numbers declined on the population-level surveys conducted at Kenai Fjords 2002–06, shoreline trend counts at this location extend much further back in time (1976) and they have been extremely variable. The long-term trend is actually positive (table 17).

Another way to analyze these data is to examine trends, standardized as percent change per year (table 17). Population trend data are available from a limited number of locations. For Southeast Alaska, we examined four different datasets to establish population trends in three ways:

1. We examined changes in abundance of murrelets over the entire Southeast Alaska region by comparing the Southeast Alaska-wide population survey of Agler and others (1998) with a series of Southeast Alaska-wide coastal surveys conducted by the USFWS (J. Hodges, U.S. Fish and Wildlife, unpub. data, 2006) over several years (1999–2001);

2. We examined trends in Icy Strait by combining data from surveys conducted by the USFWS in 1993–99 (Lindell, 2005) with identical surveys of the same area from 1999 to 2003 conducted by the USGS (Robards and others, 2003; and

Table 17. Summary of changes in *Brachyramphus* murrelet populations at eight different trend sites during summer in Alaska.

[See appendixes F-K. Weighted linear regressions were performed on log transformed annual means. *t*-tests conducted using Welch's correction for unequal variances. Significant (*p*<0.05) changes are in **bold**. The percent change in counts between years was calculated from the difference between actual counts in the first and last years of the range sampled (which does not always reflect the overall trend from multiple years of sampling)]

Site or transect route	Region	Range of years	Number of years sampled	Test	Statistic	df	*P*	Percent change between all years	Avg rate of change (percent per year)
Southeast	Southeast Alaska	1994–2001	[1]2	*t*-test	**_t_=2.71**	**1060**	**<0.01**	**-46**	**-11.5**
Icy Strait	Southeast Alaska	1993–2001	8	regression	**F=8.52**	**21,10**	**0.015**	**-65**	**-12.7**
Glacier Bay	Southeast Alaska	1991–2001	7	regression	**F=128.5**	**1,6**	**<0.0001**	**-79**	**-11.8**
Malaspina	Outer Coast	1992–2002	2	regression	**F=111.4**	**21,2**	**0.009**	**-43**	**-5.4**
Prince William Sound	South-central Alaska	1989–2005	9	regression	**F=18.7**	**1,8**	**0.003**	**-60**	**-6.7**
Kenai Fjords	South-central Alaska	1976–2006	5	regression	*F*=0.43	1,4	NS	-17	+1.8
Kachemak Bay	South-central Alaska	1993–2006	3	regression	F=0.49	1,1	NS	-14	-3.7
Adak Island	Aleutians	1995–2006	2	*t*-test	*t*=1.04	37	NS	-57	-7.4

[1] Comparison made using 1999 as mid-point for sampling of the Southeast area in 1997–2001 (see appendixes).

[2] Surveys replicated within some years, so degrees of freedom larger than expected from number of years sampled.

3. We examined trends in Glacier Bay by comparing surveys conducted in 1991 (Piatt and others, 1991), with surveys conducted by Lindell (2005) in 1993 and the USGS in 1999–2003 (Robards and others, 2003).

The paper by Agler and others (1998) is published and provides some of the comparisons. For the remaining comparisons, we have included descriptions of the surveys and details of our analyses in appendixes F-H. Table 17 shows results of these trend assessments.

Outside of Southeast Alaska, we have trend data from five other locations:

1. Kissling (U.S. Fish and Wildlife Service, unpub. data, 2006) surveyed murrelets on the outer Gulf of Alaska coast for several years, and compared their survey of the Malaspina Forelands with a similar survey conducted in 1992 by Kozie (1993). Details of this unpublished comparison are found in appendix I;
2. Our best trend data are from Prince William Sound, which has the longest time series (1972 / 1989–2005) of murrelet population surveys. This dataset has been analyzed specifically for trends in Marbled and Kittlitz's murrelet populations by Kuletz (2005), and that analysis is included here in appendix J;
3. Trends in Kenai Fjords populations were examined by Van Pelt and Piatt (2003) using data collected on four coastal surveys conducted between 1976 and 2002, and we updated that trend with data collected in summer 2006 (M. Romano, U.S. Fish and Wildlife Service, unpub. data, 2006);
4. In Kachemak Bay during 2005 and 2006, Kuletz resurveyed 46 random transects located within the bay that were originally used in the estimate of the murrelet population of Lower Cook Inlet (Agler and others, 1998), and we estimated trend from the original survey data collected in 1993 (K. Kuletz, U.S. Fish and Wildlife Service, unpub. data, 2005–06). We opted not to use the Cook Inlet population surveys of 1993 and 1996 to assess trends owing to the brief time interval between surveys (and unlikely trend of -18 percent per year); and
5. Part of the coast of Adak Island was surveyed for murrelets in 1995 (Meehan, 1996) and we surveyed the entire island in 2006 to obtain a whole-island population estimate and evaluate trends. Details of this survey and comparison with the 1995 census are provided in appendix K.

Results of these analyses indicate that there has been a rapid and widespread decline in *Brachyramphus* murrelet populations throughout Alaska (table 17). The evidence for major declines in abundance is strongest from Southeast Alaska and Prince William Sound owing to the good time-series of data in both locations. In Southeast Alaska, there is good agreement with rates of decline estimated from Icy Strait and Glacier Bay (-12.7 vs. -11.8 percent), and these estimates are supported by observed trends from a region wide survey (-11.5 percent). Declines in Prince William Sound were less extreme, but still large at -6.7 percent per year. Numbers along the Malaspina Forelands, in Kachemak Bay, and at Adak Island were all negative, and slightly positive at Kenai Fjords, but small sample sizes and highly variable data limit our ability to reach definite conclusions about trends.

Consequences of these rates of population change are indicated in table 16. We considered two scenarios based on the duration and form of long-term trends (see appendixes D-K) observed in Alaska and British Columbia: (1) that populations declined at a linear rate until about 1999, when the decline leveled off (as suggested at one trend site in Alaska and British Columbia), possibly owing to effects of a weak oceanic "regime shift" in 1999 (see section, "Discussion"); and, (2) that populations declined in linear fashion all the way to summer of 2006. We calculated rates of decline for each trend site under each scenario (table 16). We then applied those rates of decline to historical population estimates (and used rates from adjacent areas for Yakutat, Kodiak, and Gulf of Alaska) and projected what the size of populations should be in 1999 or 2006 under each scenario. The trend rate for Southeast Alaska was calculated as the average between Glacier Bay and Icy Strait (the Agler-Hodges trend estimate was excluded).

In making these projections, we are assuming that rates of decline from smaller areas are representative of a larger area and population. In Southeast Alaska, there is evidence to support that assumption. In Prince William Sound, the population level survey data are the same as used for estimating trends, so there is no uncertainty about the real extent of these projections. Finally, it is worth noting that we are not projecting far outside of our temporal window of certainty, since trend survey data in most areas were collected as recently as 2001–06 (table 17).

Taken together, the trend and population survey data suggest that populations may have declined by 56 percent between the time of original surveys and 1999, or by as much as 71 percent by 2006 (table 17). We have no trend data from one-half of the areas surveyed, and these may have decreased or increased during the same time periods. However, numbers in these areas are relatively small, and changes one way or the other would have little impact on the overall estimate. Conversely, Southeast Alaska has the largest impact on any analysis of population and trends owing to its large historic population size.

British Columbia Population

British Columbia Population Estimates

Burger (2002b) summarized at-sea and radar counts for British Columbia to estimate the provincial population (table 18). Most of the vast coastline of British Columbia did not have count data and estimates were based on several methods of extrapolating from at-sea or radar counts covering portions of each of the six conservation regions established by the CMMRT (see fig. 7). More than 32,500 birds were actually counted, and the likely population was estimated to be 55,000–78,000 birds (median 66,000 birds). Burger (2002b) stressed that there was much uncertainty in these estimates because large areas of the British Columbia coast had not been censused, many of the census data were out of date and often based on single boat transects, and extrapolations from the patchy census data were necessarily crude. There is little new information with which to update and improve the crude population estimates made by Burger (2002b). Nevertheless, we have tried to improve the population estimates in two ways: (1) by updating, where possible, the information used by Burger (2002b); and (2) by making a new estimate by applying densities derived from radar studies to estimates of total habitat area within British Columbia. Neither of these approaches is highly satisfactory and an accurate estimate of the British Columbia population remains elusive.

Table 18. Population estimates for British Columbia as reported by Burger (2002b) and updated with new information (2006).

[See Appendixes for details. Birds, not breeding pairs or nests, are the measure of population used here]

Conservation region[1]	Population estimate made in 2002 (birds)[2]	Updated estimate (birds)[3]
West and North Vancouver Island	19,400–24,500	18,700–23,600
East Vancouver Island	700–1,000	1,000–2,000
Southern Mainland Coast	6,000–7,000	6,000–7,000
Central Mainland Coast	10,000–21,000	10,000–21,000
Northern Mainland Coast	10,100–14,600	10,100–14,600
Haida Gwaii (Queen Charlotte Islands)	8,500–9,500	8,500 – 25,000
Total for British Columbia	54,700–77,600	54,300 – 92,600

[1] For details on the conservation regions see Canadian Marbled Murrelet Recovery Team (2003) available at http://www.sfu.ca/biology/wildberg/bertram/mamurt/links.htm.

[2] Range indicates the pessimistic and optimistic population estimates (Burger, 2002).

[3] See text for details on new population data and updated estimates. Note that these estimates remain relatively crude for most of the conservation regions.

The total British Columbia population of Marbled Murrelets based on the most recent information is estimated to be in the range of 54,300–92,600 birds (median 73,000 rounded to the nearest thousand). This is slightly higher than the previous estimate (55,000–78,000 birds; median 66,000 birds; Burger, 2002). It must be emphasized that both the current and the previous estimates are crude, based on extrapolations from rather sparse information in most regions and with large margins for error. It also must be emphasized that the slightly higher population estimate produced in 2006 does not indicate that the numbers of murrelets in British Columbia have risen since the last estimate or since the original estimate made by Rodway (1990; 45,000–50,000 breeding birds or about 53,000–59,000 birds—see Burger, 2002). Rather, the higher numbers reflect somewhat improved data and greater geographical coverage of surveys. All available evidence points to declining populations in British Columbia (see below).

Population estimates from the central and northern mainland, and the Haida Gwaii (Queen Charlotte Islands) are probably the least reliable. In the two mainland regions, the populations were estimated from a single year of radar counts extrapolated using correlates with areas of apparently suitable habitat. Radar surveys are underway that will improve our knowledge of these populations and their trends (D. Bertram, Canadian Wildlife Service). In all three of these regions, the numbers of murrelets per thousand ha of suitable habitat varied considerably among the sampled watersheds, and the interpretation of suitable habitat from the GIS data also has considerable scope for error. GIS mapping to improve the estimates of areas of suitable habitat across British Columbia is nearing completion (T. Chatwin and M. Mather, British Columbia Ministry of Environment), which also will help improve population estimates.

British Columbia Population Trends

Population trends of Marbled Murrelets are assessed here from surveys made at-sea in British Columbia during the breeding season (late April–mid-July). Data were available from six transect routes which were repeatedly sampled (but not in every year) within the period 1979 to 2006, and two routes sampled in 1996–2000. Most of the data cover the years 1995–2006. Seven of the transects were off southwest Vancouver Island (Clayoquot and Barkley Sounds, and the West Coast Trail) and one was in Laskeek Bay off Haida Gwaii (Queen Charlotte Islands). Methods varied somewhat among the studies but generally murrelets were counted on both sides of a small vessel running at constant speed along a fixed route, and densities were estimated either using an unlimited distance line-transect (giving densities as birds per km) or within 300 m-wide strip-transects (giving

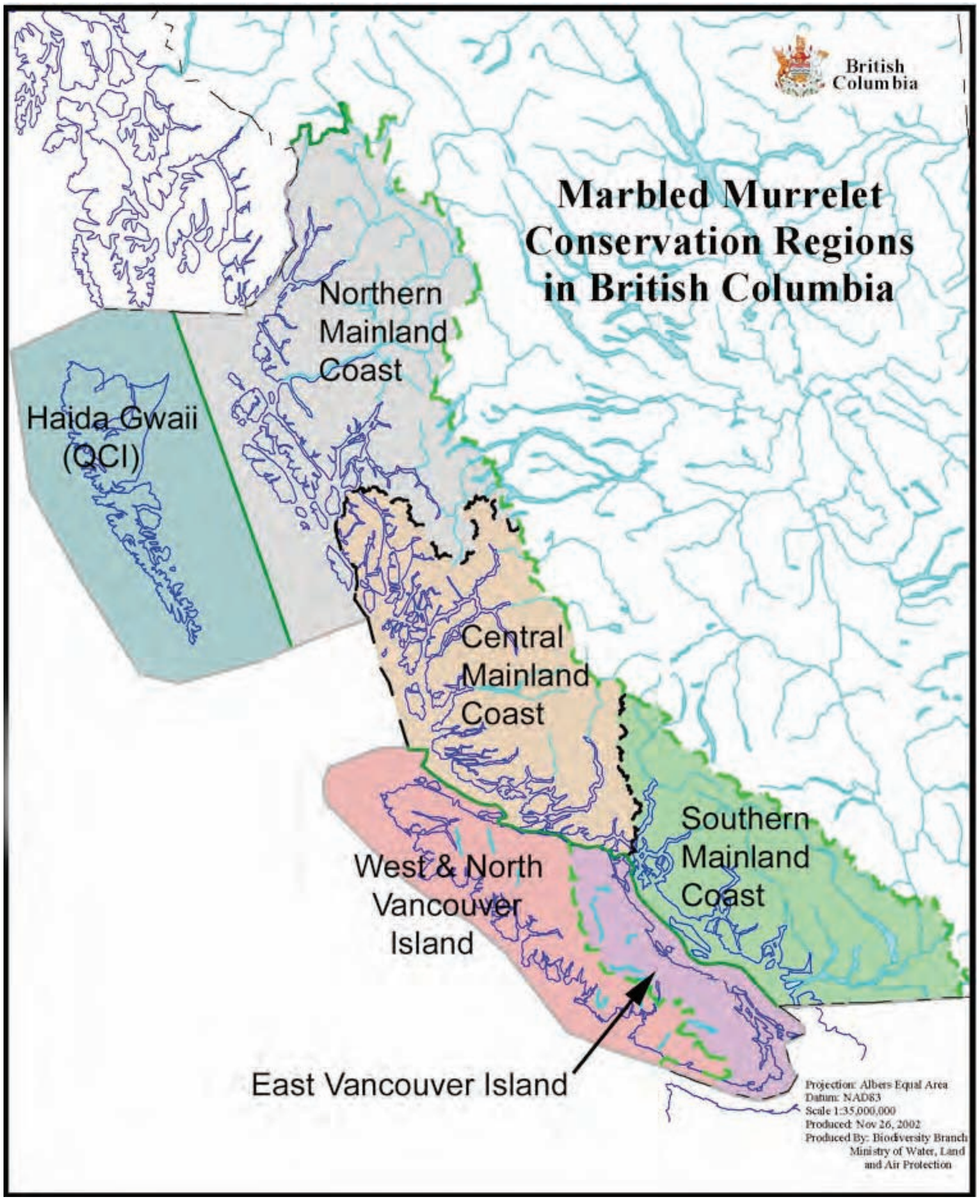


Figure 7. Six Conservation Regions established by the Canadian Marbled Murrelet Recovery Team (Bertram and others, 2003) for surveying and managing Marbled Murrelets in British Columbia.

densities as birds per km^2). More details on how surveys were conducted, and the results of each survey, can be found in appendixes D-E.

We recognize that the available data have severe limitations in their geographical scope (five of the sites are close together in Barkley Sound and adjacent West Coast Trail and the sixth is in Laskeek Bay off Haida Gwaii (Queen Charlotte Islands); fig. 8). We also include a reanalysis of previously published data from the Tofino and Flores transects done in Clayoquot Sound over 4 years (Mason and others, 2002), which help to explain the long-term trends seen in that area (Kelson and others, 1995; Burger, 2002). Although there are gaps and inconsistent survey effort in all data sets, sampling effort was sufficient to reveal likely trends. Because all six data sets were derived from fixed transect routes, spatial variation within study areas is not an issue when analyzing long-term temporal variations in these data. Portions of these data sets have been used to summarize interannual variations in earlier reviews (Burger, 1995b, 2000, 2002b; Bellefleur and others, 2005), but appendixes D-E are the most complete analysis of these data.

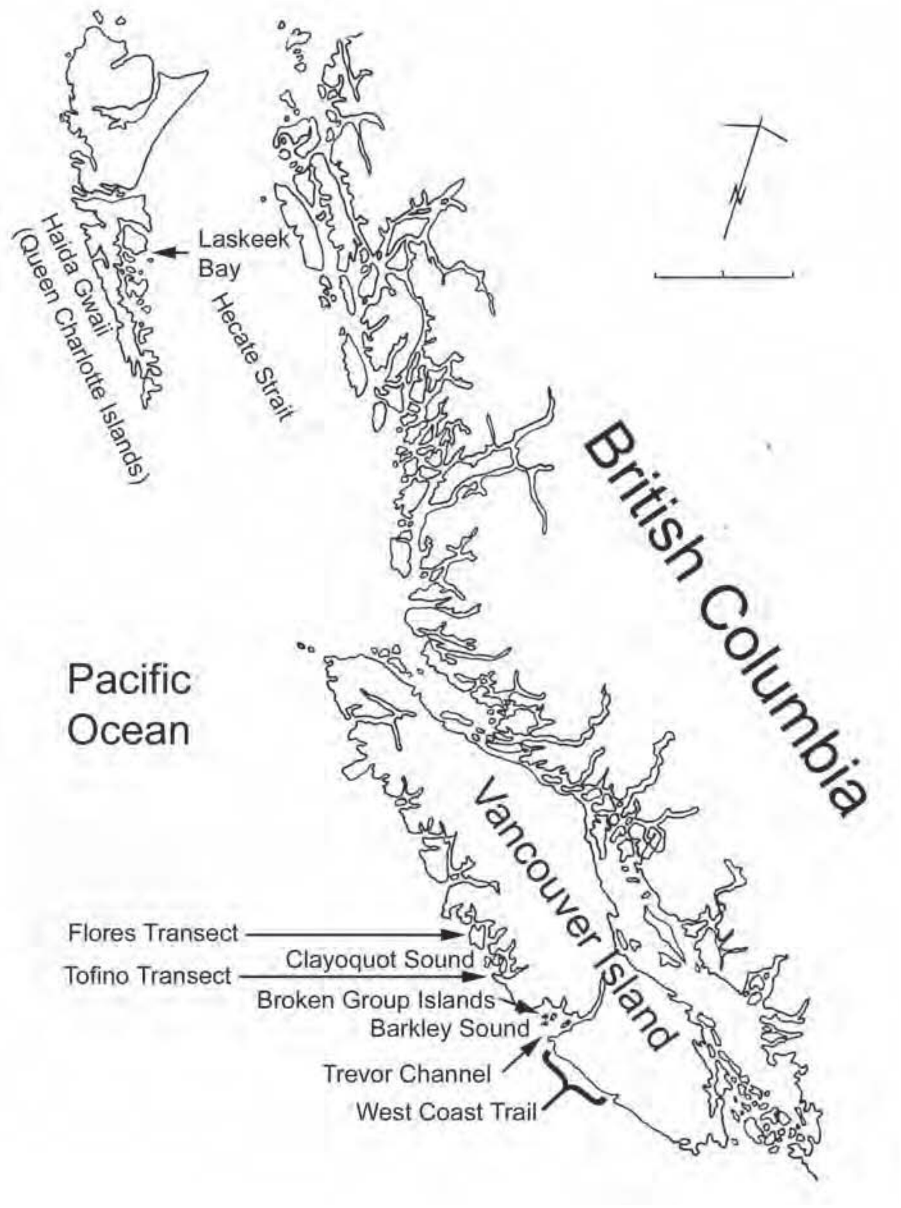


Figure 8. Location of sites where at-sea surveys were undertaken in British Columbia.

Overall we found declines in densities or counts of Marbled Murrelets in all six of the data sets covering the period 1979–2006, and the two data sets covering much shorter periods 1996–2000. Despite considerable within- and among-year variations in densities, these trends were statistically significant in five data sets (table 19). Statistically significant trends emerged from the three data sets with the most consistent sampling (Laskeek Bay, Broken Group Islands Inner, and West Coast Trail) and we feel the lack of significant trends in three data sets might be due to having insufficient sample sizes to overcome the natural variation in these at-sea data. The annual rates of decline in these data covering more than 10 years ranged from -5.8 to -14.6 percent (6.1–14.6 percent in the statistically significant data sets; table 19), and was much higher in the Tofino and Flores transects covering 1996–2000 (table 19). These estimated rates of decline are not intrinsically precise and the addition of another year or two of data will undoubtedly change the calculated rate. Nevertheless, these are high rates of decline for any population and indicate a potentially serious problem for the populations that they represent. In the four data sets with adequate sampling in recent years, we found no significant trends in densities since 1999, suggesting that the major changes occurred prior to this year.

Although some of the survey sites (Trevor Channel, Trevor-Beale-Seabird Rocks) were selected as study areas because of high densities of murrelets (Carter, 1984), there is no evidence that selection of sites with initial high densities produced a biased measure of trend. The high densities in the Trevor Channel area were well known to local residents for many years prior to Carter's (1984) study and Carter's unpublished data shows consistent high densities in both 1979 and 1980. Most of the other transects were long enough that they encompassed a wide range of habitats and murrelet densities (see Gaston, 1996; Mason and others, 2002; Bellefleur and others, 2005), reducing the likelihood that high counts in early years were spatial anomalies. Furthermore the large spatial coverage of seven transect routes on the west coast of Vancouver Island, all of which show declines, reduces the likelihood that the trends observed were due to local movements. We cannot, however, rule out larger scale emigration to other parts of the murrelet's range.

Burger (2002b) reviewed evidence for population trends of murrelets in British Columbia and the main points are briefly summarized here. Rodway and others (1992) found no clear trends in Christmas Bird Count (CBC) data from 1957 through 1988. This analysis has not been expanded to include more recent data, because few count areas overlap with significant wintering populations in British Columbia, and CBC data seem to be poor indicators of widespread population trends in this species (Hayward and Iverson, 1998b; Piatt, 1998).

There is anecdotal evidence that populations of Marbled Murrelets in the Strait of Georgia declined significantly in the early 1900s. Brooks (1926) commented on the scarcity of Marbled Murrelets along the east coast of Vancouver Island in 1925–26 compared with numbers observed in 1920 and earlier. Pearse (1946) reported a decline in numbers around Comox between 1917 and 1944, concomitant with the loss of large tracts of the surrounding coniferous forests. In more recent times, counts of birds along a 6 km stretch of shoreline at Boundary Bay, south of Vancouver, between November and August showed a decline from an average of 66 Marbled Murrelets in 1980–81 to 2 in 1994–95, and no birds in 1996 and 1997 (Cooke, 1999). Murrelets appear to have disappeared from Burrard Inlet near Vancouver since 1990 (G. Kaiser, quoted by Hull, 1999).

Table 19. Summary of trends of Marbled Murrelet counts and densities at eight marine transect routes in British Columbia.

[See appendixes D and E for details. Linear regressions were conducted on log-transformed annual means weighted by their variance. Statistically significant trends ($P<0.05$) are shown in **bold**. Sites are listed from south to north]

Site or transect route	Region	Range of years	Number of years sampled	Number of surveys	Slope	Rate of change percent per year	*R*-squared	*F*	df	*P*
West Coast Trail	West Vancouver Island	1994–2006	10	32	**-0.063**	**-6.1**	**0.53**	**9.02**	**1, 8**	**0.017**
Trevor Channel	West Vancouver Island	1980–2000	10	61	**-0.060**	**-5.8**	**0.58**	**4.93**	**1, 7**	**0.046**
Trevor/Beale/SBR	West Vancouver Island	1979–2005	6	20	-0.097	-9.3	0.48	3.72	1, 4	0.126
BGI Inner	West Vancouver Island	1991–2006	14	65	**-0.087**	**-8.3**	**0.72**	**30.85**	**1, 12**	**0.000**
BGI Outer	West Vancouver Island	1995–2006	10	41	-0.062	-6.0	0.17	1.67	1, 8	0.232
Tofino transect	West Vancouver Island	1996–2000	4	19	-0.375	-31.2	0.89	16.58	1, 2	0.055
Flores transect	West Vancouver Island	1997–2000	4	15	**-0.240**	**-21.3**	**0.98**	**86.03**	**1, 2**	**0.011**
Laskeek Bay	Haida Gwaii (Queen Charlotte Islands)	1992–2004	14	56	**-0.158**	**-14.6**	**0.39**	**7.79**	**1, 12**	**0.016**

Burger (2002b) analyzed data from audio-visual surveys made from 1991 through 1999 at 11 stations within the forest nesting habitat in the Carmanah and Walbran watersheds adjacent to the West Coast Trail on southwest Vancouver Island. A subset of the audio-visual detections, which indicate site occupancy, provided indirect measures of relative murrelet abundance. Mean frequencies of occupied detections showed a significant negative correlation with sea temperature (Burger, 2000), but Burger's (2002b) analysis, using analysis of covariance with sea temperature as a covariant, showed a significant negative trend over the 9 years (adjusted $r^2 = 0.347$, $P < 0.001$; see appendixes D and E). Since 1990, there has been no logging in the Carmanah valley, but parts of upper Carmanah were logged in the late 1980s and logging continued in the upper Walbran close to the observation stations.

Radar counts made during the breeding season at the mouth of the Bedwell-Ursus Watershed in Clayoquot Sound showed a significant decline in the years 1995–98, which corresponded to declines in annual mean detections in audio-visual surveys made in the same drainage (Burger, 2000). This could not be attributed to logging because there had not been any logging in that drainage for 40 years. There was a weak non-significant negative correlation with local sea temperatures in both the radar and audio-visual detections (Burger, 2000).

Overall, these published data and reviews show a consistent pattern of decline in numbers of Marbled Murrelets wherever there are reasonable data to test trends in British Columbia.

Demographics and Population Dynamics

This section presents an in-depth treatment of demography and population dynamics of the Marbled Murrelet. We first review the history of previous efforts to model Marbled Murrelet populations. Then, using what we felt to be reasonable vital rate estimates (for fecundity and adult survival) for Marbled Murrelets, we present potential resultant population growth rates using two models: (1) a deterministic, life table model; and (2) a matrix model incorporating stochasticity. We use the models to explore how variations in vital rates affect population trends. These modeling exercises provide context for understanding the likely significance and need for conservation concern about murrelet population trends observed empirically.

Survivorship, Fecundity, and Age at Maturity

Knowledge of a species' survival rates is essential for demographic analyses, but rates of survival of Marbled Murrelets at every life stage are poorly known. Adult survival has been estimated in two ways: (1) as a prediction from the literature based on allometric relationships observed in other alcids (Nur, 1993; DeSanto and Nelson, 1995); and (2) using data from two field investigations that used mark-recapture methods in Desolation Sound (Cam and others, 2003) and central California (Peery and others, 2006b). From the relationships among survival rate, body size, and clutch size in the alcid family, Nur (1993) predicted the survival of adult murrelets should be about 0.85. Cam and others (2003) reported two estimates derived from samples of murrelets captured by different techniques. For a sample obtained with night-lighting and dip-nets, they calculated an adult survival rate of 0.83 (95 percent CI: 0.716–0.903), whereas birds captured with a mist-net deployed over water produced a higher value, 0.93 (95 percent CI: 0.629–0.990). Trap shyness may have contributed to lower recapture rates by dip-netting. The sample was thought to include a larger proportion of subadults than the mist-netted group, which also would affect the estimation of survival if pre-breeders had lower survival or lower fidelity to the study area (Cam and others, 2003). Finally, the authors' estimated rate of population growth was 0.86 in conjunction with the 0.83 estimate of survival, i.e., a decline of 14 percent per year. That amounts to a 95 percent population decline in 20 years, or 75 percent in 10 years—the duration of the field study reported by Cam and others (2003). The authors make no mention of a large (and presumably noticeable) population decline during their study, which suggests the 0.83 estimate of adult survival is too low.

In central California, Peery and others (2006a) obtained estimated annual survival rates of 0.868 (SE = 0.074) for males and 0.896 (SE = 0.067) for females (all birds captured by dip-netting at night). Those estimates incorporated the survival of subadults (ages ≥ 1 year), because adults and subadults could not be distinguished in the field. Survival of subadults probably is lower than adult survival, but breeding success was poor in central California (Peery and others, 2004b; Peery and others, 2006b), thus the representation of subadults in the marked sample may have been small.

Little is known about juvenile survival in Marbled Murrelets. Parker and others (2003) estimated a survival rate of 0.862 for the first 80 days post-capture among recently fledged juveniles in Desolation Sound. The extrapolated annual rate of survival over the first year of life was 0.51, but that calculation assumes no change in daily survival between the first 80 days and subsequently, which is probably unrealistic (Parker and others, 2003). In the following section, "Population Models," we will model murrelet populations using survival rates for first-year juveniles (0-1 years of age) and second-year subadults (1-2 years of age) estimated by the levels (expressed as proportions of adult survival) seen in other alcids. Nur's (1993) review suggested that reasonable estimates would be 70.1 and 88.8 percent of adult survival for first- and second-year birds, respectively.

In addition to survival, fecundity, the annual production of female offspring per adult female in a population, is an essential input to population models. To estimate fecundity, nesting success is divided in one-half, and further adjustments may be needed to account for adults that skip breeding (breeding propensity) and for multiple breeding attempts within a year (double clutching or renesting). Double clutching (production of more than one brood per year) is unknown in Marbled Murrelets, but replacement laying (a second clutch following a failed first attempt) has been estimated at 13–63 percent annually (McFarlane Tranquilla and others, 2003a). The difference, if any, between the average success of first and second nesting attempts is unknown. The percentage of non-breeding adults was estimated at 22 percent in Desolation Sound (McFarlane Tranquilla and others, 2003c), whereas McShane and others (2004) suggested that it should be less than 10 percent for most Marbled Murrelet populations in most years, as is seen in other alcids. For our models, in the absence of definitive data, we will assume that the effect of a breeding propensity <1 is offset by successful renesting, and that uncorrected nesting success (divided by 2) is a reasonable approximation of fecundity.

At-sea ratios of juveniles to adults are an alternative measure of fecundity, but they suffer from a number of potential biases, as discussed earlier. The ratios also will differ from estimates of nesting success because they incorporate early post-fledging mortality.

The age of first breeding is unknown for Marbled Murrelets, but is thought to occur anywhere from age 2 to 5 and most commonly at age 3 (DeSanto and Nelson, 1995; Burger, 2002). Other studies have modeled murrelet populations using various assumptions about the breeding propensities of murrelets between 2 and 5 years of age (Beissinger, 1995b; McShane and others, 2004). In the absence of specific data, we will use a uniform value of 3 years for purposes of modeling population dynamics, below.

Population Models

When a population is monitored over a substantial period of time it typically exhibits trends – sometimes it increases, at other times it declines. Two technical elements are key when monitoring and then interpreting subsequent results:

1. Much attention is given to the issue of statistical significance. We want to be sure of statistically detecting a trend. Statistical power analysis is a helpful tool in designing sampling protocols with known probabilities of detecting trends (Kuletz and Kendall, 1998; Jodice and others, 2001; Smith and Harke, 2001; Hatch, 2003); and
2. Once a statistically significant trend is detected, how are the biological factors controlling the population trend understood? In other words, what is the biological (as opposed to statistical) significance of the trend? Is the population on a trajectory that would be unlikely to occur as an outcome of natural fluctuations in fecundity and survival?

In this section, we explore population growth outcomes for different scenarios of published biological metrics using two model approaches. These models help inform possibilities for evaluating the biological significance of trends detected through monitoring. We preface that discussion with an overview of prior efforts to model the population dynamics of Marbled Murrelets, and we demonstrate a convenient method for calculating the expected growth rate of a population.

Previous Studies

Modeling efforts pertaining to murrelet populations outside of Alaska are reviewed by Burger (2002b), Lank and others (2003), and McShane and others (2004). Briefly, models created prior to the latest review (McShane and others, 2004) used some version of a three-stage (juveniles, subadults, adults) projection model to predict population growth deterministically (i.e., no allowance for stochastic variation) given the best available estimates of fecundity, survival rates, and age at first breeding (Beissinger, 1995b; Beissinger and Nur, 1997; Boulanger and others, 1999; Boulanger; 2000; Peery and others, 2002). None of the models incorporated population density as a possible influence on birth and death rates. McShane and others (2004) developed a stochastic matrix model with multiple adult age classes to address assumptions implicit in the earlier models—namely, unlimited maximal longevity, and invariant rates of productivity and survival. All models pertaining to murrelets in the southern portion of their range (Washington, Oregon, and California) have predicted population declines of 2 to 6 percent per year. McShane and others (2004) found extinction in less than 100 years is likely within some of the conservation zones delineated in the species recovery plan.

In Desolation Sound, British Columbia, Cam and others (2003) concluded that their study population probably was declining slowly (replacement rate 0.985), but the range of model estimates included the possibility of a stable or slightly increasing trend. These results were due in part to the higher estimates of productivity and survival they obtained from their field studies.

A Deterministic Model of Population Growth—Program LIFE

The timing and magnitude of population growth (defined as a positive or negative change in population size) is an outcome of the mean values of population vital rates (fecundity, survival, age at first breeding) and the variability of those parameters. Variability can be age-related—e.g., individuals may become more productive with breeding experience, old individuals and subadults may survive at different rates than young adults –and it also can arise from environmental variation or the influence of population density. Whereas age-structured models with time-varying inputs are required to examine the complexities of population growth, it is often desired simply to calculate the expected growth rate of a population for a given set of known or hypothetical values of key demographic parameters—i.e., the question is simply whether the population of interest would be expected to grow, decline, or remain relatively stable. A tool for doing this is described below.

The expected growth rate of a population with discrete but overlapping generations can be calculated from the following equation (adapted from Fisher, 1966, p. 37):

$$\lambda^{\delta} = \alpha^{-1} + \alpha\ \beta^{\ \delta}, \qquad (1)$$

where,

λ = population growth rate (also called ‘net replacement rate’);

α = fecundity;

γ = adult survival (proportion of adults surviving from time *t* to time *t*+1);

β = juvenile survival (proportion of subadults surviving from time *t* to time *t*+1); and

δ = age at first breeding (years expressed as integer value).

This relationship applies when there is no upper limit on adult longevity (i.e., no senescence), no variation in the demographic parameters α, γ, β, and δ, and production is considered to occur in a pulsed, simultaneous manner annually (i.e., the breeding season takes “zero” time). The last assumption can be relaxed by subtracting from δ a quantity representing the fraction of a year taken up by one complete breeding cycle (about 70 days, or 0.19 year in Marbled Murrelets; Fisher, 1966). That refinement makes little sense in the present context, however, because the discrepancy is incorporated in the value of β, which is only crudely estimated anyway.

An intuitive grasp of equation (1) can be gained by considering how it applies to a stationary population. When $\lambda = 1$, the left side reduces to unity and the first term on the right reduces to γ (which also could be expressed as $1 – m$, where m is the annual mortality rate of adults). The second term on the right expresses the number of young recruited in year δ from an initial cohort of α young per adult (i.e., it is the cohort size at fledging reduced by the juvenile survival rate applied over δ years). Thus, in the special case where $\lambda = 1$, the equation is satisfied when adult mortality is exactly offset by recruitment.

Equation (1) is unrealistic insofar as survival in each of the prebreeding years is assumed to be equal to the mean value for ages 0 to δ. It generally is thought that juvenile mortality in seabirds is concentrated in the first year or two of life, after which the survival rate approximates that of adults (Lack, 1966; Nelson, 1966; Potts and others, 1980). Thus, a more realistic model is:

$$\lambda^{\delta} = \gamma\lambda^{\delta-1} + \alpha\ b_1 b_2 \gamma^{\delta-2}, \qquad (2)$$

where b_1 is first year survival (age 0–1), b_2 is second-year survival (age 1–2), and the other parameters are defined as before.

Because λ is exponentiated on both sides of equation (2), the growth rate is most readily evaluated by iterative interpolation using a computer. This solution has been implemented as a short Javascript program (appendix B), which can be used for estimating population growth rate when the other parameters are entered as known or hypothetical values. Using program LIFE, we calculated the expected growth rate of the Alaska population of Marbled Murrelets under various scenarios, ranging from the worst to the best combination of available estimates for adult survival and fecundity. For adult survival, we used the lower and higher estimates (and their mean) obtained in the mark-recapture study of murrelets in Desolation Sound (Cam and others, 2003). For fecundity, we used raw and adjusted HY:AHY ratios reported for Kachemak Bay (Kuletz and Piatt, 1999), and the estimated nesting success of murrelets in Desolation Sound, as determined by Bradley and others (2004) from radio-telemetry.

Given the amount and quality of demographic data currently available, and considered appropriate to Alaska murrelets, we can say only that predicted population growth ranges from strongly negative (about –9 percent per year) to strongly positive (about 5 percent per year), with intermediate values of the input parameters producing a population that is approximately stable (table 20).

Table 20. Predicted population growth rates of Marbled Murrelets in Alaska using the demographic model LIFE.

Scenario[1]	Adult Survival[2]	Fecundity[3]	Population Growth Rate (λ)[4]	
Pessimistic	0.83	0.19	0.911	(0.901)
		0.24	0.929	(0.923)
		0.26	0.936	(0.930)
	0.88	0.19	0.966	(0.961)
↓		0.24	0.985	(0.981)
		0.26	0.992	(0.988)
	0.93	0.19	1.021	(1.021)
		0.24	1.041	(1.039)
Optimistic		0.26	1.047	(1.044)

[1] Age at first breeding 3 years for all calculations, with first- and second-year survival estimated at 0.701(adult rate) and 0.888(adult rate), respectively.

[2] High, low, and mean values of Marbled Murrelet adult survival, as estimated by Cam and others (2003) using mark-recapture methods in British Columbia.

[3] Fecundity estimated by HY:AHY ratios in Kachemak Bay (low value; Kuletz and Piatt, 1999), the same estimate adjusted for possible inclusion of nonbreeding subadults in the ratio (high value; see text), and fecundity based on nesting success of murrelets in Desolation Sound, British Columbia (Bradley and others, 2004).

[4] Values in parentheses are corresponding rates calculated by program MATRIX for comparison; they differ from the LIFE estimates because of differing assumptions about maximal longevity (see text).

A Flexible Model of Population Growth—Program MATRIX

The deterministic life table equation (2) and program LIFE are useful for calculating the expected growth rate of a population when estimates of the basic demographic parameters are available. To project actual population levels over finite periods of time, however, it is necessary to model the demographic parameters not as constants but as variables, subject to change over time for the whole population or with the age of an individual. The common approach for doing this uses some version of the matrix model of population growth introduced by Leslie (1945). Briefly, the basic set-up is as follows:

$$\text{If } \mathrm{M} = \begin{bmatrix} f_0 & f_1 & f_2 & f_3 & f_4 & f_5 & \cdots & f_{k-1} & f_k \\ s_0 & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & s_1 & 0 & 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & s_2 & 0 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & s_3 & 0 & 0 & \cdots & 0 & 0 \\ 0 & 0 & 0 & 0 & s_4 & 0 & \cdots & 0 & 0 \\ \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & & \vdots & \vdots \\ 0 & 0 & 0 & 0 & 0 & 0 & \cdots & s_{k-1} & 0 \end{bmatrix} \text{ and } \vec{N}_t = \begin{bmatrix} N_0 \\ N_1 \\ N_2 \\ N_3 \\ N_4 \\ \vdots \\ N_k \end{bmatrix} \text{ then } \mathbf{M}\vec{N}_t = \vec{N}_{t+1}$$

The f_i are age-specific fecundities (number of offspring produced in each time interval *t* by a female of age *i*) and the s_i are age-specific survival rates. Maximal longevity is denoted by *k*—all individuals surviving at age *k*-1 are assumed to die within the next time interval. N_t is a column vector expressing the number of individuals in age class *i* alive at time *t*, and the sum of the N_i is equal to population size. The square array of fecundity values and survival rates **M** is often called the "projection matrix" because it contains the information necessary to project the population into the future. When the vector N_t is multiplied by matrix **M**, the result is a new vector N_{t+1}, potentially with a new sum (population size) and age distribution (proportions of individuals in the age classes N_o to N_k). Mathematically, the age distribution tends toward a fixed array (called a stable age distribution) that is characteristic for any fixed set of f_i and s_i. As long as the f_i and s_i remain unchanged, a population that has reached its stable age distribution retains that distribution indefinitely, even as the population grows or declines.

Originally, population biologists viewed the Leslie matrix model as a simple heuristic tool, limiting its application to cases where the f_i and s_i were modeled as constants. With the aid of a computer, however, it is possible to let the parameters change according to any hypothetical scheme and thus to model population behavior more realistically (e.g., Pollard, 1966; Searle, 1966; Goodman, 1969).

We implemented the Leslie matrix model of population growth in a Fortran program called MATRIX (appendix C). The user enters proposed mean values and SDs for α (annual fecundity), γ (adult survival), b_1 and b_2 (first and second-year survival expressed as proportions of adult survival), and δ, the age of first breeding (modeled here as a constant in MATRIX). Program outputs include:

- λ, the expected population growth rate (as in program LIFE);
- α_{adj}, the adjusted rate of fecundity needed to achieve a stationary population ($\lambda = 1$) given the survival schedule entered by user;
- The stable age distribution calculated for the demographic parameters as entered;
- The stable age distribution for a population with $\alpha = \alpha_{adj}$ and $\lambda = 1$;
- The population trajectory that results when parameters in the projection matrix are held constant at their user-entered mean values;
- Examples of population trajectories that result when parameters in the projection matrix are allowed to vary stochastically;
- Mean time to population extinction and a distribution of extinction times for the calculated λ and for the special case $\lambda = 1$; and
- Trend frequencies over intervals of 10, 20, and 30 years that result when input parameters are allowed to vary stochastically.

By allowing stochastic variation in the values of most demographic parameters, the projection of population size through time is made more realistic than is possible using a strictly deterministic model such as LIFE. As no data are available on the age-specific rates of fecundity or survival of adult murrelets, our simulations use best estimates of mean rates for all f_i and s_i. Cam and others (2003) reported two estimates of local survival. The first (0.829) they considered probably was biased low (as an estimate of adult survival) because it included subadult birds in the sample. The second estimate (0.929) they suggested possibly was biased high because it sampled primarily the successful breeding component of the population. The mean of the two estimates is 0.879. Peery and others (2006b) reported separate estimates for male (0.868) and female (0.896) murrelets, the mean of which is 0.882. We therefore used a value of 0.88 annual adult survival for applications of the matrix model. Following Beissinger (1995b) and McShane and others (2004), we assumed that first-year survival is 0.701 times the adult survival rate and second-year survival is 0.888 times the adult rate—values based on what has been reported for other alcids (Beissinger, 1995b). We included all murrelets 3 years of age or older in the adult (breeding) population, and the initial conditions for each simulation included a stable age distribution (calculated initially by MATRIX for the given set of parameter inputs). We used a mean fecundity of 0.24, corresponding to the mean nesting success (0.48) of radio-tagged murrelets over a 4-year study in Desolation Sound, British Columbia (Bradley and others, 2004; table 5).

Stochastic variability at each iteration of the model (i.e., annually) is simulated by drawing random values from distributions of annual productivity and survival, which in turn are dictated by the means and SDs supplied as inputs. The CV in annual nesting success of Marbled Murrelets was 0.357 in the study by Bradley and others (2004). In our simulations, we calculated the fecundity required of murrelets for $\lambda = 1$ (with annual survival of 0.88) to be 0.295 (see below). Applying the observed CV to a fecundity of 0.295 provides an estimate of 0.105 (SD) for interannual variation in fecundity. Annual estimates of murrelet survival (*n* = 6) in California ranged from about 0.83 to 0.97 (fig. 3 in Peery and others, 2006b), with an SD of 0.059. Thus, on the information currently available, we took 0.1 as the best estimate of interannual variation (SD) in fecundity (α), and 0.06 as the SD of survival rates (γ, b_1, and b_2) in Marbled Murrelets. To gauge the sensitivity of model results to the accuracy of those inputs, we also ran simulations using $SD_\alpha = 0.2$ and $SD_\gamma = 0.1$ (a "high variability" example) as well as $SD_\alpha = 0.05$ and $SD_\gamma = 0.02$ (a "low variability" example).

A final technical note is necessary concerning our parameterization of the MATRIX model. In a Leslie matrix model, the f_i assume that the youngest cohort includes only females that survive until the time interval in which they were produced has passed. At the end of that interval, they are all considered to be of age 0 (Batschelet, 1971). Similar to the LIFE model (see above), we make the simplifying assumption that all young are produced simultaneously, and the concomitant assumption that the first-year survival rate of juveniles applies over an entire year. The approach is sensible when juvenile survival is poorly known, and the effect on model behavior is negligible when the input parameters are set to produce an expected λ equal to 1. That special case (expected $\lambda = 1$) is the focus in the discussion to follow.

Our approach is essentially the one employed by McShane and others (2004). Their analysis predicted extinction for the California population(s) of murrelets within 100 years. McShane and others (2004) used demographic parameters considered appropriate for California Marbled Murrelets, which had been shown by Beissinger (1995b) to result in rapid population decline. One effect of adding stochasticity is that it hastens, on average, the inevitable outcome, which is extinction. It is important to realize, however, that stochastic variation of birth and death rates in such a model (with birth rates $\leq$ death rates) ensures that the simulated population eventually goes extinct, *even when the means of the input parameters are set to produce an expected* λ *equal to 1*.

To illustrate this, we ran a relatively small population of murrelets (starting population size 3,000) repeatedly through a simulated future using MATRIX. We set fecundity and survival such that the expected λ is equal to 1 ($\gamma = 0.880$, $b_1 = 0.701$, $b_2 = 0.888$, and $\alpha = 0.295$ as calculated by MATRIX for $\lambda = 1$). We resampled values for fecundity (α) and survival (γ, b_1, and b_2) annually from normal distributions of those parameters, as described above. We applied the same random variates to juvenile and adult survival on the assumption that those parameters are likely to vary concordantly. However, for this (and subsequent) applications of MATRIX, we considered two scenarios, termed 'seasonal independence' and 'seasonal concordance.' The first option models the situation in which annual survival and annual productivity vary independently—those two parameters do in fact reflect environmental factors that impinge primarily at different seasons, winter and summer—while the alternative (seasonal concordance) is a scenario in which "good" and "bad" years affect both parameters equally.

In all cases in which birth and death rates are allowed to vary stochastically, the simulated population (with expected $\lambda = 1$) goes exinct (fig. 9). That outcome happens sooner on average with seasonal concordance, because the effect of low and high values of fecundity and survival is accentuated. The reason why a "stochastic" population (with expected $\lambda = 1$) always goes extinct has to do with the multiplicative nature of birth and death rates. The population is on a "random walk." Early on there can be large changes, up or down, but eventually the population will wander to low levels from which it is simply not possible to recover because the absolute number of individuals (as opposed to percentage) being added or subtracted each year is too small to reverse the trend (given the SDs of the input parameters).

It should be noted that we took a threshold value of 5 percent of N_o as our definition of extinction. This assumption seems reasonable when starting with a small population (such as 3,000), because with a 95 percent reduction there are only 150 individuals remaining. From a practical standpoint, that equates to extinction, especially given the likelihood of an Allee effect, whereby a population that reaches a low threshold experiences negative density dependence (for logistic and behavioral reasons) and proceeds rapidly to extinction (Boyce, 1992). Mathematically, however, it may take considerably longer for a population to walk randomly to its literal extinction (i.e., less than one individual remaining) than what is suggested by the end points depicted in figure 9.

By running a large number of simulations, it is possible to show the expected distribution of extinction times (fig. 10). As mentioned, extinction occurs sooner with seasonal concordance – the mean time to extinction is 616 years versus 1,030 years in the alternative model – but is highly variable in either case. There is a small possibility of a population with $N_o = 3,000$ going extinct in fewer than 100 years. To reiterate, this outcome applies to a population with mean rates of fecundity and survival that predict a stationary population.

The concept of inevitable extinction in a stochastic model may be unfamiliar, so it is worth mentioning that this outcome is well-grounded in mathematical theory (Pielou, 1969; Krebs, 1978). For a population with instantaneous birth and death rates (denoted b and d, with $d = 1 - \gamma$) that are subject to stochastic variation, the probability of extinction is a finite value that approaches $(d/b)^{No}$ as time becomes very large (Krebs, 1978). That is, extinction probability depends on initial population size and the ratio of birth and death rates. For the special case in which birth and death rates are equal, the expression reduces to 1, regardless of population size. Given enough time, extinction is the inevitable fate of such a population. [Readers who try the formula in relation to murrelet population models will find that the relatively rapid extinction observed in many simulations seems inconsistent with theory. There are two reasons for this discrepancy: (1) the formula predicts literal extinction (<1 individual remaining), whereas we use a threshold of 5 percent of N_o remaining as our functional definition of extinction; and (2) the theory is expressed in terms of instantaneous rates, whereas the model rates are finite—i.e., birth and death are measured on time intervals of 1 year. The principle is the same, but extinction will occur sooner on average in a discrete time population model.

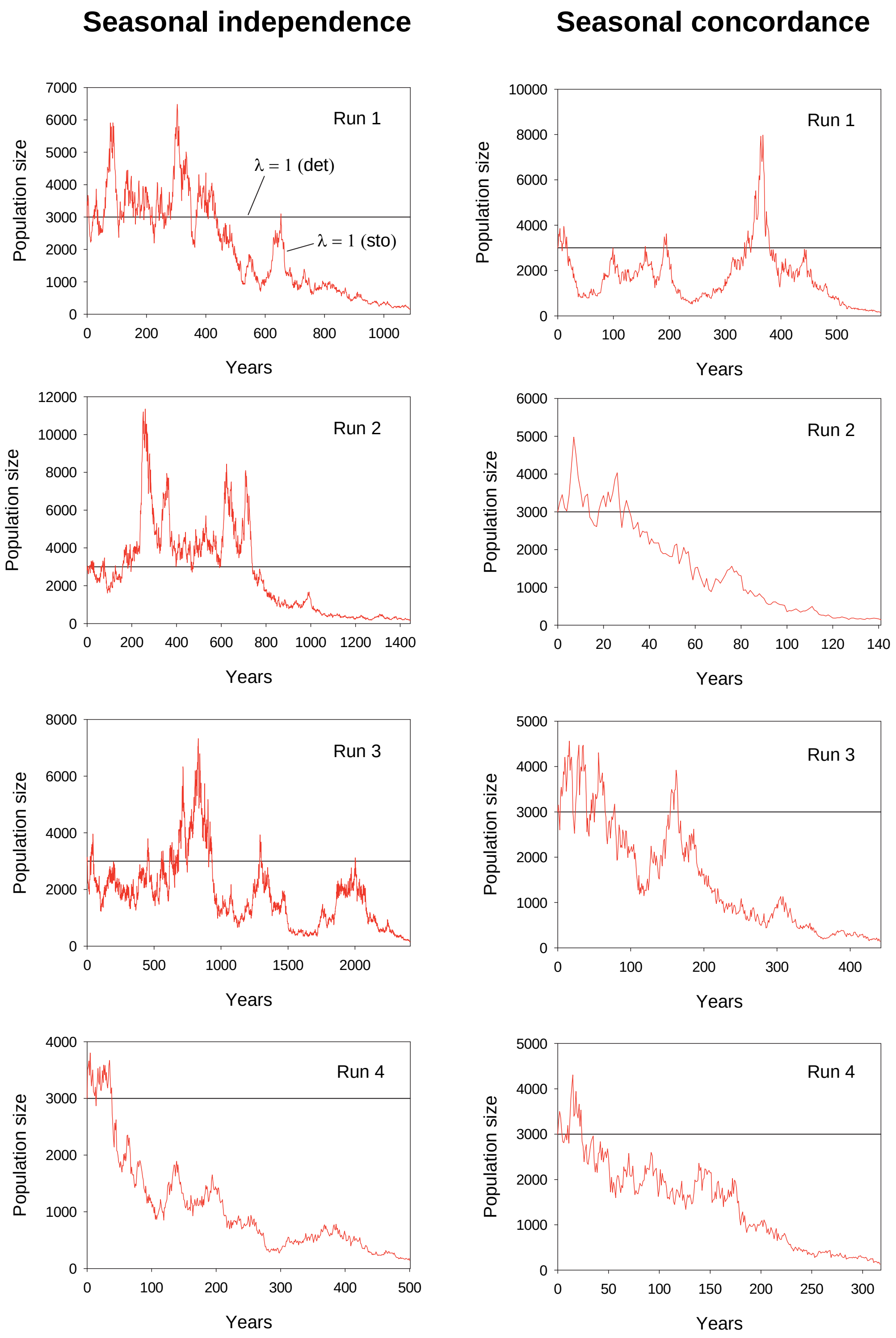


Figure 9. Examples of projected numbers for a population of 3,000 Marbled Murrelets with and without stochastic variation in survival and fecundity. Mean values of demographic parameters are the same for the "deterministic" (det) and "stochastic" (sto) populations. "Seasonal concordance" and "seasonal independence" indicate linkage or absence of linkage between the annual variations in fecundity and survival. Initial conditions and model procedures are the same for all runs.

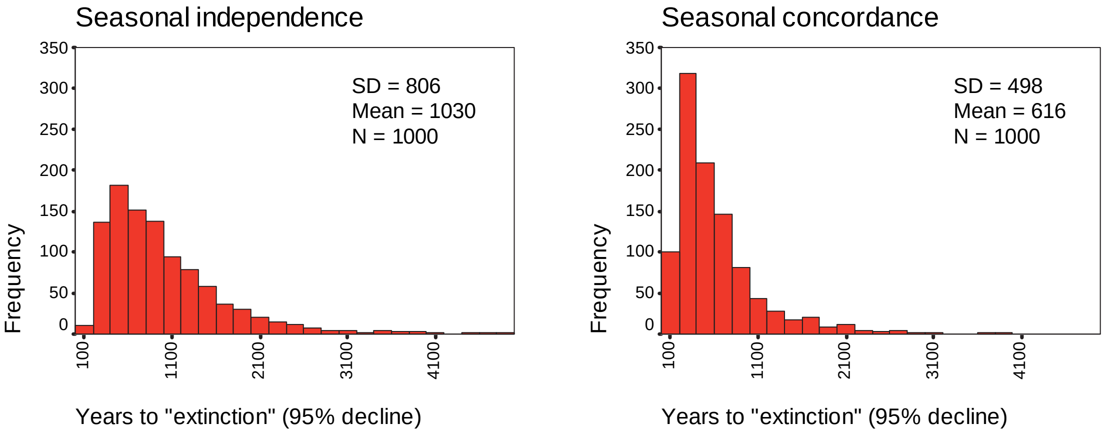


Figure 10. Variability of extinction times for a small population of Marbled Murrelets (No = 3,000) when $s_u$rvival and fecundity are subject to stochastic variation. Distributions reflect the frequency of outcomes in 1,000 trials under conditions of seasonal independence and seasonal concordance.

In natural populations, birth and death rates often vary in a manner that appears outwardly to be stochastic, yet those populations ordinarily do not go extinct over observable periods of time. The explanation of this paradox lies in density dependence—variation in birth and death rates is in fact not entirely stochastic, but is mediated to some extent by population size, or density. The interplay of stochastic and deterministic controls on demographic parameters is shown schematically in figure 11. It would seem like a good idea to model density dependence by superimposing on the stochastic variation a certain amount of density dependent regulation. The problem is that we know virtually nothing about the functional relationships between birth and death rates and population density for most natural populations, and Marbled Murrelets are no exception. We could achieve different outcomes using the models, depending on what we are inclined to believe about density dependence. Unfortunately, our applications of MATRIX omit this essential, but unknown effect, as have previous models for murrelets.

We point out that the estimates of λ from programs LIFE and MATRIX are not identical for the same inputs (table 20). This is because an upper bound is placed on longevity in the matrix model but not in the life table equation. In our implementation, the size limit of the projection matrix is established by the age at which fewer than 5 percent of a cohort remain alive—all adults of that age are assumed to die within 1 year. The resulting maximal longevity (with an age-constant γ = 0.880) is 27 years. This difference in model assumptions affects the predicted λ to a small degree, even when birth and death rates are modeled as constants in MATRIX.

Applying a matrix model to Marbled Murrelets is a qualitatively different exercise in Alaska than in California, because the subject population is much larger in Alaska. If we use the same model inputs as before but start with a population of 300,000 individuals (as an example), the mean time to extinction (5 percent of original population remaining) is unchanged—all populations, regardless of size, have the same distribution of “extinction” times depicted in figure 10. However, when our hypothetically large population declines to 5 percent of original numbers, it still contains some 15,000 individuals, which is not a reasonable definition of extinction. The population would likely exhibit episodes of recovery, perhaps repeatedly, before reaching a realistic measure of extinction, such as 150 individuals remaining.

When dealing with a large population of murrelets, as in Alaska, the issue is not so much whether or when the population will become extinct. A more practical application of MATRIX in this situation is the estimation of stable-age distributions. When any combination of inputs (α, γ, b_1, b_2, and δ) are entered, MATRIX reports the stable-age distribution that results from those parameters, and also the stable-age distribution that would occur at λ = 1 (α having been adjusted to achieve that outcome). This information can be used to estimate the size of the subadult population —an important statistic about which little is known directly. Although the estimates are no better than the quality of inputs for productivity and survival, they can be useful as a working approximation. In the present case, an Alaska population with α = 0.24 and γ = 0.880 is expected to be slowly declining (table 20) and to have about 26 percent of total numbers in the subadult year classes (fig. 12). MATRIX calculates that

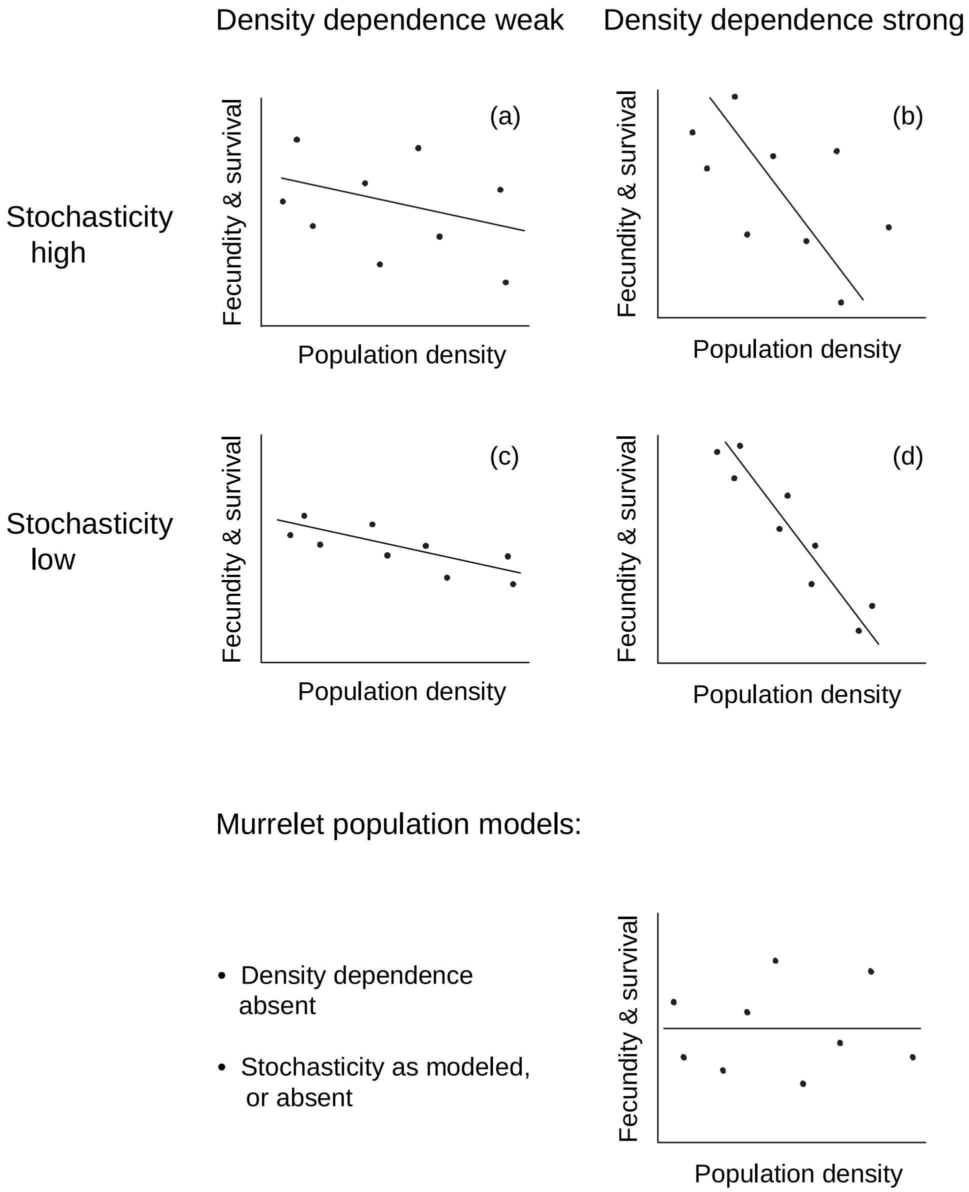


Figure 11. Contributions of stochastic and density-dependent effects to variability in population size. A population in long-term equilibrium exhibits large deviations when birth and death rates are highly variable but unresponsive to density (a), or small deviations when stochastic effects are slight and density dependence is strong (b). Intermediate conditions are depicted in (c) and (d).

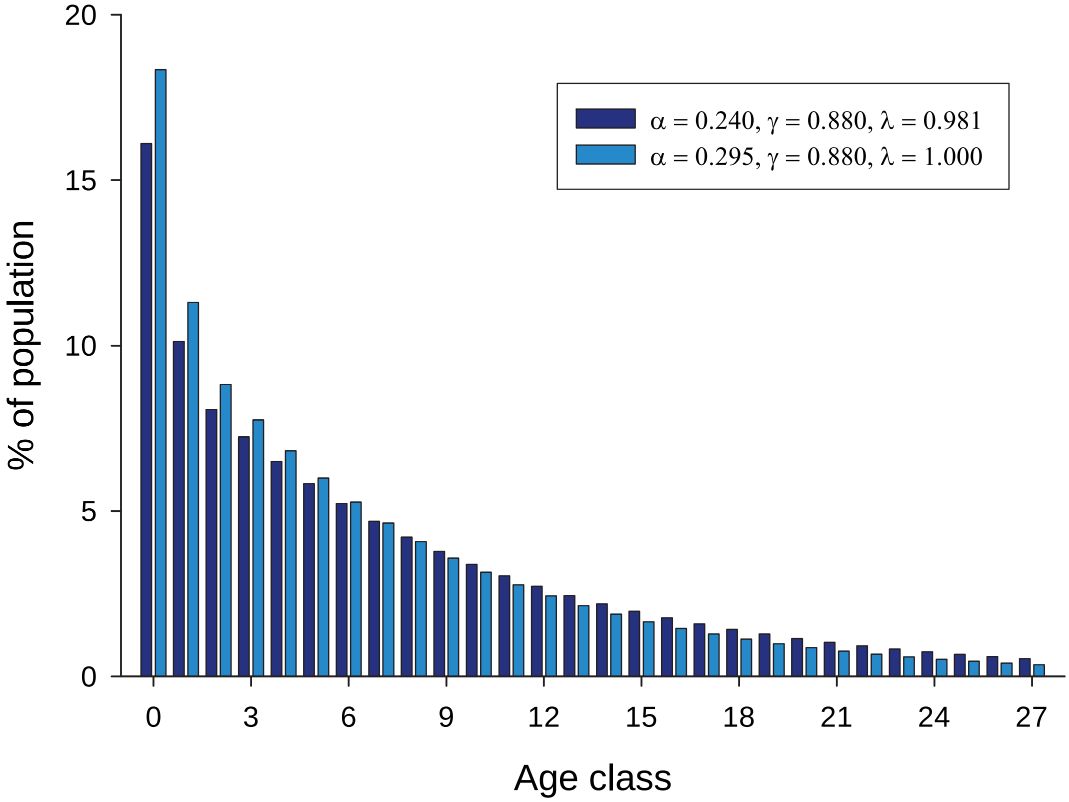


Figure 12. Stable-age distributions calculated by MATRIX for a stationary population of Marbled Murrelets ($\lambda = 1$) and another declining at the rate of 2 percent per year.

a fecundity of 0.295 is required for a stationary population, given $\gamma = 0.880$, $b_1 = 0.701$, $b_2 = 0.888$, and $\delta = 3$. In that case, the cohorts of subadults are 18.3 percent 1-year-olds and 11.3 percent 2-year-olds (fig. 12), for a total of 29.6 percent subadults in the population. Therefore, subadults (excluding juveniles, age 0) compose an estimated 22–25 percent of AHY murrelets. Applying that information to field data, a HY:AHY ratio can be adjusted for the proportion of AHY birds that are non-breeding subadults, giving a better estimate of fecundity. A necessary assumption is that adults and subadults are distributed similarly with respect to the areas surveyed. For Kachemak Bay (Kuletz and Piatt, 1999), the juvenile index of 0.192 (all transects combined) means that productivity was not 19 young per 100 adults, but something closer to 19 young per 75 adults (0.255) or 19 young per 78 adults (0.245). That is the basis for the most "optimistic" scenarios considered in table 20.

In Alaska, the most important application of MATRIX concerns the problem of interpreting the biological significance of trends. When we consider the variability of animal numbers from a conservation perspective, we have only two options for deciding what is normal, or natural: (1) we can monitor populations under natural conditions for a sufficient period of time that the range of natural variation (in trends, not numbers) has been observed and quantified statistically—in the case of long-lived animals such as seabirds, a study duration of hundreds, or even thousands of years may be needed to do the job; or (2) we can model populations in ways that predict the frequency of trends of any given duration and magnitude. In that case, we would compare an observed trend with the expected distribution of trends and judge its biological significance in a manner analogous to the conventional use of probability in statistics. This is where a program such as MATRIX can contribute, because it allows us to calculate for the modeled population the frequencies of trends to be expected purely by chance. In the stochastic model, trends arise from the chance juxtaposition in time of high and low levels of productivity and survival and, especially in the case of seasonal concordance, the chance concatenation of “good” and “bad” years into runs that produce either favorable or unfavorable trends in a population.

For Marbled Murrelets, we calculated the distributions of trends arising by chance in a population with its demographic parameters set so that $\lambda = 1$, but with stochastic variation in fecundity and survival causing variability around a short-term equilibrium value (short-term, that is, in relation to the mean extinction time, as discussed previously). The input values, as before, were $\gamma = 0.880$, $\alpha = 0.295$, $b_1 = 0.701$, $b_2 = 0.888$, and $\delta = 3$. The stochasticity arises from SDs of 0.1 and 0.06 in fecundity and survival rates, respectively. This was done for study intervals of 10, 20, and 30 years, which may be thought of as typical benchmarks in a monitoring program for wildlife populations. Distributions are generated by running the same starting population to extinction (<5 percent remaining) a large number of times ($n = 1{,}000$) and calculating for every interval of 10, 20, or 30 years the percentage change in population that occurs from beginning to end of the interval.

On average, the change over any 10-, 20-, or 30-year period is approximately 0 (as expected), but ranges from more than +100 percent (a population doubling) to declines greater than 60 percent that arise solely from the stochastic variation in birth and death rates (fig. 13). The probability (biological significance) of an observed trend can be interpreted from the graphs. The sensitivity of this analysis to the SDs of survival and fecundity (SD_γ and SD_α) is characterized in figure 14 (a higher variance example) and figure 15 (a lower variance example). One general conclusion from these simulations of random-walking effects may be counterintuitive—the longer a population has been observed, the more likely it is that any observed trend is due to chance.

What should be the rarity of a given trend before we would consider it biologically significant, i.e., what is an appropriate action threshold? Should we follow the usual convention in statistics and label a trend as significant only if it would be expected to occur by chance fewer than 5 times in 100 trials? Probably not—from a conservation standpoint, we may prefer to err on the safe side, treating trends of lower magnitude as probably unnatural and requiring attention. Also, there is a built-in tendency for the distributions depicted in figures 13, 14, and 15 to be wider than they are in nature, because no effect of density dependence is included in the model. In that sense, this application of the MATRIX program can be viewed as “non-alarmist” – the possibility of accepting a trend as normal, when in fact it is not, is more likely than deciding that a trend requires action, when in fact it reflects normal population dynamics. As always, the conclusions one derives from modeling are only as sound as one’s assumptions and inputs. The approach described here may be applied with increasing confidence as our knowledge of the means and variability of vital parameters, including their responses to population density, increases for species of concern – such as Marbled Murrelets—through further research.

To conclude this section on demographic models, we offer the following perspective on the relevance of models that pay only indirect homage to habitat availability to conservation issues. If a population is declining, not because of relatively subtle changes in birth and death rates of the kind considered here, but rather because some portion of its living space is being modified by humans or nature so as to become wholly unsuitable for reproduction or survival, then the population will decline in direct proportion to the amount of habitat that becomes unusable. In that situation, no mathematical models are really necessary to understand the process.

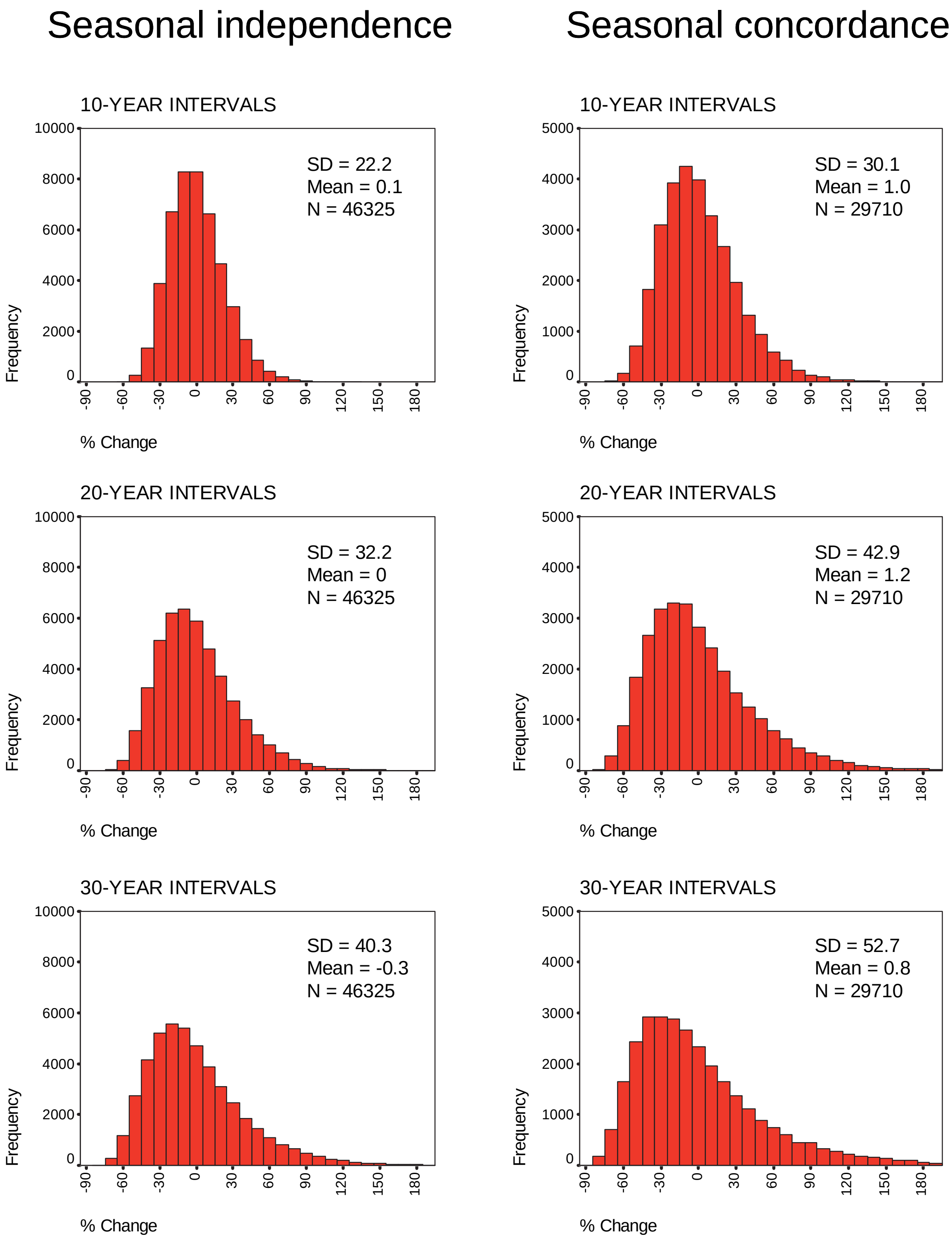


Figure 13. Expected distributions of trends over 10-, 20-, and 30-year intervals arising stochastically from interannual variation in the fecundity and survival of Marbled Murrelets, as modeled in program MATRIX.

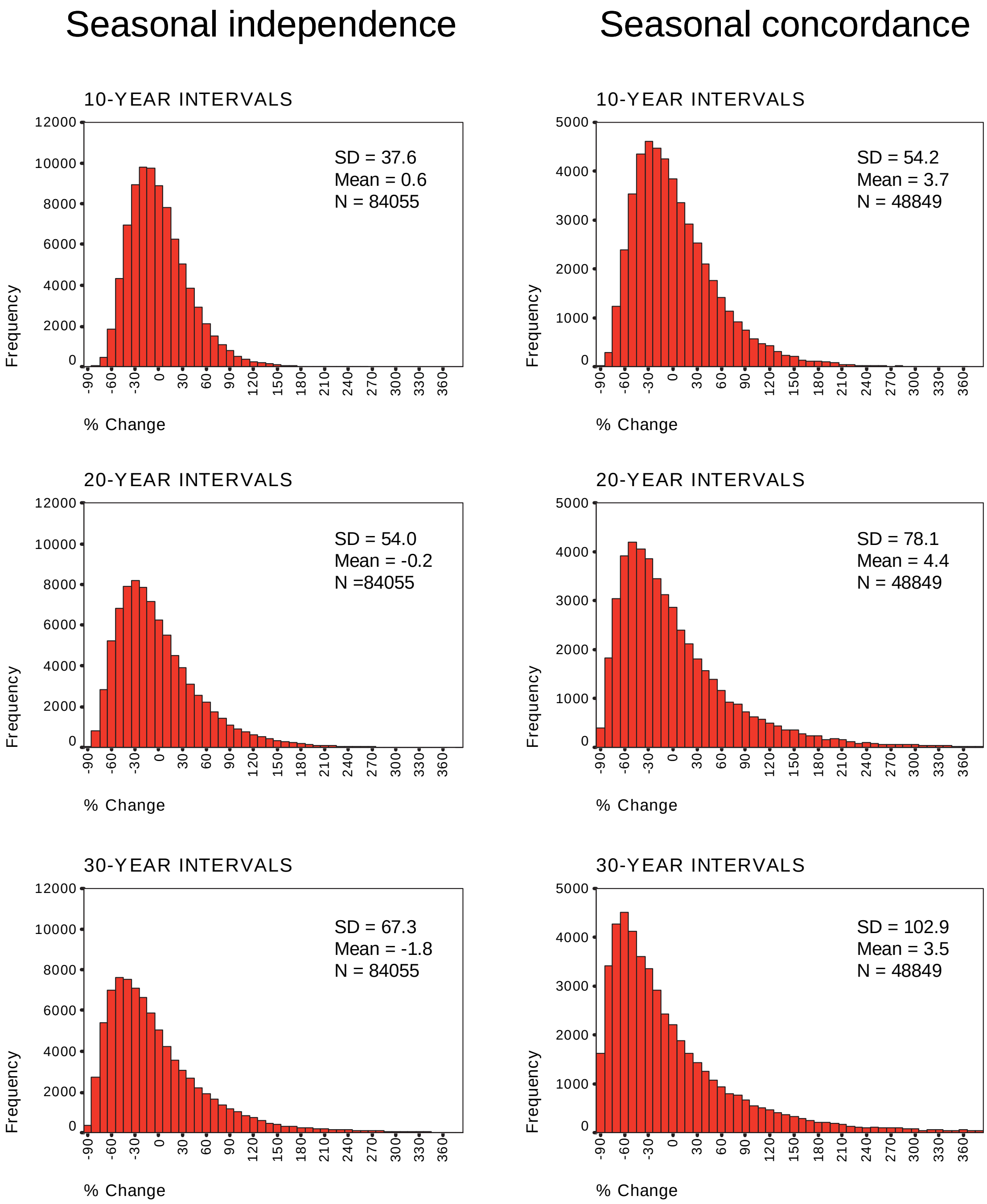


Figure 14. Expected distributions of trends arising stochastically over 10-, 20-, and 30-year intervals when interannual variation in fecundity and survival is comparatively high.

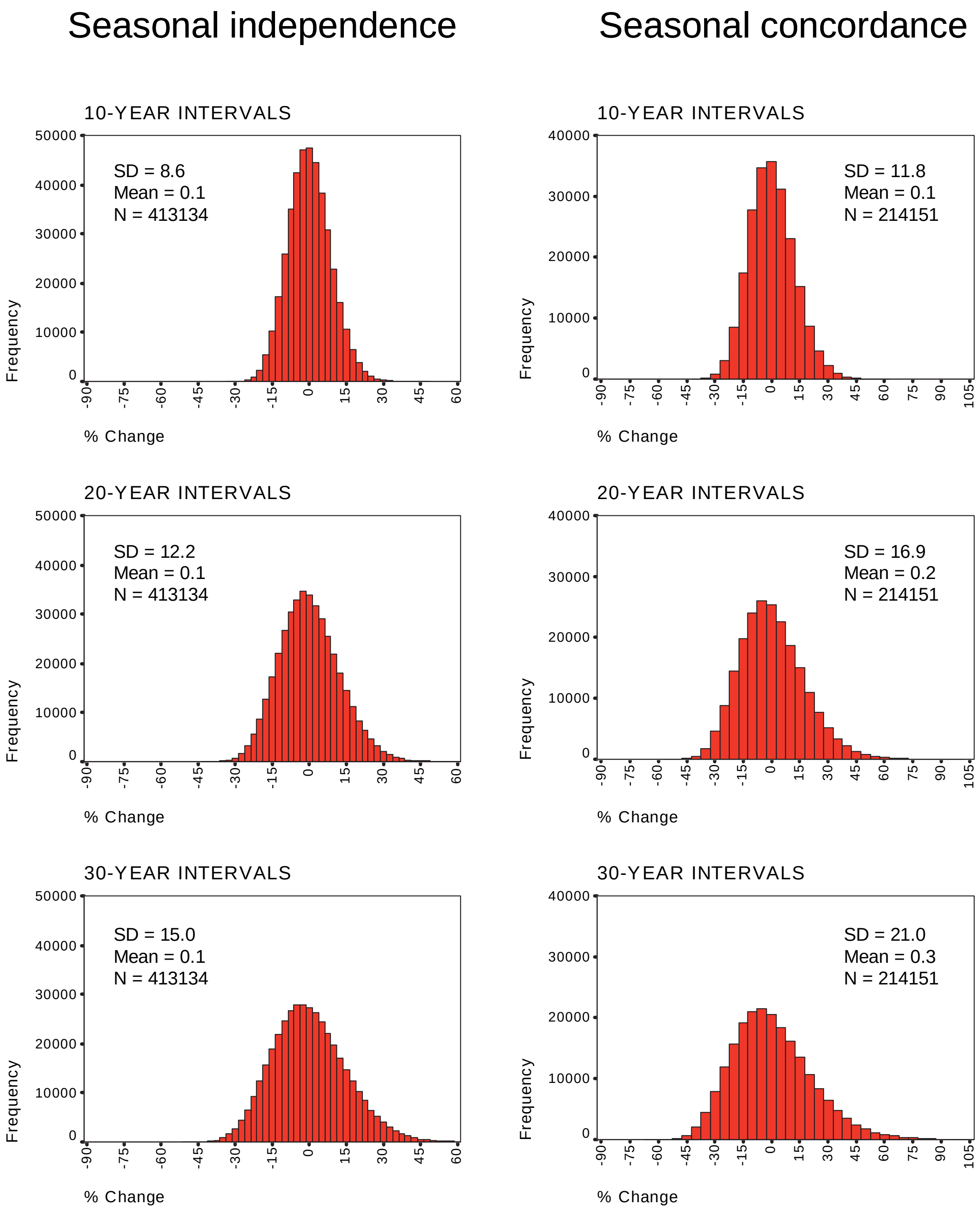


Figure 15. Expected distributions of trends arising stochastically over 10-, 20-, and 30-year intervals when interannual variation in fecundity and survival is comparatively low.

Marine Habitat: Characteristics and Threats

Marbled Murrelets spend most of their lives in the coastal marine environment, although they will feed occasionally in freshwater lakes near suitable nesting habitat (Carter and Sealy, 1986; Hobson, 1990). Our knowledge of the marine habitat of this species, though limited, has increased dramatically during the past few decades. In this section, we first describe the general features of marine habitats used by Marbled Murrelets in Alaska and British Columbia. We then consider the potential effects of climate-driven changes in marine food webs on murrelet prey species. Finally, this chapter examines anthropogenic threats to murrelets in their marine habitats, including oil pollution, incidental take in fisheries, effects of commercial fishing on their prey, vessel disturbance, and research activities.

Characteristics of Marine Habitats Used by Marbled Murrelets

The marine range of the Marbled Murrelet is primarily in coastal waters of southern Alaska, British Columbia, and Washington, Oregon, and California. In Alaska, these marine waters include the Aleutian Islands (from Attu to Unalaska islands), the south side of the Alaska Peninsula, the Kodiak Archipelago, Cook Inlet, Prince William Sound, and throughout Southeast Alaska (Piatt and Naslund, 1995). Small numbers of Marbled Murrelets also occur on the southeast Bering Sea shelf and along the north side of the Alaska Peninsula to Bristol Bay. Two major offshore current systems affect marine habitats of the Marbled Murrelet: (1) the Alaska Current/Alaska Stream (from northern British Columbia to the western Aleutian Islands); and (2) the California Current (from southern British Columbia to California). On the north side of the eastern Aleutian Islands, the smaller Aleutian North Slope Current acts as an extension of the Alaska Stream in the eastern Bering Sea.

Two major atmospheric pressure systems, the North Pacific High and the Aleutian Low, create major currents in the North Pacific Ocean (Weingartner, 2005). The Aleutian Low, strongest between September and January, creates a counter-clockwise current flow in the Gulf of Alaska, dominated by the Alaska Stream which follows the shelf-edge westward. This flow, combined with the onshore movement of water caused by the Coriolis Force, causes downwelling along the northern Gulf coasts of Alaska (Weingartner, 2005). Storms generated by the Aleutian Low result in high precipitation in the coastal mountains bordering the Gulf of Alaska (Mundy and Olsson, 2005), which in turn create conditions suitable for the coastal rainforests of this region. Outflow from the numerous coastal rivers feeds and defines the Alaska Coastal Current (Weingartner, 2005), which flows north and then west along the inner third of the continental shelf from northern British Columbia to about Samalga Pass in the eastern Aleutian Islands (Mundy and Olsson, 2005). The current is highly productive in spring and summer, and delivers plankton to nearshore waters, inlets, and fjords. Waters to the west of Samalga Pass are more oceanic and more strongly influenced nearshore by the Alaska and Aleutian North Slope Currents (Weingartner, 2005). South of the Gulf of Alaska, the North Pacific High creates clockwise winds and a current that travels south along the coasts of British Columbia, and Washington, Oregon, and California (Freeland, 1992; Benson and Trites, 2002), and winds produce upwelling along the coast (Freeland, 1992).

The coasts of southern Alaska and British Columbia have consistently high rainfall throughout most of the year (Weingartner, 2005). In Washington, Oregon, and California, rainfall becomes more seasonal with decreasing latitude. Major ENSO events can dramatically affect marine habitats used by murrelets in Washington, Oregon, and California (McShane and others, 2004). Every 4 to 7 years, warm water flows along the coast and changes the depth of the mixed layer as well as local weather. During ENSO events, many seabirds experience reduced reproduction if they reproduce at all (Ainley and others, 1995b). Fewer Marbled Murrelets are seen at-sea and inland during events, suggesting that reproductive success is reduced to some extent (Ainley and others, 1995a; Burger, 1995b, 2000; Strong and others, 1995). However, murrelet productivity may be impacted less than many other seabirds, because they can use prey that are less affected by ENSO conditions (Kelson and others, 1995; U.S. Fish and Wildlife Service, 1997). Timing of major ENSOs can vary by year between central-northern and southern parts of the California Current. Major ENSOs do not appear to project into the Alaska Current System nor have much effect on murrelets there (Piatt and Naslund, 1995), however, the impact of such periodic climatic-driven events on murrelets remains largely unknown.

Meso-Scale Characteristics

With respect to seabirds and their prey, oceanic processes at the meso-scale are defined as occurring spatially at 100–1,000 km (Hunt and Schneider, 1987). This spatial scale is used here to define ‘regions’ of murrelet populations within Alaska and British Columbia. Marine habitat varies considerably among regions, and the distribution of murrelets relative to shoreline, water depth, and other physical characteristics also varies among regions. For example, Marbled Murrelets in the Aleutian Islands use protected waters in large bays and inlets around the islands but do not use deeper waters in major passes between islands. Most murrelets occur in nearshore waters, generally within 5 km of shore (Piatt and others, 2005; Romano and others, 2005a). The shelf break is very narrow along the Aleutians and water surrounding the islands remains ice-free year-round. Water flowing between and around islands creates tidal fronts and currents that create upwelling, water mixing, and high productivity. In contrast, the marine habitat of the northern Gulf of Alaska shelf (including Prince William Sound), Southeast Alaska, and British Columbia is extremely complex. Numerous forested islands, fjords, inlets, and estuaries all provide sheltered, stratified coastal waters favored by murrelets. Most murrelets occur within 5–10 km of shore in these regions (Burger, 1995b; Piatt and Naslund, 1995).

Between Prince William Sound and Southeast Alaska, there are only a few large bays and a large shallow shelf, and Marbled Murrelets were found along exposed coasts out to at least 5 km (M. Kissling, U.S. Fish and Wildlife Service, unpub. data, 2003). However, Marbled Murrelets have been found as much as 300 km from the coast in the central Gulf of Alaska during summer and winter (Piatt and Naslund, 1995; North Pacific Pelagic Seabird Database, 2005), and it may be that some post-breeding birds move to offshore waters during winter (Nelson, 1997). A modeling exercise using only marine environmental parameters for British Columbia murrelet distribution found murrelets associated with sandy substrates, estuaries, and cooler sea temperatures (Yen and others, 2004a). South of British Columbia and along the outer coasts of Washington, Oregon, and California, marine habitats used by Marbled Murrelets are more homogeneous. There are no major islands, relatively few coastal rocks, and little shallow, nearshore water. Murrelets tend to use nearshore waters and numbers decline rapidly with distance from shore.

A description of murrelet use of marine habitats must consider the distribution of their nesting habitat, because throughout most of their range, Marbled Murrelets occur in waters adjacent to old-growth forest (Piatt and Naslund, 1995; Nelson, 1997; Miller and others, 2002). For example, in California, the most important variable influencing Marbled Murrelet abundance at-sea was proximity to large, unfragmented tracts of old-growth conifers bordered by second-growth forest (Miller and others, 2002). In Alaska, most (about 95 percent) murrelets are found in association with large coastal old-growth forests in Southeast Alaska, Prince William Sound, and Kodiak Island (Piatt and Ford, 1993). At a smaller scale, however, in Alaska and British Columbia abundance at-sea is often not well correlated with adjacent terrestrial breeding habitat (Marks and others, 1995; Speckman, 1996; Whitworth and others, 2000; Burger, 2002).

Small-Scale Characteristics

Throughout much of their range, most Marbled Murrelets are observed during summer within 5 km of shore and in shallow (less than 60 m) water (Nelson, 1997; Day and others, 2003). However, in Cook Inlet (Agler and others, 1998) and Kachemak Bay (Kuletz, U.S. Fish and Wildlife Service, unpub. data, 2006), Marbled Murrelets are often found 5–30 km from shore (fig. 16) and in water greater than 100 m deep. In Southeast Alaska and Prince William Sound, murrelets are more closely associated with the shoreline, but murrelets also can be found in waters 100–600 m deep in some bays and fjords (Agler and others, 1998; Kuletz, 2005). But for the most part, Marbled Murrelets in Alaska use sheltered waters in bays, fjords, leeward sides of islands, and island passes (Piatt and Naslund, 1995; Kuletz, 2005). In British Columbia, similar marine habitats are used, and murrelets also are found in exposed or channel habitats (Sealy and Carter, 1984; Savard and Lemon, 1992). Within British Columbia, murrelet numbers in the protected Strait of Georgia region (i.e., east coast of Vancouver Island and adjacent mainland British Columbia) are low compared to other similar areas, which may reflect removal of most old-growth forests around the Strait.

From British Columbia to California, feeding aggregations of murrelets tend to occur in similar areas over multiple years, and their occurrence may be related to persistent local prey availability (Carter, 1984; Sealy and Carter, 1984; Carter and Sealy, 1990). There is some evidence that murrelets have some forage site fidelity and stay more or less within ‘home ranges’ (Lank and others, 2003; Kuletz, 2005). In Prince William Sound, the minimum-area polygons of 33 radio-tagged Marbled Murrelets averaged 143 ± 37 km^2 (counting the nest sites), but most relocations of individuals on the water were usually within a 5-km radius (Kuletz, 2005). Consistent use of a bay also has been recorded for radio-tagged Marbled Murrelets in Southeast Alaska (Quinlan and Hughes, 1992) and in British Columbia (Hull and others, 2001; Lougheed and others, 2002a). The evidence for site fidelity shown by murrelets in these studies suggests that familiarity with an area and learned behavior may influence the use of certain marine habitats.

The characteristics of Marbled Murrelet foraging habitat appear to vary depending on location. In general, Marbled Murrelets in Alaska were considered to be most abundant in cooler water, and in stratified, rather than strongly tidally-mixed, coastal water (Piatt, 1994; Piatt and Naslund, 1995).

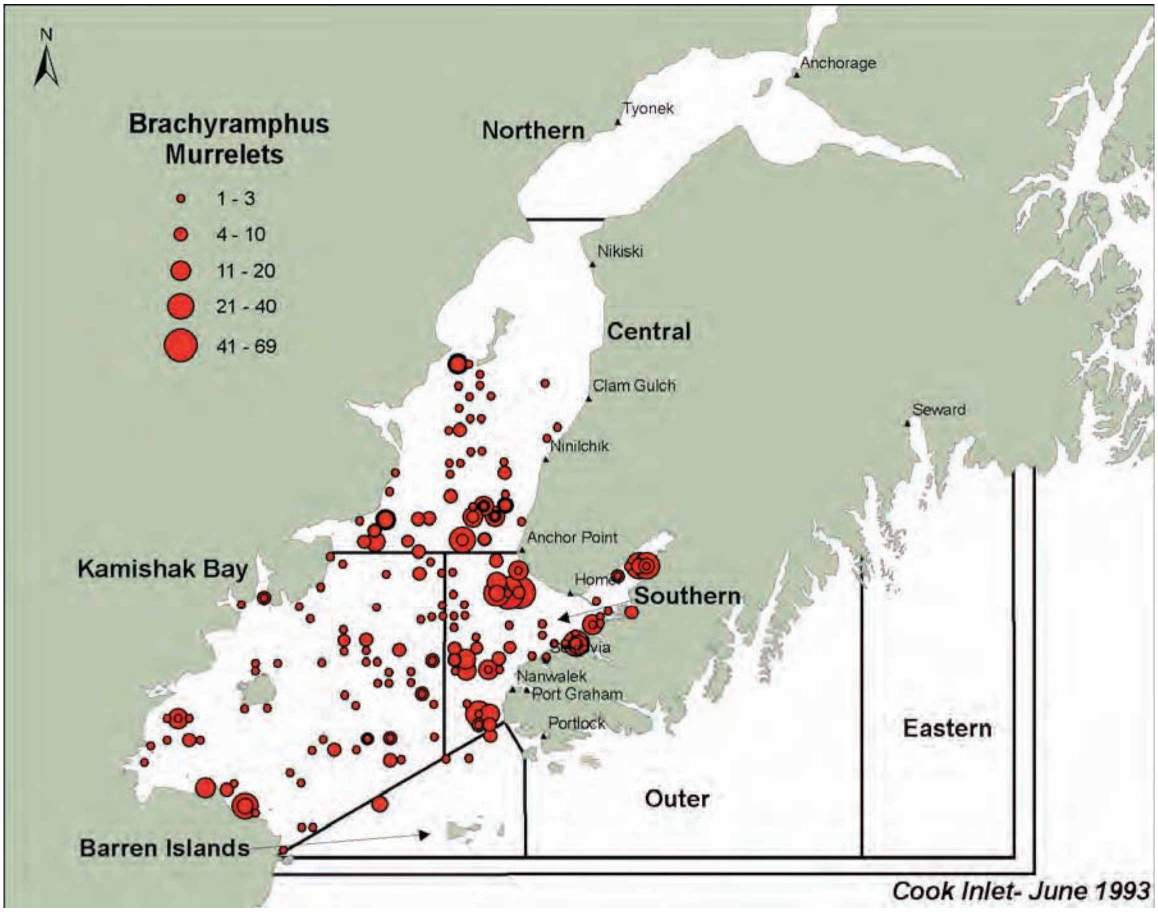


Figure 16. *Brachyramphus* murrelet distribution in lower Cook Inlet in June 1993, relative to salmon fishing districts in the Cook Inlet area.

However, murrelets also are often associated with areas of upwelling created by underwater shelves, mouths of bays, and island passes and wakes, which may serve to aggregate prey (Carter, 1984; Sealy and Carter, 1984; Day and Nigro, 2000; Day and others, 2003; Kuletz, 2005). Murrelets are associated with sand and gravel substrate, also habitat of the Pacific sand lance, an important prey item (Carter, 1984; Burger, 1995b; Speckman and others, 2000). There is evidence that juvenile Marbled Murrelets have a more limited range of habitats, at least in the first weeks or months following fledging (Andersen and Beissinger, 1995; Kuletz and Kendall, 1998; Speckman and others, 2000). Juveniles tend to be found close to shore in well protected, shallow waters or in nearshore areas with kelp beds (Kuletz and Piatt, 1999).

In Alaska, Marbled Murrelets are often found in waters adjacent to glaciers, where they co-occur with Kittlitz's Murrelets (Agler and others, 1998; Day and others, 2003; Kuletz and others, 2003b; Robards and others, 2003), but they are less likely to be associated with glaciers in British Columbia (Burger, 2002; Yen and others, 2004a). In Barkley Sound, British Columbia, murrelets aggregated in traditional juvenile herring rearing areas that were near spawning areas (Carter, 1984), although murrelets generally are not found in other herring spawning areas of British Columbia (Yen and others, 2004a).

Use of foraging habitat may vary temporally. Carter and Sealy (1990) suggested that murrelets forage in productive waters at considerable distance from breeding sites in morning hours, but later shift to feeding areas that are closer to nest sites where they can capture prey for delivery to chicks (Carter and Sealy, 1990), and evidence was found for this pattern of behavior in Southeast Alaska (Speckman and others, 2000) and British Columbia (Bradley, 2002; Rodway and others, 1995). Murrelets may choose some feeding areas where they can feed on fish that migrate vertically to the surface at dawn or dusk (Speckman and others, 2000; Kuletz, 2005). Ostrand and others (1997) noted changes in the depth of water and distance from shore used by murrelets in apparent response to changes in habitat use by their prey. Major changes in murrelet habitat use occur after the breeding season is completed, although the characteristics of the autumn and winter habitats are not well known. Details on the seasonal dispersal of murrelets were addressed under the section, "Breeding Biology."

Marine Ecosystem Change

The abundance of forage fishes is known to fluctuate in response to oceanographic conditions such as water temperature (Chavez and others, 2003; Rose, 2005), salinity and depth (Abookire and Piatt, 2005), daylight (Beamish and others, 1999), tidal influences (Zamon, 2003), and frontal mixing (Maravelias and Reid, 1997). For example, Speckman and others (2005) found that turbidity, temperature, salinity and interannual variability in marine climate (e.g., ENSO and La Niña events) played an important role in structuring forage fish communities in lower Cook Inlet. Similarly, the seabird community reflected the physical and biological structure of the Cook Inlet ecosystem (Speckman and others, 2005).

Large-scale shifts in marine climate have been linked to biological regime shifts (Benson and Trites, 2002; Chavez and others, 2003) that resulted in changes in the abundance of forage fish important to Marbled Murrelets and other seabirds in the North Pacific (Anderson and Piatt, 1999). The 1977–78 regime shift was driven by decadal-scale changes in atmospheric forcing of the Aleutian Low, which affected current flow and ocean temperatures (Francis and others, 1998). Coincident with fluctuations in seawater temperatures and changes in primary and secondary productivity, populations of small forage species (e.g., capelin, shrimp, and Pacific sandfish) declined after the late 1970s, whereas populations of large predatory fish (walleye pollock [*Theragra chalcogramma*], Pacific cod [*Gadus macrocephalus*], and flatfish) increased (Anderson and Piatt, 1999). Marbled Murrelets have a fairly generalist diet and show an ability to switch prey when the availability of some prey changes (e.g., Ostrand and others, 2004). Nontheless, there is evidence that changes in prey affect murrelet distribution and productivity (Peery and others, 2004b; Becker and Beissinger, 2005).

Population and diet data from a variety of marine birds suggest that an ecosystem change occurred in Prince William Sound in the 1980s that negatively affected fish-eating birds (DeGange, 1996; Kuletz and others, 1997; Agler and others, 1999). Marbled Murrelets ate mostly sand lance during the late 1970s, whereas they started to feed almost entirely on lipid-poor gadids from 1989 to 1991, with capelin disappearing as a dietary item (DeGange, 1996; Kuletz and others, 1997; table 3). Linked with these changes in diet, Marbled Murrelets and other piscivorous seabird populations declined, although not all the declines were significant (Klosiewski and Laing, 1994; Agler and others, 1999). However, mortality from oil spills and fisheries also occurred during these decades (Carter and Kuletz, 1995; Carter and others, 1995; Piatt and Naslund, 1995; see below). Recent data indicate that Marbled Murrelets were feeding primarily on herring and sand lance in the late 1990s (Kuletz and others, 1997; Day and Nigro, 2000; appendix A), and suggest that ecological conditions in Prince William Sound may have changed to a more productive environment for fish-eating birds.

A shift in diet also appears to have occurred along the Alaska Peninsula and around Kodiak Island. In these areas, Marbled Murrelets collected in the 1970s–1980s during summer were feeding largely on capelin (Piatt and Anderson, 1996; appendix A). In contrast, capelin were nearly absent in Marbled Murrelets collected in the same areas during the 1990s (appendix A).

The effects of marine ecosystem change on Marbled Murrelets also have been observed in British Columbia, with warmer ocean temperatures associated with the ENSO negatively affecting Marbled Murrelet reproduction (Burger, 2000; Becker and Beissinger, 2003). More recently, Becker and Beissinger (2005) have demonstrated a large change in the trophic level and diet of Marbled Murrelets in California over the last century, with birds shifting to lower trophic level prey items (such as krill, rockfish, and sand lance) in response to a decrease in the abundance of higher trophic level prey species associated with declines in fisheries. High predation rates and limited nesting habitat also likely contribute to poor reproduction in central California (Hamer and Nelson, 1995; Nelson and Hamer, 1995), and more work is needed to assess fully the reasons for their poor reproduction. These studies highlight the important effects that changes in marine community composition (whether due to over-fishing or natural variation in the marine environment and patterns of upwelling) can have on the prey base and demographic response of Marbled Murrelets.

Although there are possible links between climate and murrelet reproductive success or population trends, we do not know the mechanisms involved. There is, however, growing understanding of climate effects on the lower trophic levels on which murrelets depend.

A major reorganization of the marine food web occurred in the Gulf of Alaska during the decade following a 1977 regime shift (Hollowed and Wooster, 1995; Hare and Mantua, 2000; Hollowed and others, 2001). The 1980s to 1990s is approximately the period when murrelet populations showed evidence of declines (this volume), which supports the hypothesis that changes in the marine environment have been one component of the conditions leading to murrelet declines (Burger, 2000; Peery and others, 2004b; Becker and Beissinger, 2005; Kuletz, 2005). However, climate-driven shifts in marine food webs are not new. In the North Pacific, regime shifts may have occurred in 1925, 1947, 1977, and 1989, with a weaker shift in 1998–99 in the Gulf of Alaska (King, 2005). Paleo-ecological records suggest that the duration of regime shifts have diminished from 50 –100 years to 20–30 years (in historical times), and more recently to 10 years. Thus, it is possible that changes in the North Pacific climate and ocean ecosystems have increased in frequency (King, 2005), which could stress even generalist foragers such as the Marbled Murrelet.

Most of the fish species used by Marbled Murrelets (this volume) feed on macro-zooplankton, primarily copepods and euphausiids, and thus are linked to environmental fluctuations that influence zooplankton abundance, distribution, and species composition (Zebdi and Collie, 1995; Williams and Quinn II, 2000). In the Gulf of Alaska, zooplankton timing, abundance, and community composition has changed on a decadal scale, with apparent links to changes in ocean and climate conditions (Mackas and others 1998, 2001; Boldt and others, 2005). Concurrently, fish communities have changed (McGowan and others, 1998), followed by changes in seabird prey species, notably after the 1970s (Piatt and Anderson, 1996; Anderson and Piatt, 1999).

One of the most important prey for murrelets in British Columbia and Alaska, particularly for birds raising chicks, is Pacific herring. Juvenile herring feed on copepods, and after their first year, they eat more euphausiids. Survival of juvenile herring depends on their ability to acquire enough food during summer and autumn to survive their first winter (Foy and Paul, 1999). Warm water and poor body condition from insufficient food can facilitate the spread of diseases that may be limiting recovery of the herring population in Prince William Sound (Marty and others, 1998). Warmer water temperatures between the 1970s and 1990s also may have been responsible for declines in capelin in the Gulf of Alaska (Anderson and Piatt, 1999) and the subsequent disappearance of capelin from the diet of Marbled Murrelets (Piatt and Anderson, 1996). In contrast, walleye pollock abundance increased in the Gulf of Alaska during this period (Boldt and others, 2005) and also in the diet of murrelets. Although adult murrelets will eat juvenile pollock, they select higher quality prey for their chicks (Kuletz, 2005).

There are substantial differences among forage fishes in the fat content, energy density, and quality of forage fish (Anthony and others, 2000). In addition, there can be differences in energy density within the same fish species, depending on sex, breeding condition, season, location, or annual changes in environmental conditions (Robards and others, 1999a; Anthony and others, 2000). As a result, birds provisioning their chicks may show delivery rates and prey species selection similar to historical records, yet show lower chick growth and survival, such as occurred in the North Atlantic (Wanless and others, 2005). Providing high-quality prey has been shown to increase chick growth and improve fledging success in seabirds in Prince William Sound (Golet and others, 2000; Suryan and others, 2002) and under laboratory conditions (Romano and others, 2006).

Prey quality may be more important than quantity for chick growth in seabirds (Kitaysky and others, 1999; Wanless and others, 2005), and thus the body condition of forage fish, as well as their abundance, could impact murrelet productivity. For example, Kuletz (2005) used published energetic values to estimate the number of fish deliveries required daily to raise a Marbled Murrelet chick. The daily rate varied from approximately two 1-year old herring to nine male capelin. Over the course of the 27–40 day nestling period (with presumably longer fledging periods where food is more scarce), estimated total fish deliveries could range from less than 60 herring to more than 250 capelin to raise a chick. Hypothetically, if a murrelet pair had access to high-quality prey while raising their chick, they would work less to capture and deliver prey, risk fewer trips inland past avian predators, and be more likely to fledge the chick by reducing exposure to nest predators.

In California, murrelets have been shown to alter their foraging locations in response to ocean conditions (Becker and Beissinger, 2003), and they spent more time foraging when food availability was low (Peery and others, 2004b). The murrelet's ability to adapt to changes in ocean conditions appeared to have costs to reproductive success (Peery and others, 2004b). There also may be costs to adult body condition. In Prince William Sound, during a period of population decline, mean adult murrelet body mass declined between 1977 and 1999 (Kuletz, 2005).

Threats in Marine Habitats

Anthropogenic activities that could affect Marbled Murrelets in the marine environment include oil and other contaminant pollution, incidental take in commercial fisheries, secondary or indirect effects of commercial fisheries (such as displacement or impacts on murrelet prey), vessel disturbance, and research activities. Here we review these threats using available information from various sources. Anthropogenic effects may not drive large-scale population changes in murrelets, but their cumulative effects, in conjunction with natural events (as discussed above), could be significant. We attempted to be thorough in evaluating anthropogenic threats, and the amount of information provided on each topic does not necessarily reflect the potential impact on the murrelet population.

Oil Pollution

Alaska

Marbled Murrelets are considered highly vulnerable to oil spills in Alaska (King and Sanger, 1979) and the Pacific Northwest (Carter and Kuletz, 1995), because they remain on the sea for most of their lives, forage by diving, and prefer nearshore habitats (usually less than 5 km offshore). Throughout the range of the Marbled Murrelet, oil pollution has been and remains a significant problem (Carter and Kuletz, 1995; McShane and others, 2004), and this has been particularly evident in Alaska. The 1989 EVOS was the single largest mortality event for Marbled Murrelets, killing a minimum of 8,400 murrelets (Carter and Kuletz, 1995; Kuletz, 1996). In addition to catastrophic events, smaller spills (i.e., chronic oil pollution) frequently kill large numbers of murrelets in Washington, Oregon, and California (McShane and others, 2004). Based on reports from regions with larger human populations, it is possible that tens to hundreds of murrelets per year are killed in Alaska and British Columbia by chronic oil pollution without documentation. Where rehabilitation of oiled murrelets has been attempted, there was little success. During the EVOS, only 3 of 33 treated Marbled Murrelets survived to be released (Carter and Kuletz, 1995).

In the cold waters of Alaska, even small amounts of oil can cause mortality or metabolic problems for seabirds (Nero and Associates, Inc., 1987). During the EVOS, Ford and others (1996) found that about 25 percent of the small alcid carcasses retrieved (primarily murrelets) had no discernable oiling on their bodies. Although crude oil is most often associated with seabird mortality from spills, diesel also is a common contaminant (table 21). Diesel is lighter and disperses more quickly than crude oil, and there is no evidence that its effect on plumage and thermoregulation on seabirds is less problematic.

Exxon Valdez Oil Spill

The EVOS began with the grounding of the oil tanker in northwestern Prince William Sound on March 24, 1989 and release of 11 million gallons of crude oil. Over the next 2 months oil spread southwest with prevailing currents, covering 30,000 km^2 of coastal and offshore waters (Piatt and others, 1990). Alcids were the avian taxon most affected by the spill, and Marbled Murrelets had the highest mortality among six species of small alcids that were identified from carcass recoveries (Piatt and others, 1990; Ford and others, 1991, 1996). The EVOS occurred when most murrelets had not yet entered Prince William Sound for the breeding season, and thus estimated mortality for regions farther south were actually higher than for Prince William Sound (table 22).

Estimating mortality of Marbled Murrelets was complicated by the large number of unidentified murrelets and other small alcids, but the minimum estimate of direct mortality was 8,400 *Brachyramphus* murrelets, most of which were Marbled Murrelets (table 22). This represented approximately 7 percent of the known population in the spill zone (Kuletz, 1996). However, based on re-examination of a sample of carcasses of murrelets and ‘unidentified’ small alcids, larger numbers of Marbled Murrelet carcasses were identified (Ford and others, 1991, 1996). Using revised carcass counts, murrelet mortality was 10,000–22,000, with a best approximation of 12,800–14,800 (Kuletz, 1996). These latter estimates represented 7 to 12 percent of the murrelet population in the spill zone. Details of the estimates of murrelet mortality and subsequent damages are available in Carter and Kuletz (1995) and Kuletz (1996).

Windy Bay Oil Spill

Although relatively small, the *Windy Bay* oil spill was the largest spill in Prince William Sound since the EVOS, and provided information on the types of risks posed by small spills. On August 4, 2001,the fishing tender *F/V Windy Bay* struck a reef and sank in northern Prince William Sound. The vessel held 35,000 gal of diesel fuel, 100 gal of lube oil, and 300–500 gal of hydraulic fluid. An estimated 60 percent of the fuel evaporated and 11,000 gal were recovered by response operations. Light sheen was observed over approximately 40 mi^2. By August 9, approximately 10–20 gal of diesel per

Table 21. Summary of spills between 1979 and 2005 in coastal Alaska, by substance category.

[Data from Alaska Department of Environmental Conservation. These records include those that occurred in marine areas, and do not include the *Exxon Valdez* oil spill. The amount of substance spilled was recorded as gallons or pounds, depending on the substance or environmental conditions]

Substance	Vessel spills			Other sources		
	Number	Gallons	Pounds	Number	Gallons	Pounds
Agricultural Chemical	14	1,530	25,008,957	132	1,210	303,332
Chemical—Other	10	37	179	221	131,710	20,822
Fuel—Diesel, Gasoline, Aviation	1,145	245,040		649	113,573	502
Fuel—Other	9	148		43	22,213	212
Oil—Crude	24	8,924		231	23,361	
Oil—Marine, Other	528	589,026		586	9,914	
Other or Unknown	90	45,182	44,000	331	155,380	46,078
Water—Oil, Refinery, Ballast	11	79		119	174,172	
Total	1,831	889,966	25,053,136	2,312	631,533	370,946

Table 22. Estimates of direct mortality of *Brachyramphus* murrelets from the *Exxon Valdez* oil spill in Alaska in 1989.

[Reprinted from Kuletz (1996)]

Region	Estimated recovery rate	Marbled Murrelets		Kittlitz's Murrelets		Unidentified murrelets		Estimated[1] total mortality
		Number of carcasses	Estimated mortality	Number of carcasses	Estimated mortality	Number of carcasses	Estimated mortality	
Prince William Sound	0.35	289	826	23	66	21	60	952
Kenai Peninsula	0.14	113	807	23	164	73	521	1,492
Barren Islands	0.49	17	35	4	8	14	29	72
Kodiak Island	0.06	64	1,066	1	17	71	1,183	2,266
Alaska Peninsula	0.02	45	2,250	0	0	27	1,350	3,600
Total		528	4,984	51	255	206	3,143	8,382

[1] Excludes Ancient Murrelets, based on carcasses identified to species.

day were still leaking from the vessel, and between August 10 and 16, an estimated 60–100 gal/d leaked from the vessel. A large and rapid response to the event limited the damage.

Surveys that were done the week prior to the spill, and days afterwards, showed that Marbled Murrelets were abundant throughout the spill zone, and murrelets were the species most often observed in oil sheen (Kuletz, 2001). Of seven bird carcasses retrieved during response operations, six were Marbled Murrelets, and these were retrieved from oil-containment booms that had skimmed heavily oiled waters. Two of the dead murrelets were adults and four were newly fledged juveniles. The six murrelet carcasses probably represent a very low proportion of total mortality (Kuletz, 2001). Several hundred murrelets were observed in waters with some sheen present, and six others were obviously impaired but eluded captors (K. Brenneman, U.S. Fish and Wildlife Service, oral commun., 2001). Based on recovery estimates for small alcids and local conditions, Kuletz (2001) suggested that a conservative estimate of direct mortality for this spill was 100 murrelets.

The *Windy Bay* spill occurred when both adult and juvenile murrelet numbers in Prince William Sound were at their peak (Kuletz and Kendall, 1998). Juvenile murrelets appeared to be more vulnerable to oiling and direct mortality than adults. During pre-spill surveys, juveniles represented about 3–7 percent of all murrelets, but 4 of the 6 oiled murrelets found dead were juveniles. Juveniles prefer, and often aggregate at, shallow, rocky locations with kelp (Kuletz and Piatt, 1999), such as existed in the primary spill zone (Kuletz, 2001). Fledgling physiology and behavior likely contributed to the disproportionate juvenile murrelet mortality. Juvenile murrelets typically have less than 70 percent adult body mass (Nelson, 1997), do not dive well, and rarely fly (Kuletz and Kendall, 1998). Newly fledged juvenile murrelets would not likely fly away from the presence of diesel, nor escape from skimming booms.

Secondary and Long-Term Effects

A secondary impact from spills is the extremely high number of vessels that concentrate in the affected area during response, clean-up, and monitoring activities. This was noted following the 1989 EVOS, during which boat presence appeared to displace Marbled Murrelets from key foraging areas (Carter and Kuletz, 1995; Kuletz, 1996). Similarly, in 2001, the highest number of boats encountered during surveys occurred while conducting post-*Windy Bay* spill surveys in the spill zone (Kuletz, 2001). Spills affect bird distribution, as evidenced by increased seabird abundance in un-oiled bays and inlets of the spill-affected areas of Prince William Sound (Piatt and others, 1990). A similar pattern was observed during the *Windy Bay* spill (Kuletz, 2001).

Oil spills and contaminants can potentially cause immediate and long-term damage to forage fish populations. Herring and sand lance, both key prey species for murrelets in Alaska (this volume), may have been impacted in Prince William Sound by the EVOS (among other stressors) and may still be experiencing perturbations from the EVOS (Petersen and others, 2003). Perhaps related to impacts to forage species, and direct mortality prior to the breeding season, there was evidence of fewer fledged juveniles at Naked Island, Prince William Sound in 1989 and 1990 (Kuletz, 1996).

Herring spawn nearshore and juvenile herring aggregate in protected bays (Norcross and others, 2001). In oiled areas of Prince William Sound, herring showed sublethal damage and larval malformations, and did not spawn in some historical spawning locations (Norcross and others, 2001). Herring in Prince William Sound peaked in estimated adult biomass in 1988, at 100,000 metric tons, followed by an erratic but ultimately dramatic decline. The herring stock collapsed in 1993, declining to an estimated 16,082 metric tons in 1993 and by 2001 to a low of 6,384 metric tons (Thomas and Thorne, 2003). There is no agreement on the cause of the collapse, and it could have been due to a combination of factors in addition to the EVOS (Paine and others, 1996; Spies and others, 1996). There is less information on sand lance because it is not a commercially fished species. Sand lance is a valuable prey species for seabirds because of their high energy-density (Van Pelt and others, 1997), and in Prince William Sound it comprises 50 percent of the prey fed to murrelet chicks (Kuletz, 2005). Sand lance occupy nearshore waters and burrow daily into sandy substrates, where they may be exposed to contaminants settled into benthic habitats (Robards and others, 1999b).

Chronic Oiling and Other Types of Contaminant Spills

Small spills are more frequent, and though limited spatially, have the potential to cause mortality under different wind and sea conditions, particularly when spills occur in preferred foraging locations during sensitive periods in the breeding season. In addition to the *Windy Bay* spill, the fishing vessel *Vanguard* sank in northern Prince William Sound in July 2001, releasing 3,000 gal of fuel. The cumulative effects of incidents like these fishing-related spills could be significant in areas with high vessel activity. Records of vessel spills in coastal Alaska from 1979 to 2005 (Alaska Department of Environmental Conservation, unpub. data, 2005) indicate that vessel-related spills of oil and other contaminants peak slightly during the summer, as recreational, tourist, and fishing activities increase (fig. 17). This also is when murrelets occupy inshore waters of Alaska. During autumn and winter months, spills into coastal waters from other sources (such as oil rigs, harbor operations, fish processors, mining, logging, etc.) contribute a higher percentage of total spills.

The spills recorded by the ADEC ranged from a single gallon to tens of thousands of gallons, and include a variety of contaminants (table 21). Records were scarce prior to 1995, and thus we used 1995–2005 to examine annual trends in spills. In terms of numbers of spills, vessel-related spills peaked in 1999, declined sharply in 2000, and remained relatively stable in 2001–05 (fig. 17). Other sources of spills peaked in 1996, also declined in 2000, and increased again during 2002–04.

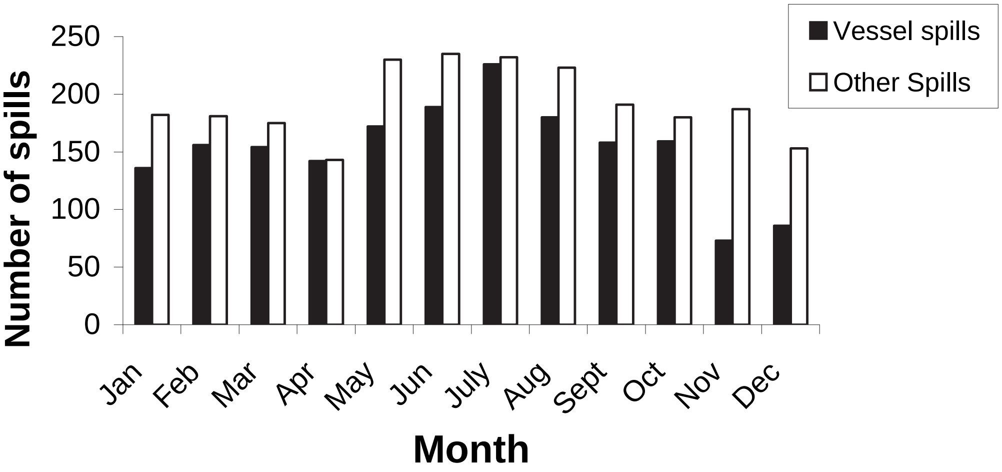
Southeast Alaska had the highest number of vessel-related spills, followed by the Aleutian Islands, with the latter having the largest total gallons of contaminants between 1979 and 2005. However, a single incident in Cook Inlet in 1997, the rollover of the *Crowley Oregon* barge resulted in more than 25 million lb of solid urea being released into coastal waters. Spills from non-vessel sources were highest in numbers in Cook Inlet, followed by Southeast Alaska, which had the largest total release of contaminants (table 23). Southeast Alaska is much larger in area than the other regional categories used by ADEC, which may partly account for the larger number of spills in Southeast Alaska. There are no records of murrelet mortality in Southeast Alaska from spills of oil or other contaminants, but there also is not generally a damage assessment response to small spills. Total spill levels also were high in Prince William Sound and Cook Inlet (table 23), both important murrelet breeding areas. Southeast Alaska has the largest proportion of Marbled Murrelets throughout their range (Agler and others, 1998; McShane and others, 2004), and thus the high incidence of spills in this region is of concern. While the oil-tanker traffic through Prince William Sound is well-known, tankers also traverse along the outer coasts of Southeast Alaska. To date, there have been no tanker accidents in this region.

The U.S. Coast Guard (USCG) is another source of information on contaminant spills, however, reports summarizing spill events, locations, or amount of discharge per event requires a Freedom of Information Act request of USCG internal reports. A summary of marine water spills (petrochemical and chemicals) for 2005 and 2006 shows 255 and 229 cases, respectively, occurred between Dixon Entrance and Cook Inlet (USCG Marine Safety Office, December 5, 2006). Of these spills, 31 were more than 100 gal.

Table 23. Summary of spills between 1979 and 2005 in Alaska, by subarea.

[Data from Alaska Department of Environmental Conservation (ADEC). These records include those that occurred in marine areas. Only 35 records were made prior to 1995, and the data file did not include the 1989 *Exxon Valdez* Oil Spill. The amount of substance spilled was recorded as gallons or pounds, depending on the substance or environmental conditions]

DEC subarea	Vessels			Other sources		
	Number	Gallons	Pounds	Number	Gallons	Pounds
Aleutian	351	583,128	5,700	88	26,665	2
Bristol Bay	57	7,308		35	15,999	
Cook Inlet	179	10,465	25,044,220	1,079	137,122	315,671
Kodiak Island	136	16,962	179	119	2,450	
Prince William Sound	231	86,914	2	255	35,940	6,326
Southeast Alaska	877	185,189	3,035	736	413,357	48,947
Grand Total	1,831	889,966	25,053,136	2312	631,533	370,946



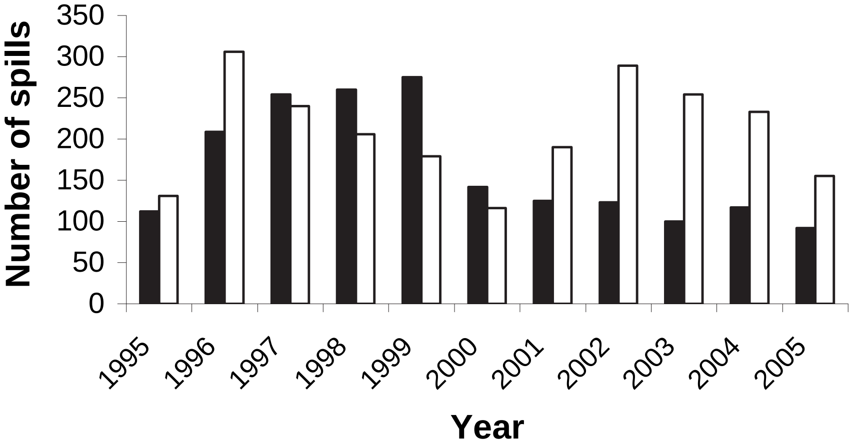


Figure 17. Number of spills in coastal Alaska waters by month (top) and year (bottom), 1995–2005, for vessel-related spills and other spill sources.

Spills from non-vessel sources included a high proportion of those related to oil-rig operations and transport activities (Alaska Department of Environmental Conservation, unpub. data, 2005). Spills related to oil extraction are reflected in the high number of spills from non-vessel sources in Cook Inlet, where 12 to 15 production platforms operate. Cook Inlet oil production peaked at 230,000 bbl/d in 1970, declined to 30,000 bbl/d by 1999, and since 2003 has been about 7,000 bbl/d (Historical and Projected Oil and Gas Consumption, Alaska Department of Natural Resources [ADNR], May 1999). These fields are expected to continue operations into the next century. Cook Inlet oil is refined in Nikiski, Alaska, and produces a variety of fuel types. Nikiski refineries include gas liquefaction and fertilizer plants, and therefore are another potential source of contaminants that could threaten murrelets in Cook Inlet.

Marbled Murrelets are not common in upper Cook Inlet, where most oil-related operations occur, but prevailing currents may carry spills into lower Cook Inlet and Kachemak Bay, where murrelet densities can be locally high. The estimated *Brachyramphus* population in lower Cook Inlet in 1993–94 was approximately 58,000 in summer and 12,000 in winter (Agler and others, 1998). A 2005 survey in Kachemak Bay estimated approximately 9,000 Marbled Murrelets present in July (Kuletz, U.S. Fish and Wildlife Service, unpub. data, 2006). Plans to open lower Cook Inlet to oil exploration have been debated for decades, with fishery, tourism, and conservation stake-holders attempting to exempt the region from further development. In 2002, the Secretary of the Interior issued a Final 5-Year Offshore Oil and Gas Leasing Program for lower Cook Inlet (2002–07), for which lease sale bids have been accepted and future operations are being negotiated (Minerals Management Service [MMS], 2003).

The shipment of crude oil and gas from Alaska production and transfer sites, and the high level of cargo or container ship traffic, result in frequent port visits to Alaska's four main industrial ports. In 2005, Valdez (Prince William Sound) had 399 tanker visits, and 81 percent of those contained crude oil (U.S. Department of Transportation [USDOT], 2006). That same year, Anchorage (Cook Inlet) received 215 cargo ships and barges. The ports of Nikiski and Homer (Cook Inlet), ranked 7th and 15th in the Nation in Gas Carrier visits, with 51 and 18 port calls, respectively, in 2005 (U.S. Department of Transportation, 2006). Three of these sites have year-round glacial (Valdez) or seasonal pack ice (Anchorage, Nikiski) that increase shipping risks. The Nikiski port has had several major spills or accidents that posed high pollution risks. The risk of spills from tankers or large vessels entering or exiting ports is thus greatest in Cook Inlet and Prince William Sound, both of which have sizable murrelet populations (Agler and others, 1998).

Documenting Mortality and Damages

Documenting murrelet mortality from oil spills is difficult; murrelets are less likely than larger seabirds to be retrieved during rescue operations because of their small size, high sink rate offshore, and high rate of carcass loss to scavengers on shorelines (Piatt and others, 1990; Carter and Kuletz, 1995; Ford and others, 1996). Scavenger rates are particularly high in Alaska, because of large populations of carnivores and avian predators (Ford and others, 1996). In a Prince William Sound study, the rate of daily loss to scavengers was 30–50 percent, with no carcass lasting more than 4 days (Ford and others, 1996). More recent studies of carcass persistence on beaches in California and Oregon determined average persistence time on beaches for small-bodied carcasses similar to Marbled Murrelets of 1.17 and 3.70 days (Ford and Ward, 1999).

Ability to document murrelet mortality from catastrophic events will depend on weather, and marine and coastal habitat. Length of time at sea greatly increases carcass loss due to sinking, but in the relatively calm waters of Prince William Sound bird carcasses stayed adrift longer than in the Gulf of Alaska, with some floating birds kept adrift for 15 to 20 days (Ford and others, 1996). For all bird species combined, the carcasses found during the EVOS were estimated to represent 10 to 30 percent of actual mortality (Piatt and others, 1990). Murrelets, however, were more difficult to find than other birds on rocky, boulder beaches common in Prince William Sound (Ford and others, 1996). More recent studies (Ford and Ward, 2000) found that small birds such as murrelets also had the lowest ratio (1:25) of found to oiled carcass retrieval during searches of flat, sandy beaches. Thus, it would be difficult to document murrelet morality from a spill even if it occurred near large, sandy beaches (i.e., the Copper River Delta to the Yakutat region).

British Columbia

The risks and actual mortality from catastrophic and chronic oil spills to seabirds in British Columbia were reviewed by Burger (1992) and Burger and Fry (1993), but these data are somewhat out of date. There likely has been an increase in the volume and rates of shipping in British Columbia waters, but perhaps balanced by improved handling and shipping techniques, increased vigilance, and better monitoring of oil pollution.

Recent major spills affecting British Columbia murrelets included the *Nestucca* spill off Grays Harbor, Washington, in December 1988, which killed at least 145 Marbled Murrelets off northern Washington and Vancouver Island (Burger, 1993a), and the *Tenyo Maru* spill at the entrance to the Strait of Juan de Fuca on the British Columbia–Washington border in July 1991, which killed at least 45 murrelets and likely many more (Carter and Kuletz, 1995). These are almost certainly underestimates, because the small carcasses of murrelets are easily missed in clean-up operations.

The risks of large, catastrophic spills within areas used by murrelets in British Columbia are high. Annually in the early 1990s there were more than 7,000 transits of freighters and tankers in British Columbia waters, including at least 1,500 tanker trips to or from Alaska, and more than 350 loaded tankers entered the Strait of Juan de Fuca (Burger, 1992). The volume of shipping is certainly higher now. Risk models for southern British Columbia and northern Washington predicted that spills exceeding 1,000 bbl could be expected every 2.5 years for crude oil and every 1.3 years for all petroleum products, with longer intervals between larger spills (Cohen and Aylesworth, 1990). The actual frequency of large spills affecting British Columbia between 1974 and 1991 was fairly close to that predicted (Burger, 1992).

In addition to well-publicized catastrophic spills, many seabirds are killed by small, often unreported spills. Many hundreds of small spills occur each year in British Columbia, from fishing vessels, recreational craft, marinas, and fueling barges (Burger, 1992). Monthly beached bird surveys between 1989 and 1997 showed that oiled birds composed 12.3 percent of the 198 carcasses with reported causes of mortality (Burger, 2002). This percentage is undoubtedly an underestimate of the actual number of oiled birds because evidence of oiling might be easily missed in carcasses that had been partly scavenged or were decomposed. Small quantities of oil were reported on the beaches in 8 percent of all surveys in British Columbia and for 17 percent of surveys on west Vancouver Island (Burger, 2002). Marbled Murrelets were not among the oiled birds identified to species in the beach surveys. Murrelets should experience similar risks of being oiled as other coastal alcids, but because they are one of the smallest seabirds their carcasses are likely to be overlooked in beach surveys.

Most (77 percent) of the oiled birds in the beach surveys were from West Coast Vancouver Island (9 beaches), with 10 percent each from southern Vancouver Island (2 beaches) and Strait of Georgia (1 beach), and a single bird (3 percent) from Langara Island, Haida Gwai (Queen Charlotte Islands) (Burger, 2002). Oiling was the most common cause of death reported for carcasses found on West Coast Vancouver Island and was attributed to 56 percent of the 54 carcasses with reported causes of death there. Oiling was responsible for 13 and 12 percent of carcasses with known causes of death in southern Vancouver Island and Strait of Georgia, respectively, and was the sole cause of death reported for Haida Gwaii (Queen Charlotte Islands). Taking all years into account, the density of oiled birds was highest for West Coast Vancouver Island (0.041 oiled birds per km surveyed), followed by Haida Gwaii (Queen Charlotte Islands) (0.015), Strait of Georgia (0.010), and southern Vancouver Island (0.007). All other regions reported no oiled birds. The mean density of oiled birds (0.014 per km surveyed) was low compared to most other coasts surveyed in North America and Europe (Burger, 1993b, 2002b), but the high volumes of logs and other wrack on local beaches reduced the chances of finding oiled birds. Annual mean oiled carcass density declined on west Vancouver Island between 1990–95, but showed no trend in other regions or for British Columbia as a whole (Burger, 2002). The percentage of oiled birds showed no changes over the years in any region.

A major concern in British Columbia is the relatively high frequency of chronic oiling on the west coast of Vancouver Island and possibly also for Haida Gwaii (Queen Charlotte Islands) (which was not adequately sampled; Burger, 2002). Both of these regions support high densities of Marbled Murrelets.

Overall, chronic oil pollution is likely to kill small numbers of Marbled Murrelet in British Columbia each year, although the actual number is not known, and the impact on the population thus remains unknown. The risks from a large catastrophic oil spill, similar to the *Nestucca* spill (Burger, 1993a) or the EVOS (Piatt and others, 1990), are, however, significant and if such a spill coincided with seasonal aggregations of murrelets it could cause a serious local population decline. Oil spills would kill a large proportion of adult birds, resulting in significant demographic impacts (Boulanger and others, 1999).

Monitoring of marine oil pollution has improved in British Columbia water over the past 5 years, with increased surveillance flights and the use of satellite radar to track large spills (P. O'Hara, University of Victoria, oral commun., 2006).

Incidental Take in Fisheries

Alaska

Commercial fishing is an important component of Alaska's economy and is critical to many communities. Commercial, subsistence, and recreational fisheries occur in Alaska, including gillnet fisheries. Incidental capture of Marbled Murrelets in gillnets is the best-documented effect of fisheries on Marbled Murrelets and has been documented widely in Alaska, British Columbia, Washington, and California (Carter and Sealy, 1984; Carter and others, 1995; Melvin and Parrish, 2001). In British Columbia, an estimated 6 percent of the breeding population of Marbled Murrelets in Barkley Sound was taken annually in gillnets in 1980, although mortality was likely lower in preceding years (Carter and Sealy, 1984; Carter and others, 1995). *Brachyramphus* murrelets are susceptible to mortality in gillnet fisheries due to their nearshore feeding using pursuit-diving behavior (Carter and others, 1995; Day and others, 1999). McShane and others (2004) indicated that gillnet mortality has been reduced in Washington and California due to highly reduced fisheries in recent years, but they used demographic models and conservative estimates of mortality to show that gillnet mortality has significantly impacted some populations in the past. Below, we review murrelet-fisheries interactions in Alaska, with an emphasis on salmon gillnet fisheries.

Salmon Fisheries

Salmon fisheries are managed by the ADFG, with nine salmon regional districts that potentially overlap with Marbled Murrelets (fig. 18). Regional districts are managed separately by local offices, with each region divided into subdistricts and statistical areas for management of fishery openings. The two types of gillnet fisheries used for salmon in Alaska are drift gillnets and setnets, both of which currently use multifilament mesh. Total gillnet length (generally 150 fathoms) per permit varies among fisheries. Drift gillnets are deployed from boats (typically <12 m), and are deployed for 15 min to 4 hr at a time (Wynne and others, 1991). Setnets are stationary surface-hanging nets anchored to shore or the bottom substrate, and usually are checked and picked, but not always removed, during slack tides.

Most salmon gillnet fisheries operate from early June-August, although seasons vary locally and with the target salmon species (fig. 19). These summer months span the breeding season of the Marbled Murrelet in Alaska, and late July through early August is when peak numbers of birds are in nearshore waters, including newly fledged juveniles (Kuletz and Kendall, 1998; Kuletz, 2005). Fisheries that extend into late August–October also may overlap with the murrelet's pre-basic molt period. The molt period for these murrelet populations extends throughout this late summer and early autumn period, and individual murrelets are flightless for about 1 month (Carter and Stein, 1995).

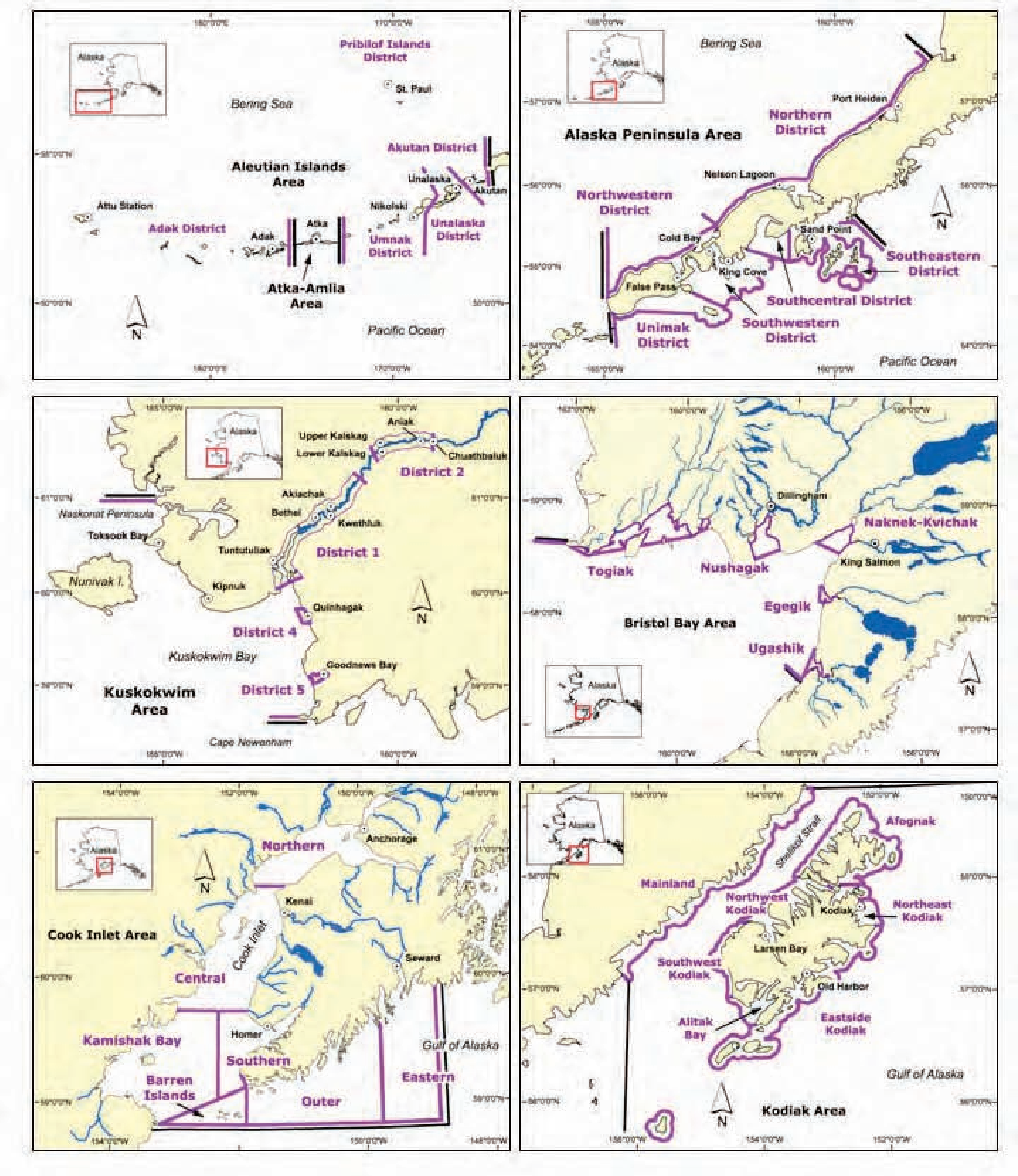


Figure 18. Alaska Department of Fish and Game salmon fishing districts for Aleutian Islands, Alaska Peninsula, Kuskowim, Bristol Bay, Cook Inlet, Kodiak, Prince William Sound, Yakutat, Juneau, Sitka, and Ketchikan Areas.

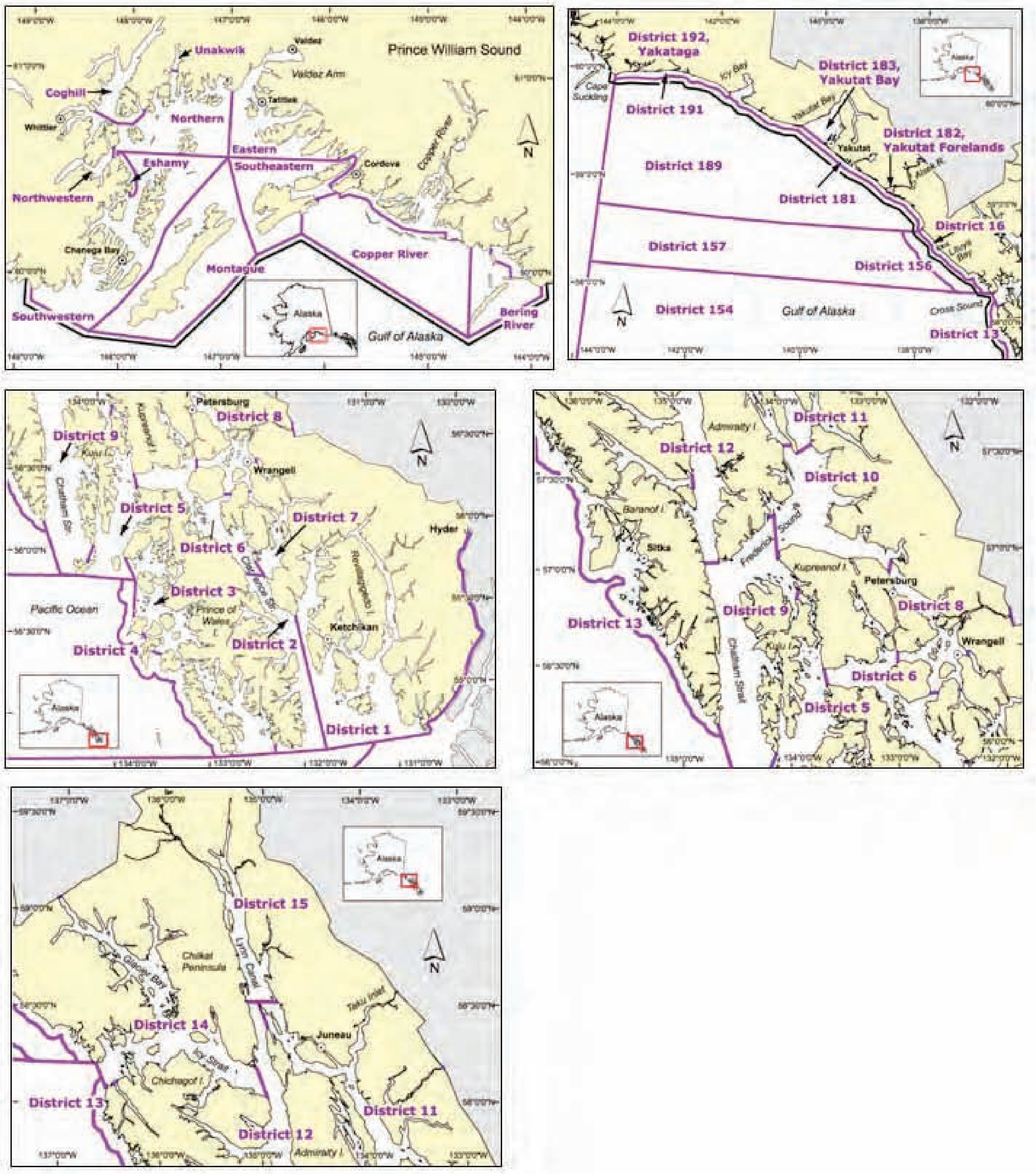
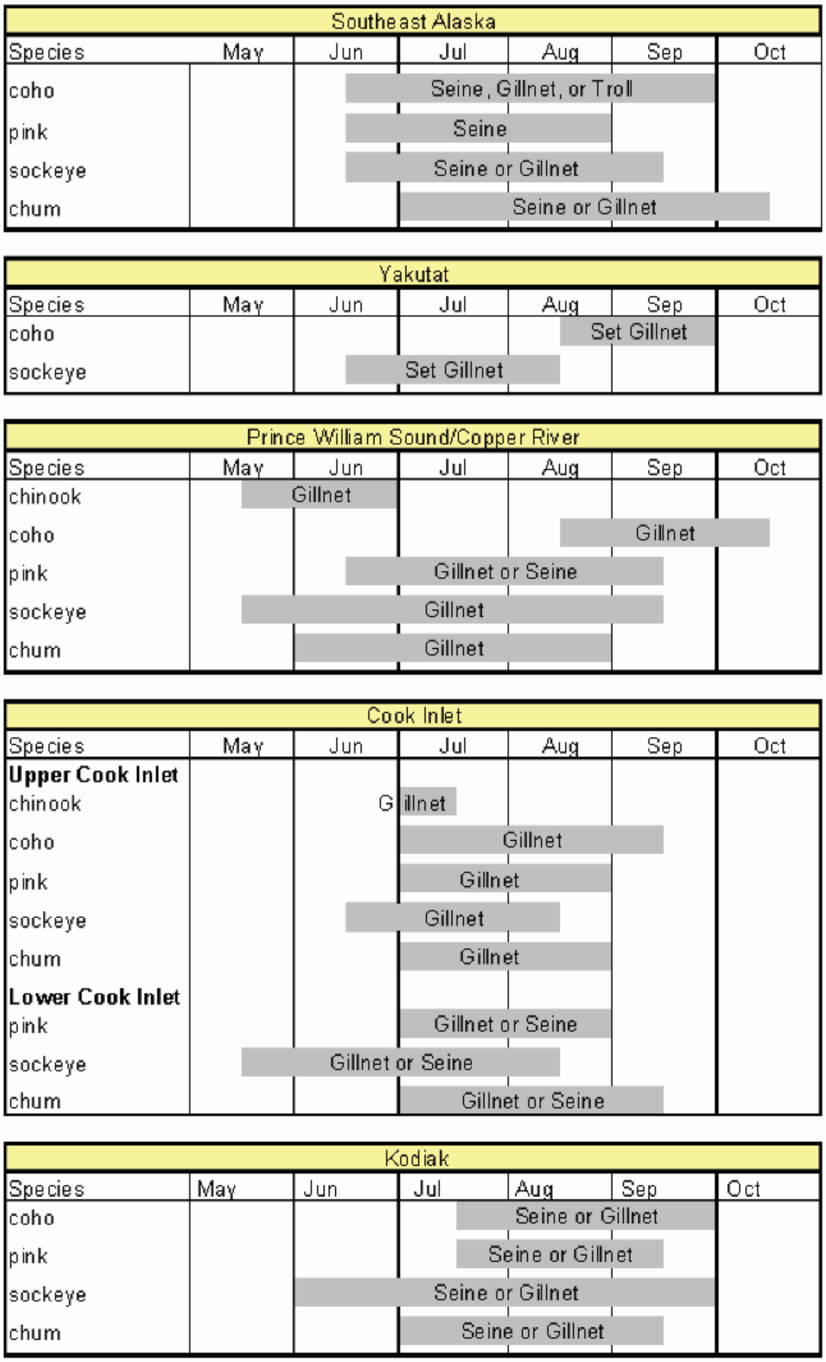


Figure 18. Continued.



Southeast Alaska

Species	May	Jun	Jul	Aug	Sep	Oct
coho		▨	▨	Seine, Gillnet, or Troll	▨	
pink		▨	Seine	▨		
sockeye		▨	Seine or Gillnet	▨	▨	
chum			▨	Seine or Gillnet	▨	▨

Yakutat

Species	May	Jun	Jul	Aug	Sep	Oct
coho				▨	Set Gillnet	
sockeye		▨	Set Gillnet			

Prince William Sound/Copper River

Species	May	Jun	Jul	Aug	Sep	Oct
chinook	▨	Gillnet				
coho				▨	Gillnet	▨
pink		▨	Gillnet or Seine	▨	▨	
sockeye	▨	▨	Gillnet	▨	▨	
chum		▨	Gillnet	▨		

Cook Inlet

Species	May	Jun	Jul	Aug	Sep	Oct
Upper Cook Inlet						
chinook			Gillnet			
coho			▨	Gillnet	▨	
pink			Gillnet	▨		
sockeye		▨	Gillnet			
chum			Gillnet	▨		
Lower Cook Inlet						
pink			Gillnet or Seine	▨		
sockeye	▨	▨	Gillnet or Seine			
chum			▨	Gillnet or Seine	▨	

Kodiak

Species	May	Jun	Jul	Aug	Sep	Oct
coho			▨	Seine or Gillnet	▨	
pink			▨	Seine or Gillnet	▨	
sockeye		▨	Seine or Gillnet	▨	▨	
chum			▨	Seine or Gillnet	▨	

Figure 19. Commercial salmon fishing seasons in Alaska, for those fisheries using gillnets.

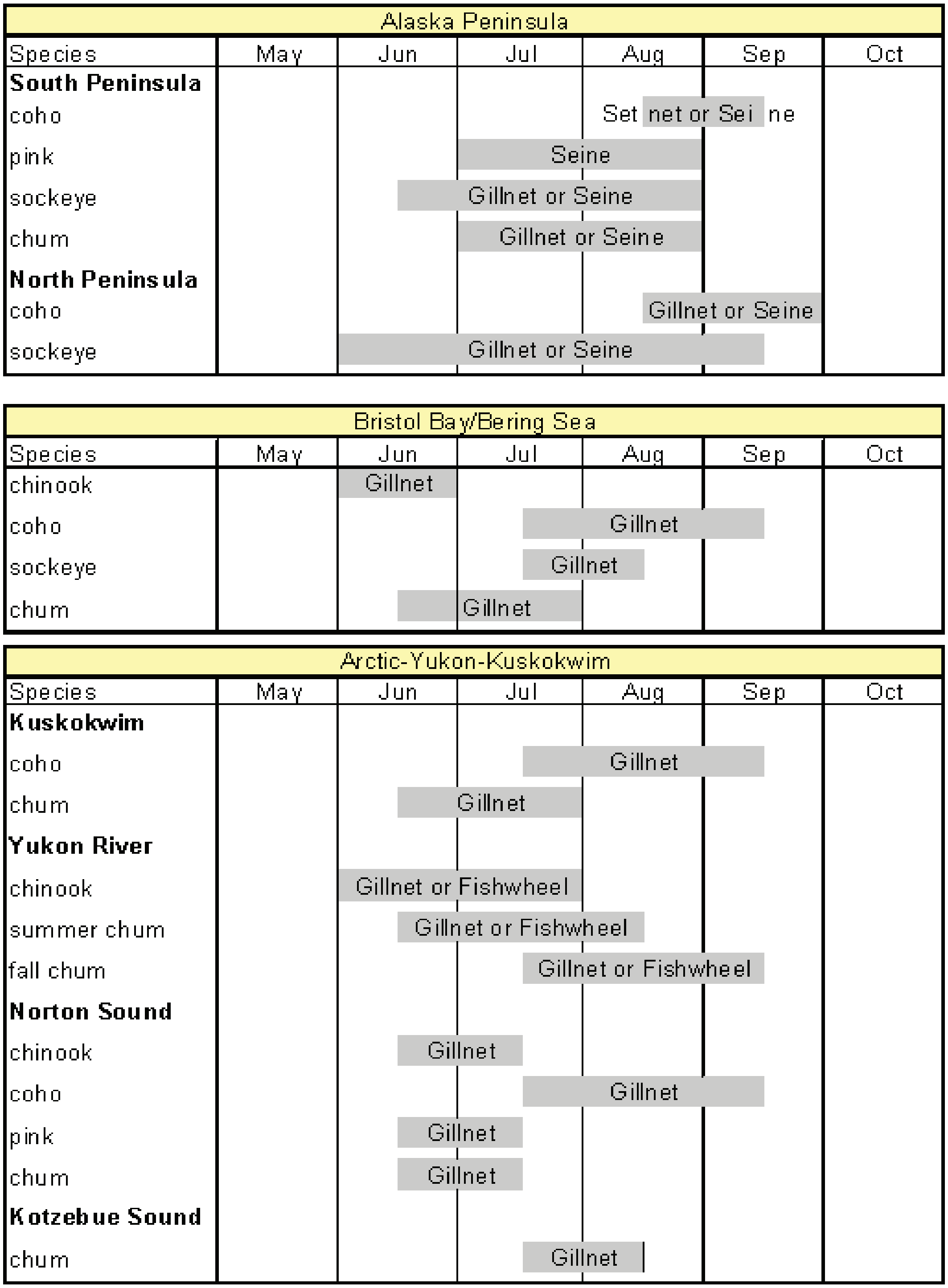


Figure 19. Continued.

The number of salmon permits held throughout the State (including gillnet, seine, and troll fisheries) has a 5-year (2000–04) average of 7,432 permits (Woodby and others, 2005; table 24). Of these permits, 3,438 (46 percent) are in regions with substantial populations of Marbled Murrelets, including Southeast Alaska—Yakutat, Prince William Sound, Cook Inlet, and Kodiak Island. Smaller murrelet populations, and thus lower densities and potentially lower encounter rates, may overlap with gillnet fisheries in Bristol Bay, the Aleutian Islands, and along the Alaska Peninsula (fig. 18).

The number of salmon permit holders and salmon landings increased dramatically in the 1980s, and remains strong today (fig. 20). In Prince William Sound, this growth in the salmon fishery was facilitated by Pink salmon (*O. gorbuscha*) hatcheries, which began in 1977 and reached full production in the mid-1980s (Pearson and others, 1999; Thomas and Thorne, 2003).

Murrelet and Gillnet Fisheries Overview

For three of the major ADFG fishing areas, Cook Inlet, Prince William Sound, and Southeast Alaska, the USFWS has survey data (1993, 2005, 1994, respectively) on murrelet distribution (North Pacific Pelagic Seabird Database [NPPSD], 2006). We mapped the numbers of *Brachyramphus* murrelets (93–99 percent Marbled Murrelets) with respect to fishing district boundaries[2]. Not all areas of a fishing district are fished, and annual and seasonal differences in fishing effort are dramatic, thus these maps are only for general reference.

In Cook Inlet, murrelets occur throughout the central portion of central Cook Inlet, with the heaviest concentrations in the Southern District, which includes Kachemak Bay (fig. 16). In Prince William Sound, murrelets tend to be in nearshore waters, are fairly evenly distributed, and overlap with all districts to some degree (fig. 21). Numbers of murrelets are high in the Southwestern District, including the southern Eshamy District, but this is partly an artifact of more USFWS transects in this region (U.S. Fish and Wildlife Service, unpub. data, 2006). Murrelets are locally abundant in the upper fjords of the Coghill District as well. There is no murrelet survey data for the Copper River, Bering River, or the outer waters of Southeastern and Montague districts, all of which are considered part of the Prince William Sound Area.

Southeast Alaska is divided by the ADFG into the northernmost Juneau Area, the central Sitka Area, and the southernmost Ketchikan Area, totaling 16 subdistricts (fig. 22). Areas that are traditionally fished include Districts 15 (Lynn Canal and adjoining inlets), District 11 (Stephens Passage and adjacent inlets), Districts 6 and 8 (passages between northeastern Prince of Wales Island, southern Kupreanof Islands, and the mainland). Marbled Murrelets occur throughout Southeast Alaska, but the 1994 survey shows high concentrations in the southern portion of District 15, District 11, and the northern portion of District 10 (fig. 22). Murrelets were scattered throughout District 6, with a large concentration near the confluence of the Sumner and Stikine straights (northwestern Prince of Wales Island). Similar overlap between murrelets and gillnet fisheries in the inside waters were described by Carter and others (1995), based on non-standardized surveys conducted by fisher-biologist Mike McAllister. In the 1994 survey, murrelets also occurred along the outer coast, particularly in District 3 (northeastern Prince of Wales Island) and the northern portion of District 13 (northern Baranof Island). District 14, which includes Icy Straight, also has large numbers of murrelets (this volume), and may attract murrelets nesting as much as 100 km to the south (Whitworth and others, 2000).

---

[2] District maps available at http://www.cf.adfg.state.ak.us.

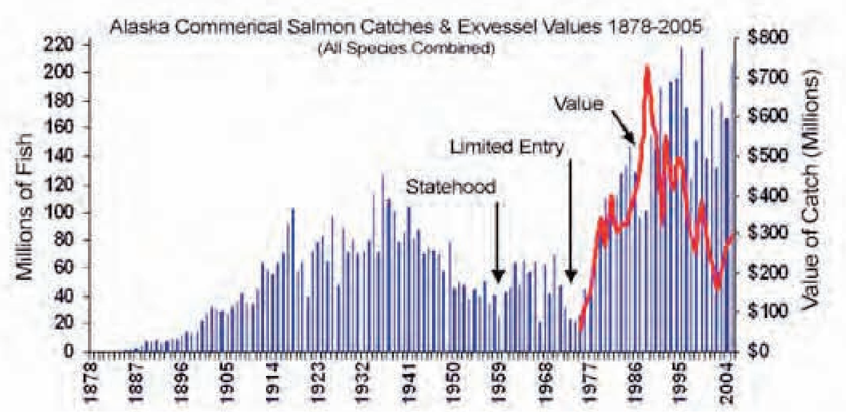


Figure 20. Salmon harvest in Alaska, 1878–2005. From Alaska Department of Fish and Game.

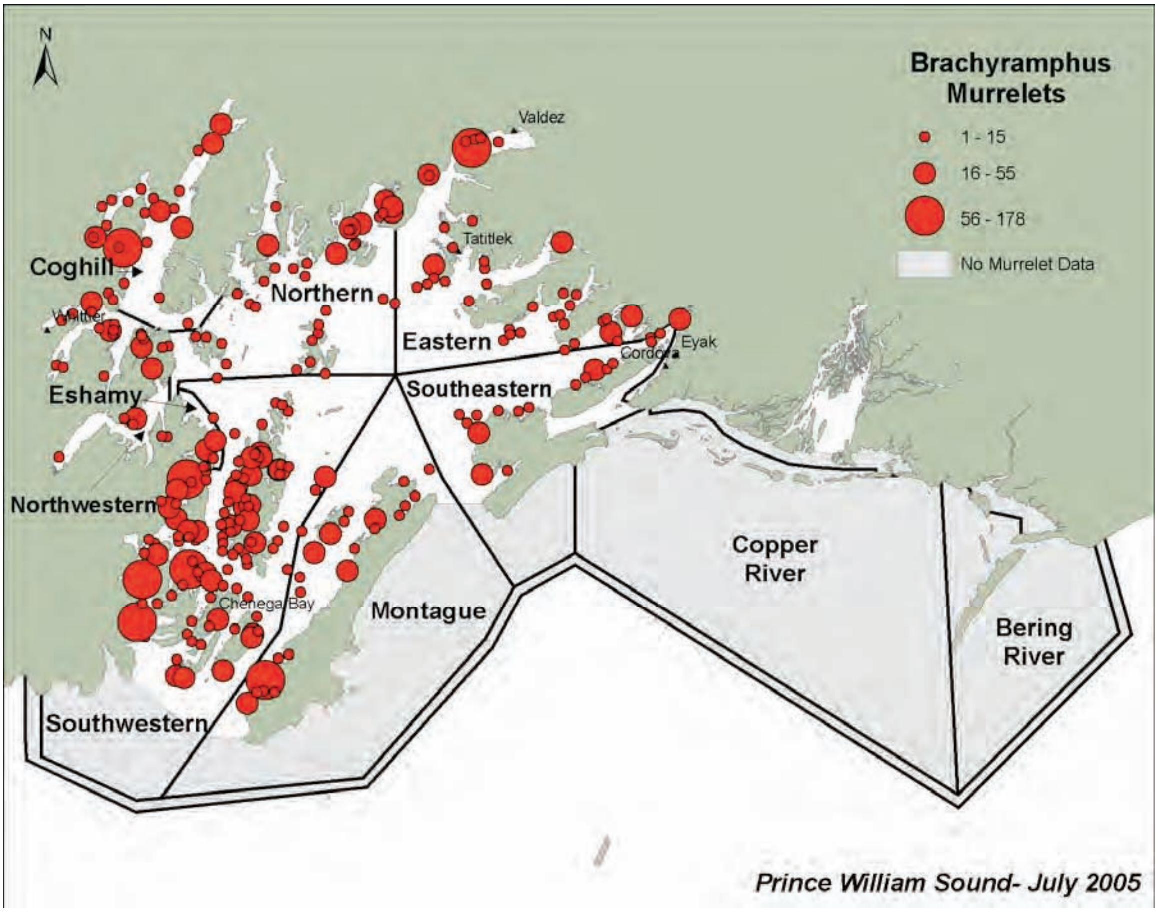


Figure 21. *Brachyramphus* murrelet distribution in Prince William Sound in July 2005, relative to salmon fishing districts in the Prince William Sound Area. Surveys for murrelets were not conducted in the outer waters of the Sound, nor in the Copper River and Bering River districts.

Gillnet Mortality

Prior to 1990, records of murrelet mortality in gillnets were mostly anecdotal, and suggested that total murrelet mortality in gillnets in Alaska was in the low thousands annually (Mendenhall, 1992; Carter and others, 1995). Carter and others (1995) report observations by fisher-biologist Pete Isleib, that ‘several hundreds’ of murrelets were killed annually in Prince William Sound (including the Copper River district). Isleib also estimated, based on his estimates of fishing effort, locations, and what he observed in Prince William Sound, that as many as 1,000 Marbled Murrelets were killed annually in gillnet fisheries of Southeast Alaska (DeGange and others, 1993). Isleib reported that gillnet mortality of birds was rare in the Bristol Bay area, and he had not encountered murrelets as bycatch in that fishery.

Because distribution of fishing effort, habitat types, and murrelet abundance varies among regions, differences in encounter rates between murrelets and gillnet fisheries would be expected. Based partly on the results of the Prince William Sound studies, and anecdotal reports of murrelet mortality in gillnets, Piatt and Naslund (1995) estimated that as many as 3,300 Marbled Murrelets were killed in gillnets annually in Alaska during the 1990–91 period. This estimate assumed similar encounter rates between gillnet fishers and murrelets in all fishing areas, and operation of all available fishing hours, and thus could have inflated the murrelet bycatch estimates. However, additional information for Cook Inlet and Kodiak Island suggest that the Piatt and Naslund (1995) estimate was at least within the same order of magnitude. Based on the estimated take of murrelets in Prince William Sound, south Unimak, Cook Inlet, and Kodiak Island (table 25), and assuming that declines in murrelet populations since the 1990–91 studies have reduced encounter rates, it is likely that at least 500 birds are taken annually in those four fisheries. Because of the larger area, higher number of permits, and larger murrelet population in Southeast Alaska, it is possible that twice that number is taken annually there. However, a proper estimate would require a monitoring effort for Southeast Alaska–Yakutat areas, and an update for the Prince William Sound–Copper River areas.

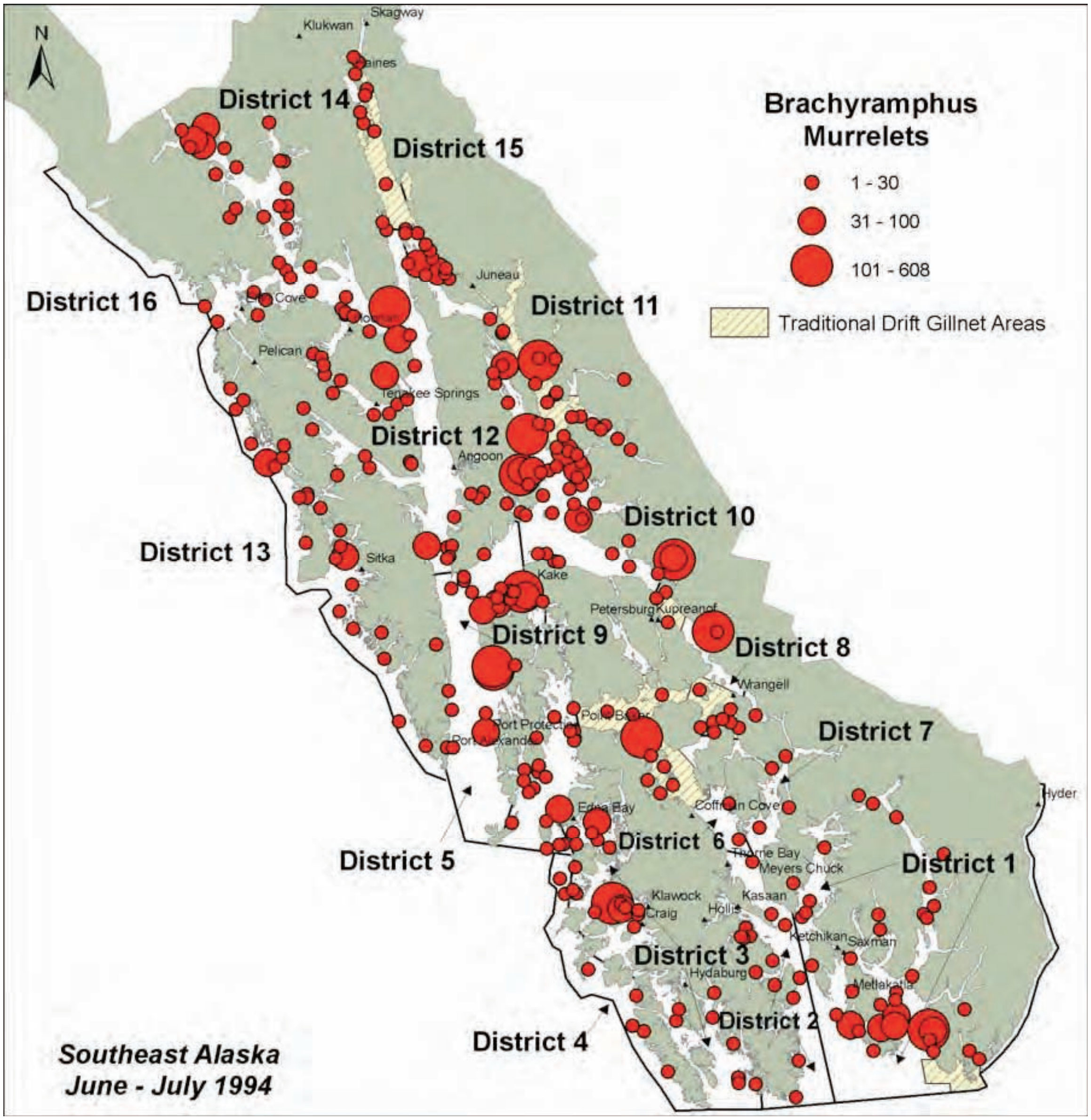


Figure 22. *Brachyramphus* murrelet distribution in Southeast Alaska in June and July 1994, relative to salmon fishing districts in the Southeast Areas.

The number of ADFG commercial salmon permits provides an indication of relative fishing effort among areas, but not all permits are used in a given year, and fishers may not fish during all openings. Daily, seasonal, and annual fishing vessel-hours can vary dramatically depending on achievement of escapement goals, and actual fishing effort is not tracked by the ADFG (Wynne and others, 1991, 1992; Manly and others, 2003). For example, a 2006 pilot study of the Yakutat gillnet fishery by West, Inc. (B. Manly, oral commun., 2006), found that roughly one-third of the maximal potential net-hours (based on number of permits and openings) were actually fished. Thus, estimates of fishing effort should be based on surveys of fishing effort conducted concurrent with studies of incidental take. Tracking of actual fishing effort during gillnet bycatch studies was conducted for the Cook Inlet and Kodiak studies. Extrapolating total bycatch mortality for murrelets throughout Alaska would require more detailed knowledge of fishing effort, local fishing patterns, and would ideally include data on current murrelet distribution and abundance.

Table 24. Recent 5-year average harvests, value, and permits fished for selected Alaska commercial salmon fisheries.

[From Commercial Fisheries in Alaska, Woodby and others, 2005, with updated data. http://www.cf.adfg.state.ak.us/geninfo/finfish/salmon/catchval/blusheet/salmon_00-04table.php. Averages are for 2000–04]

Fishery	Harvest (number of fish)	Harvest (lb)	Value($)[1]	Permits
Southeast and Yakutat	61,727,291	286,506,541	$72,573,000	1,781
Prince William Sound	40,563,838	169,733,170	$43,841,000	680
Cook Inlet	5,337,269	28,301,597	$14,657,800	982
Kodiak	21,262,985	87,729,099	$19,744,000	322
Chignik	1,856,583	11,593,697	$6,978,000	62
Alaska Pen. and Aleutians	8,476,735	40,999,253	$13,668,000	285
Bristol Bay	18,070,428	112,058,010	$56,097,000	2,285
Kuskokwim	430,566	3,274,628	$1,149,800	491
Yukon River[2]	50,182	682,624	$1,268,800	465
Norton Sound	64,026	298,277	$71,600	42
Kotzebue	91,401	786,247	$129,000	37
Statewide	157,931,303	741,963,142	$230,178,000	7,432

[1] Exvessel value of landed catch.

[2] No Yukon fishery in 2001.

Although the Alaska salmon fishery is managed by the State, the National Oceanographic and Atmospheric Administration (NOAA)-Fisheries is responsible for monitoring threats to marine mammals, which also are caught in gillnets. In 1990, the NOAA-Fisheries initiated the Alaska Marine Mammal Observer Program. The original intent was to rotate among state gillnet fisheries, sampling a given fishery with an observer program for 2 years. However, funding of NOAA gillnet studies is allocated at the National level, and depends on the status of mammals at risk and costs of monitoring a fishery. In Alaska, with a large, dispersed fishery and remote locations with difficult access, the cost of conducting bycatch studies has hindered adequate coverage, even when a study was implemented (Wynne and others, 1991).

Between 1990 and 2006, gillnet fisheries were monitored during six seasons at south Unimak on the Alaska Peninsula (1990), Prince William Sound (1990, 1991), Cook Inlet (1999, 2000), and Kodiak Island (2002, 2005; see table 25). The NOAA-Fisheries estimated that ideally 20–35 percent of a fishery should be sampled, but where this is not possible, they accept 5 percent coverage as a minimum for adequate statistical analyses (Wynne and others, 1991). In Alaska salmon fisheries, observer coverage has been limited because of the use of small boats, distribution of boats over large areas, and potentially dangerous seas (Wynne and others, 1991). The 1990 study was estimated to have sampled 2.7–4.1 percent of three fisheries that year, and 5 percent in 1991 (Wynne and others, 1991, 1992). In Cook Inlet, less than 2 percent of the fishery was monitored, resulting in wide CIs and suspect mortality estimates (Manly, 2006a). Manly determined that adequate sampling of most fisheries would require observation of approximately 5 to 7 percent of the fishing effort (Manly and others, 2003). However, based on results from the Kodiak fishery, power to detect significant differences in bycatch of Marbled Murrelets between regions or years would take four times that level of coverage (Manly and others, 2003). The wide CIs of the resulting bycatch estimates (table 25) illustrate the relatively rare occurrence of seabird bycatch to individual fishers. Nonetheless, the size and geographic extent of Alaska's salmon fisheries could make it a conservation issue.

Table 25. Salmon gillnet fishing regions, the 5-year average (2000–04) for number of permits by region, and available data on Marbled Murrelet incidental take in those fisheries.

[Bycatch rate for PWS and Unimak were derived from data in report, using number of birds taken per net hauls observed. Bycatch rate for Kodiak and Cook Inlet were calculated by the source author, using number of birds taken per net-hour fished. nd, no data]

Region	5-year average number of permits	Year of study	Percent of total birds	Incidental take of Marbled Murrelets			Source of bycatch data
				Bycatch rate	per year take	95-percent confidence limit	
Southeast and Yakutat	1,781	nd	nd	nd	nd	nd	
PWS / S. Unimak	680						Wynne and others, 1991
PWS driftnet[1]		1990	91.9	0.020	1,350	768–1,930	
PWS setnet[1]		1990	0	0	0	0	
S. Unimak driftnet[1]		1990	6.3	0.003	21	10–33	
PWS driftnet[2,3]		1991	32.1	0.012	318	107–671	Wynne and others, 1992
Cook Inlet[4]	982						Manly, 2006a
Upper CI setnet[4]		1999	0	0	0		(author notes insufficient coverage to determine bird bycatch)
Lower CI setnet[4]		1999	0	0	0		
Central driftnet[4]		1999	0	0	0		
Upper CI setnet		2000	33.3	0.001	37	0–111	
Lower CI setnet		2000	0	0	0		
Central driftnet		2000	0	0	0		
Kodiak Island	322						
setnet		2002	11.4	0.013	56	3–110	Manly and others, 2003
setnet		2005	10.9	0.011	143	8–277	Manly, 2006b
AK Penin / Aleutians	285	nd	nd	nd	nd	nd	
Bristol Bay	2,285	nd	nd	nd	nd	nd	

[1] Based on data in Wynne and others, 1991, using weekly bycatch rates for all birds, and percent Marbled and unidentified murrelets.

[2] Based on data in Wynne and others, 1992, using 17 birds taken during 22 percent of 5,875 sets (not total net hours).

[3] Includes one unidentified murrelet, but not the Kittlitz's Murrelets.

[4] Less than 1 or 2 percent of fishery was observed; insufficient for sampling bird bycatch, and estimates not reliable (Manly, 2006a).

Bycatch Estimates

Murrelet bycatch in the 1990 south Unimak fishery was relatively low, with murrelets composing about 6 percent of total bird bycatch and annual take ranging from 10 to 33 birds (95 percent CI). The low proportion of murrelets among the bird bycatch likely reflects the relatively low murrelet density in the Alaska Peninsula Area (Van Pelt and Piatt, 2005).

In the Prince William Sound-Copper River drift gillnet fishery, estimated incidental take of *Brachyramphus* murrelets ranged in magnitude from approximately 2,000 to several hundred in 1990 and 1991. Different treatment of data in Wynne and others (1991, 1992) have resulted in differences in annual estimated bycatch of murrelets for Prince William Sound. Piatt and Naslund (1995) estimated that *Brachyramphus* murrelet mortality was 923 and 714 murrelets in 1990 and 1991, respectively. However, using Wynne's more detailed analysis of total bird bycatch in 1990 using mean bycatch rates per week and gillnet effort (Wynne and others, 1991) resulted in an estimated 1,468 (95 percent CI, 813–2,043) total bird take, which would equate to 1,423 *Brachyramphus* murrelets (Piatt and Naslund, 1995). Based on the percentage of bird bycatch in 1990, Marbled Murrelets composed 84 percent of the total bycatch, or 92 percent if unidentified murrelets were included, which equated to 1,350 murrelets (table 25). In 1991, Marbled and unidentified *Brachyramphus* were 32 percent of total bird bycatch, or 318 birds. Estimated mortality of Kittlitz's Murrelets added an additional 79 birds in 1990 and 133 birds in 1991.

In both 1990 and 1991, bycatch was highest in the Copper River District, but there also was greater coverage in that district, and bycatch occurred regularly in the Coghill District (Wynne and others, 1991). Anecdotally, fishers reported that murrelet abundance and bycatch in the Copper River District were much higher than normal in 1990 (Wynne and others, 1991). Wynne and others (1991) observed that murrelets were taken in all Prince William Sound districts, mortality occurred throughout the summer, but was highest in late July, and was most frequent in nearshore sets. Estimates of seabird bycatch are highly variable among years even at the same site (Melvin and others, 1999, 2001). The high variance is believed to be partly the result of changes in environmental or fishery-related factors, but also reflects the generally low probability of detecting bycatch (Manly and others, 2003).

Seabird bycatch in the three Cook Inlet fisheries was very low, with the exception of the Upper Cook Inlet setnet fishery in 2000 (table 25). However, the 2000 estimate of 37 murrelets was based on a single bird taken in a study with very low observer coverage. The low coverage level in this fishery compromised estimates of bird bycatch (Manly, 2006a). In the Kodiak setnet fishery, Marbled Murrelets composed about 10–11 percent of total bird bycatch, with estimated per annum mortality of murrelets of 56 and 143 in 2002 and 2005, respectively (table 25). The higher estimated morality of murrelets in 2005 appeared to be due to greater fishing effort, not a higher bycatch rate (Manly, 2006b).

Murrelets taken in the Kodiak fishery were examined by University of Alaska and USFWS researchers. The Marbled Murrelets all had brood patches (in various stages), and thus were likely breeding adults, with equal proportions of males and females (Manly, 2006b). Piatt and Naslund (1995) reported that 18 murrelets examined from the Prince William Sound study included 16 adults and 2 juveniles. However, based on anecdotal reports from Alaska, Carter and others (1995) reported that juvenile murrelets may be particularly susceptible to gillnet mortality when fishing occurs later in the breeding season.

Other Coastal Fisheries

Some components of the sac-roe (herring eggs) fishery also use gillnets, although the majority of herring are taken by purse-seine. The herring fishery has not been monitored for bycatch, but it is not likely to be a significant contributor to murrelet mortality. Compared with salmon fisheries, herring gillnet fisheries are relatively brief, and occur in spring (primarily April), before many murrelets aggregate in nearshore waters in parts of Alaska. However, some birds are resident over the winter and could be impacted in Southeast Alaska. The mesh used for herring typically is about one-half the size of that used for salmon, which may reduce or preclude murrelet entanglement. Murrelets also can become trapped inside purse-seine nets as they are encircled and hauled in during salmon and herring fishing operations, but anecdotal observations suggest murrelets can escape (Carter and others, 1995).

Efforts to Reduce Gillnet Mortality

There is considerable evidence that where murrelets overlap with gillnet fisheries, mortality occurs at some level. Although monitoring bycatch is a useful management tool, the best approach at this stage would be to determine how best to mitigate incidental take in these fisheries. Area closures have proven to be successful for reducing seabird bycatch in central California and Washington. Between 1979 and 1990, a series of fishing closures gradually reduced gillnet mortality of seabirds and marine mammals throughout the breeding range of the Marbled Murrelet in central California (i.e., Marin to northern Monterey County) where murrelet mortality had been documented (Wild, 1990; Carter and Erickson, 1992; Carter and others, 1995). Alternative fishing gear (modified otter trawls) were investigated and used for several years by a few fishers but later abandoned. By the mid-1990s, fishing effort shifted farther south off the coasts of southern Monterey and San Luis Obispo Counties, and seabird and marine mammal mortalities resumed (Forney and others, 2001). In 1997, radio-marked Marbled Murrelets were first found to disperse to this area (E. Burkett, California Department of Fish and Game, unpub. data, 1997), and concern about possible gillnet mortalities to murrelets resumed but no carcasses were recovered. In 2000, gillnet fishing was banned from all nearshore waters (i.e., waters <100 m deep; McShane and others, 2004).

In Washington, several studies in 1993–96 found low entanglement of seabirds; however, fishing effort already had been reduced to less than 50 percent of levels in the 1980s (McShane and others, 2004). Area and temporal closures were implemented in 1995, and alternative gear was investigated and later implemented. Bycatch of birds, primarily Common Murres and Rhinoceros Auklets (*Cerorhinca monocerata*), in the gillnet fishery in Washington has been reduced by as much as 75 percent (Melvin and others, 1999; Melvin and Parrish, 2001). However, whether or not Marbled Murrelet mortality was reduced by alternative gear was not determined (McShane and others, 2004). Very reduced fishing effort after 1997 has likely led to low levels of gillnet mortality in Washington over the last decade.

In British Columbia, restrictions to prevent fishing in murrelet aggregation areas or to prevent crepuscular and night-time fishing have been proposed to reduce incidental take of murrelets in gillnets (Carter and Sealy, 1984; Burger, 2002). Carter and others (1995) also recommended daylight fishing and proposed that area restrictions might reduce murrelet bycatch in Alaska. It is unknown whether the gear modification or temporal restrictions would work in Alaska, where daylight patterns differ from lower latitudes, water clarity varies tremendously among fishing areas, and fishers are dispersed over larger areas. However, Isleib did report that as much as 80 percent of the mortality he observed in Prince William Sound occurred during night sets. Murrelets have been observed diving and foraging near gillnets, and they have been entangled at various depths, from the surface to 10 m below the surface (Carter and others, 1995). In the Kodiak fishery, Manly and others (2003) did not find time of day to be a significant factor for all alcid bycatch combined. Manly will be conducting a more detailed analysis with the inclusion of 2005 data, and will attempt to examine murrelets separately (B. Manly, WEST, Inc., oral commun., 2006).

Alaska Groundfish Fisheries

This is Alaska's largest fishery, in biomass harvested and monetary value, and is one of the largest in the world (National Oceanic and Atmospheric Administration, 2004). The NOAA-Fisheries Observer Program deploys observers onboard selected ships to monitor bycatch, including seabirds. At the request of the USFWS, the NOAA-Fisheries trains observers to identify marine birds taken incidentally in fishing gear and record opportunistic observations of presence or interactions with fishing operations. The Marbled Murrelet is one of seven bird 'species of special interest,' meaning that observers are requested to record observations of the birds, and to salvage carcasses for species confirmation. Most of these fisheries operate in offshore waters where interactions with murrelets are rare. The estimated take for all alcids in these fisheries averages less than 400 birds annually, primarily in the trawl fisheries of the Gulf of Alaska (National Oceanic and Atmospheric Administration, 2006). No identified Marbled Murrelets have been caught incidentally, although between 1993 and 2005 incidental takes of 'small unidentified alcid' were recorded on 20 occasions (S. Fitzgerald, Alaska Fisheries Science Center, oral commun., 2006).

Separate from the official incidental take records, fisheries observers opportunistically record bird observations, which are entered into the Seabird Observer Notes Database maintained by the USFWS in Anchorage, Alaska. A query of the 4,249 records in Seabird Observer Notes between 1993 and 2003 (U.S. Fish and Wildlife Service, unpub. data, 1993–2003), found 12 records of Marbled Murrelets, and 11 of unidentified murrelets. Of these, 13 were sightings of birds on the water, 2 were diving near gear lines, 7 were on the vessel and unable to fly away without assistance, and 1 was a vessel strike that died. These records suggest that Marbled Murrelet interactions with groundfish fisheries are rare, but may include vessel strikes on occasion. Vessel strikes in Alaska are more common for small auklets and shearwaters, and are often associated with lighted vessels during stormy nights or high winds (e.g., Dick, 1979).

British Columbia

Information on interactions between fisheries and Marbled Murrelets in British Columbia was summarized by Burger (2002b), but a new report (Smith and Morgan, 2005) provides additional data. Of the more than 15 types of fisheries operating in British Columbia, salmon gillnets appear to be the greatest threats to Marbled Murrelets. Possible impacts of sports fishing (angling), the purse-seine fishery, and aquaculture remain poorly known. Based on the review and data provided by Smith and Morgan (2005), murrelets appear to be at low risk to being caught in long-line fisheries (either for halibut or rock cod), the salmon troll fishery, the sablefish trap fishery, or the trawl net fishery.

In Canada, two Federal agencies have regulatory authority with regards to the issue of bycatch—Environment Canada (EC) and the Department of Fisheries and Oceans (DFO). EC has a mandate for seabird conservation and the responsibility to enforce the statutes of the Migratory Bird Convention Act and the SARA. Nationally, seabird management priorities are set by EC headquarters, with input from the various regions; and management activities are implemented regionally (e.g., through the CWS). The DFO is the Federal authority over all fishing activities, and is responsible for the enforcement of the Fisheries Act, the Oceans Act, and Canada's role in implementing International fisheries agreements. Canada is a signatory to the UN International Plan of Action for Reducing the Incidental Catch of Seabirds in Longline Fisheries (UN Food and Agriculture Organization [FAO], 1999) and the UN Code of Conduct for Responsible Fisheries (Food and Agriculture Organization, 1995). The DFO also is responsible for implementing a Pacific Region Selective Fisheries Policy and the Canadian Code of Conduct, an industry led initiative.

There is currently a modest effort to study bycatch issues in British Columbia, beginning with the formation of the interagency Pacific Seabird Bycatch Working Group in 2000. The group's goals were to increase the understanding of seabird bycatch in longline and net fisheries, and to promote the use of mitigation measures to reduce seabird bycatch in British Columbia. Efforts have been made to train fisheries observers to identify seabirds and a seabird salvage program was initiated in 2000 to collect birds killed by the gillnet fisheries. The review and analysis by Smith and Morgan (2005) is the first step in identifying the scope of the bycatch problem in British Columbia. A more detailed effort is underway to document fisheries interactions with Marbled Murrelets (D. Bertram and K. Charleton, Candian Wildlife Service), but results from this study are not yet available.

Gillnets

Bycatch in gillnets was cited as one of the major threats to murrelets in British Columbia when they were listed as Threatened (Rodway, 1990) and in subsequent reviews (Hull, 1999; Burger, 2002). The main salmon species targeted in the commercial gillnet fishery in British Columbia are pink, sockeye (*0. nerka*), and chum (*O. keta*) salmon. The DFO statistical areas are combined into eight License Areas, of which three (Areas C, D, and E; figs. 23, 24, and 25) pertain to gillnet fisheries. Areas of the British Columbia coast where gillnetting activity might overlap with Marbled Murrelet aggregations were identified by Carter and others (1995) and Burger and others (1997), but fishing effort changes frequently from year to year making it difficult to predict where problems might arise.

Gillnet vessels in British Columbia generally are less than 15 m in length and are operated by a crew of one or two. Gillnets are set below the surface and typically have a multi-strand mesh comprised of 30 or more filaments in each twine. In recent years, Alaska Twist mesh has been tested in some fisheries. This mesh is made from six or more filaments twisted together in each twine.

The first detailed study on gillnet mortality of murrelets in British Columbia was by Carter and Sealy (1984), who reported bycatch of Marbled Murrelets during gillnetting in June–August for sockeye salmon in Barkley Sound in 1979–80. Carter and Sealy (1984) estimated that a minimum of 175–250 murrelets was killed in 1980, which represented 6.2 percent of the local breeding population, or 7.8 percent of the potential autumn population (taking into account the additional loss of chicks whose parents had died). Most mortality occurred at night at depths of 2.0–8.5 m. Approximately 90 percent of the dead birds were breeding adults, 5 percent non-breeding, and 5 percent HY birds. In the 1980s and early 1990s there typically were 300–400 gillnet vessels fishing 24 hours per day, 1-4 days per week, in Barkley Sound (Burger, 2002; Smith and Morgan, 2005). Gillnetting of this intensity which overlaps with the time of maximal numbers of murrelets (April–August) is now rare in Barkley Sound, although some bycatch mortality continues (Carter and others, 1995; Alan E. Burger, University of Victoria, personal observation). Since the mid- to late-1990s, the fishing effort has been about 100 gillnet vessels fishing only in daylight, only for 1–2 days per week (Smith and Morgan, 2005).

In their analysis of more recent data, Smith and Morgan (2005) found bird mortality to be highly variable in the British Columbia salmon gillnet fisheries; bycatch rates ranged between 0.019 and 0.219 birds per hour fished. Common Murres and Rhinoceros Auklets were the species most often reported caught, composing about 90 percent of the bycatch. Marbled Murrelets were reported caught in at least three fisheries. A high proportion of the birds caught was left unidentified and not salvaged. Smith and Morgan (2005) stressed that species-specific bycatch may be underestimated due to the high number of unidentified and non-salvaged birds.

The most detailed recent analysis of seabird bycatch from salmon gillnets in British Columbia is from the 7-year (1995-2001) test fishery for chum salmon in Area 21 off Nitinat Lake, southwest Vancouver Island in late September to early October (Smith and Morgan; 2005; J. Mitchell, Department of Fisheries and Oceans, unpub. data, 1995–2001). Concentrations of murrelets are high in this area during summer but tend to be low during the months of the test fishery (Alan E. Burger, personal observation, 1995). The Nitinat fishery area is within 40 km of the Barkley Sound sockeye fishery studied by Carter and Sealy (1984). In total, the 1995–2001 data cover 106 days of fishing using 4–8 vessels, 5,425 sets, and 10,248 hours of soaking (Smith and Morgan, 2005). A total of 392 birds were caught. Bycatch rates varied greatly among the years but averaged 0.092 ± 0.063 (SD) birds per set (range = 0.040–0.183) or 0.054 ± 0.042 (SD) birds per net-hour (range = 0.019–0.117). Out of 295 identified birds, 6 were recorded as Marbled Murrelets (i.e., 2.03 percent). Most (89 percent) of the identified birds were Common Murres. If we assume that 2.03 percent of all birds, including those not identified, were Marbled Murrelets, then the estimated rate of mortality in this test fishery would be 0.0019 ± 0.0013 birds per set or 0.0011 ± 0.0008 murrelets per net-hour. Test fisheries probably do not reflect mortality rates in commercial openings (Smith and Morgan, 2005). More vessels are present in commercial fisheries, which may cause fewer birds to remain in the area, resulting in lower bycatch rates. However, commercial vessels generally do not use gear that might reduce fish bycatch (e.g., drop weed-lines, Alaska twist), some of which also might reduce incidental seabird mortality (J. Smith, Canadian Wildlife Service, oral commun., 2006).

Smith and Morgan (2005) also summarize less-detailed data from other test, selective, or commercial gillnet fisheries. During an 11-day test fishery for coho salmon in Area 4, 1,834 sets gave bycatch rates of 0–0.01 birds per set (average 0.004) of which 2 of the 5 identified birds were Marbled Murrelets (Smith and Morgan, 2005). This translates roughly to a mean catch rate of 0.0016 murrelets per set. In a sockeye salmon selective fishery in Area D, a total of 417 sets were made in 9 days, representing 416 hours of fishing. Overall, 91 birds were caught giving an overall bycatch rate of 0.219 birds per net-hour, but none of the 86 identified birds was a Marbled Murrelet. Finally, in the Barkley Sound sockeye salmon commercial fishery, 126 sets were observed from a possible 256 licensed vessels during two 1-day openings. Observers reported no bird bycatch and no other fishery data were available.

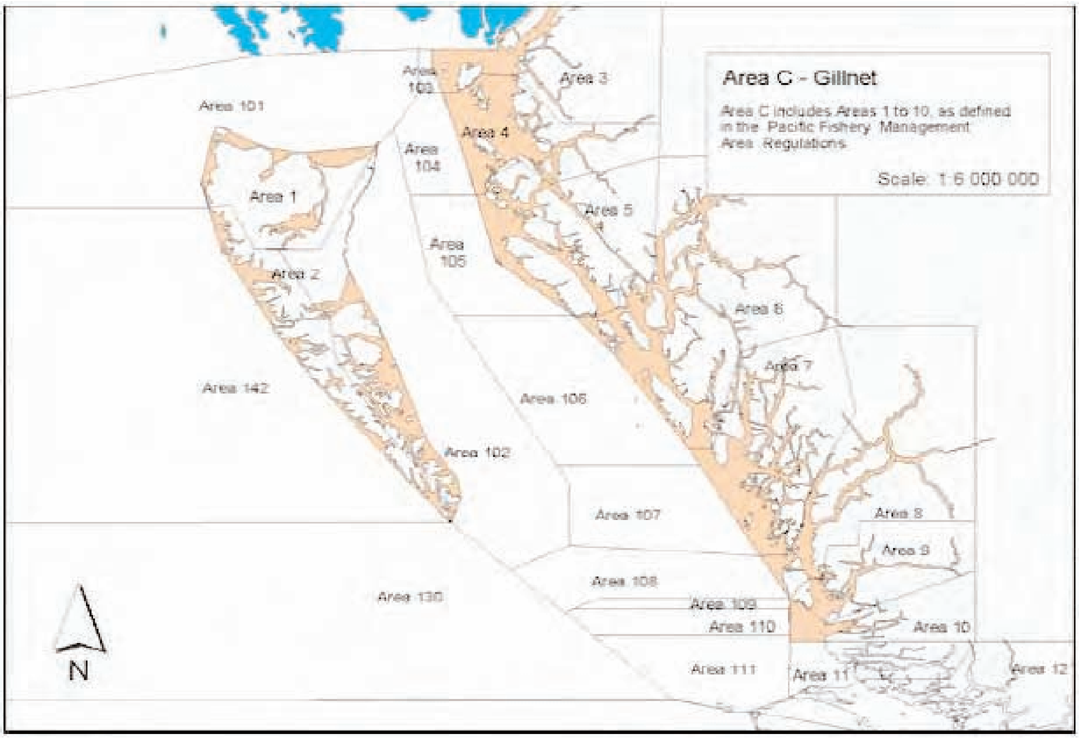


Figure 23. Department of Fisheries and Oceans salmon gillnet license Area C—areas 1–10, subarea 101–107 (from Smith and Morgan, 2005).

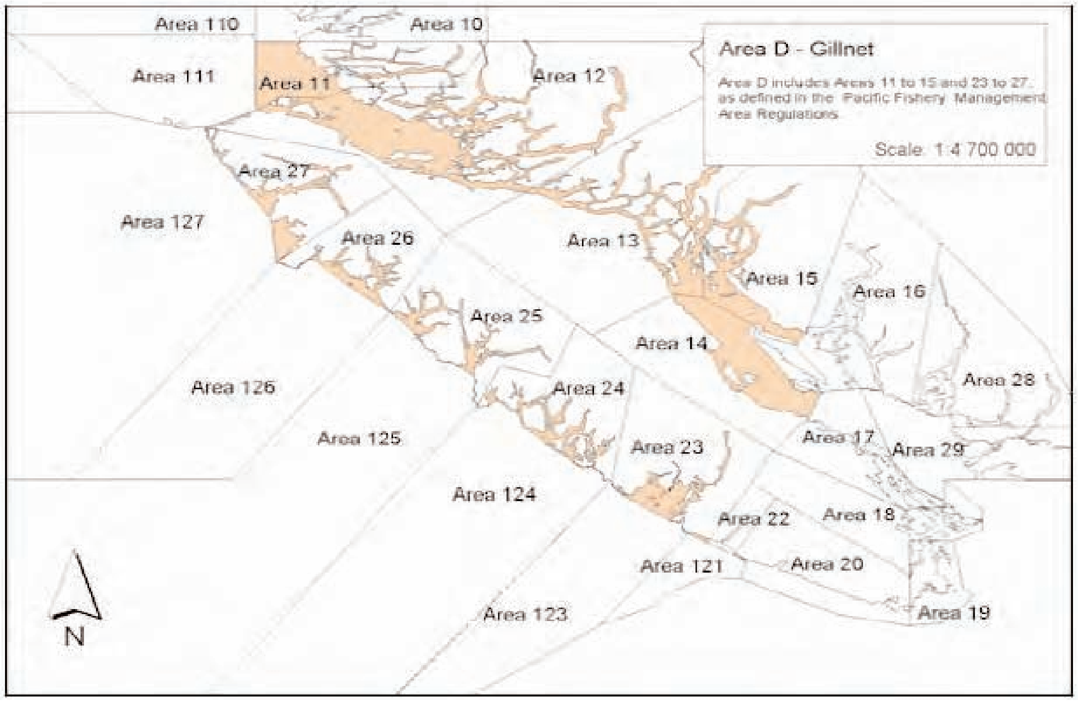


Figure 24. Department of Fisheries and Oceans salmon gillnet license Area D—areas 11–15 and 23–27 (from Smith and Morgan, 2005).

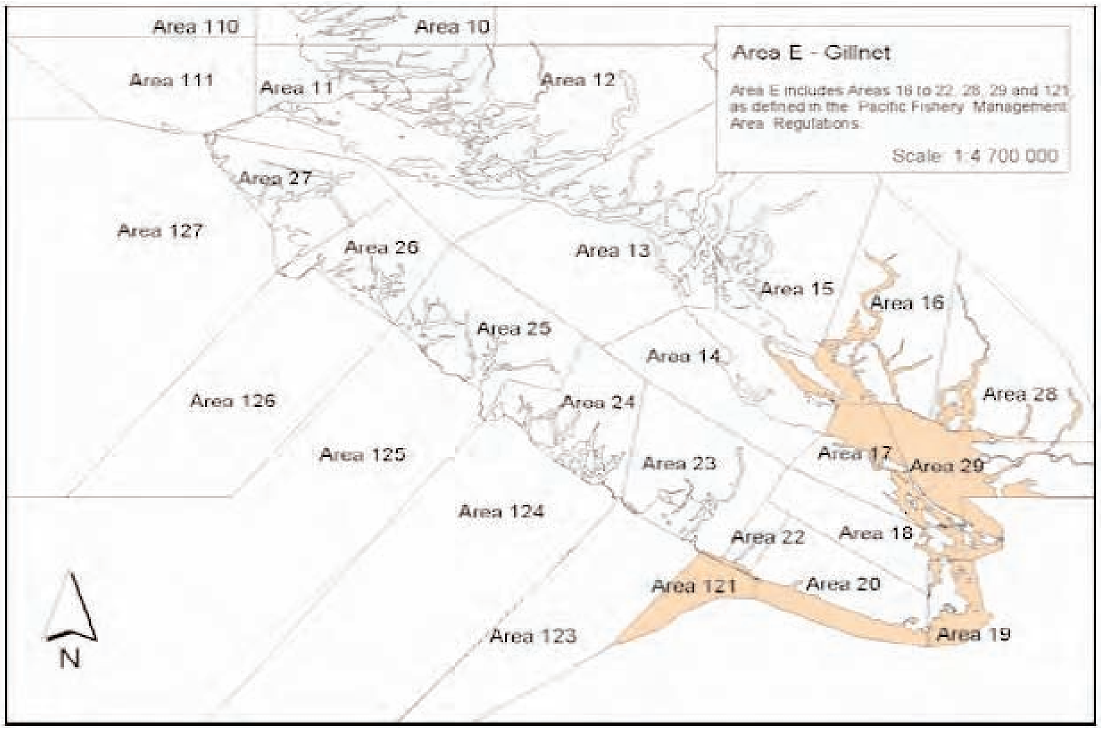


Figure 25. Department of Fisheries and Oceans salmon gillnet license Area E—areas 16–22, 28, 29 and 121 (from Smith and Morgan, 2005).

Smith and Morgan (2005) estimated the total bycatch from the entire commercial gillnet fishery in British Columbia taking into account the total hours fished in 2001–04 (annual mean = 167,206 ± 7,369 [SD] set-hour) and the mean of the bycatch data from the three observed fisheries in 1995–2001 (annual mean = 0.0723 ± 0.0652 [SD] seabirds caught per hour of fishing). This resulted in a predicted annual bycatch of 12,085 seabirds (range = 1,129–24,002), of which 95 percent died. Assuming that the proportions of birds identified and the predicted total number of seabirds caught, are representative of ‘normal’ commercial fishing, their analysis predicted as many as 552 Marbled Murrelets could become entangled each year.

Increasingly, salmon gillnet fisheries in British Columbia are under pressure to be more selective and reduce the bycatch of non-target salmon species, marine mammals, and other taxa, including seabirds (Smith and Morgan, 2005). The DFO regulates fishery time, location, target species, net configuration, and soak time (the length of time that the net fishes). Most commercial salmon fisheries in British Columbia have very little observer coverage, with the exception of test (stock assessment), experimental (gear testing), and selective (species selectivity) fisheries, where observer coverage is high (approaching 100 percent in some cases), and all collect seabird bycatch data (Smith and Morgan, 2005).

There has not been the same intensive research effort made to reduce seabird bycatch in gillnet fisheries in British Columbia as there has been for gillnet fisheries in Washington (Melvin and others, 1999). Currently in British Columbia, the DFO is testing gillnets with no mesh in the upper 2 m, as well as other modifications aimed at reducing bycatch of marine mammals and sockeye salmon, but which also are likely to reduce seabird bycatch (Smith and Morgan, 2005). Eliminating night and crepuscular gillnetting seems to have reduced bycatch of seabirds in the chum fishery off southwestern Vancouver Island (Smith and Morgan, 2005). The reduction in the abundance of target species and increased closures, have caused a decline in the annual salmon fishing effort and landings, and a series of commercial license retirement programs has has contributed to a decrease in the number of vessels fishing for salmon (Smith and Morgan, 2005).

In summary, the available evidence suggests that risks of widespread and significant mortality to Marbled Murrelets from gillnets are currently low in British Columbia, but there are few data. The high mortality recorded in Barkley Sound in 1979–80 (Carter and Sealy, 1984) and the strong impacts of bycatch in population simulation models (Beissinger, 1995a; Boulanger and others, 1999) are reminders that murrelets are highly vulnerable to gillnet fisheries.

Purse-Seiners

In Washington, two Marbled Murrelets were entangled in seine nets during a pilot study (Pierce and others, 1994). Purse-seine fisheries in Barkley Sound killed hundreds of Common Murres in 1979–82, but occurred in areas with few Marbled Murrelets, and no dead murrelets were recovered from this fishery (Carter and others, 1995). In July–August 2000, fisheries observers recorded data for 135 purse-seine sets in four subareas in Area 4 off the Skeena River on the northern mainland (Smith and Morgan, 2005). No birds were reported caught, but observers were not trained to do bird observations and many did not report seabird bycatch data. Purse-seining in areas with high murrelet concentrations might cause significant mortality, but again there are too few data to make any conclusions on its impact. Murrelets tend to avoid boats and are therefore less at risk than Common Murres and Rhinoceros Auklets.

Sports Fishery

There are anecdotal reports of Marbled Murrelets hooked on sports-fishing lures off Campbell River, in Barkley Sound, and in Clayoquot Sound (Campbell, 1967; Carter and others, 1995; Alan E. Burger, University of Victoria, personal observation, 2005). Many of these birds are released alive, but may suffer mortal injuries when removed from hooks. The numbers of birds caught and the likely impact of this fishery in British Columbia remains unknown, but requires investigation in areas where there is overlap between sports fishing areas and murrelet concentrations (e.g., in Barkley, Clayoquot, and Desolation sounds, off the West Coast Trail, and off Haida Gwaii [Queen Charlotte Islands]). Increased disturbance caused by the growing number of fast recreational fishing boats in nearshore waters is another concern (see section, “Effects of Vessel Disturbance”).

Aquaculture

Aquaculture within the nearshore waters frequented by Marbled Murrelets is increasing in British Columbia. Murrelets may be affected negatively by shellfish and finfish farms when these facilities are built in sheltered waters normally used for foraging and resting by murrelets. Disturbance from people and boats is the greatest problem, although there also might be highly localized reductions in prey due to fecal pollution from finfish facilities (Vermeer and Morgan, 1989 or mortality to prey fish (e.g., salmon smolts) caused by disease and parasites emanating from the fish pens (Krkosek and others, 2006). Potential conflicts between seabirds and aquaculture through disturbance and habitat changes were identified in Sechelt-Sunshine Coast, Campbell River-Desolation Sound, Barkley Sound-Alberni Inlet, Clayoquot Sound, Kyuquot Sound, and Queen Charlotte Strait, but in most coastal areas it was difficult to assess the degree of interference (Booth and Rueggeberg, 1989; Rueggeberg and Booth, 1989). Marbled Murrelets are common in all these identified areas, either seasonally or year-round. The numbers and size of aquaculture facilities in the British Columbia coast has increased greatly since the reviews done in the late 1980s.

Effects of Commercial Fishing on Prey

Alaska

The secondary effects of commercial fisheries on murrelets are mostly speculative and inferential. Several important forage fishes are not commercially fished in Alaska, and are barred from future commercial exploitation. The ban on exploitation of forage fishes, and the regulated take of ‘protected’ species such as Pacific herring in the groundfish fisheries, were implemented following passage of the Magnuson-Stevens Fishery Conservation and Management Act in 1976 (Witherell and Pautzke, 1997; Witherell and others, 2000). The lack of a targeted fishery on forage fishes removes, at a minimum, direct competition between humans and murrelets for those resources. For regulation purposes, the NOAA-Fisheries considers forage species to include (among others) sand lance, capelin, and myctophids, all of which are important prey species for murrelets (this volume). However, other important prey consumed as juveniles by murrelets are fished commercially as adults, in particular Pacific herring, walleye pollock, and Pacific cod.

One of the most important prey for Marbled Murrelets in Alaska is Pacific herring, and juvenile herring may be essential to successful chick rearing in some areas of Alaska (Kuletz, 2005). The commercial herring fishery could have an impact on murrelets by reduction of local populations and harvest of herring roe on kelp. Harvest of herring in Alaska peaked in the 1930s at 125,000 metric tons per year, and this level of harvest may have contributed to a stock decline between the 1950s and 1960s. Between the 1960s and 1970s, a foreign fishery in the Bering Sea created a second peak in herring harvest levels (Woodby and others, 2005). Since the 1980s, the primary fishery has focused on sac-roe and bait fisheries. Herring are an important food for a variety of marine species in Alaska. As a result, harvest levels have been managed conservatively by the State, but conflicts with other fisheries and marine mammals continue (Woodby and others, 2005). Another potential impact to herring stocks include discharges from pulp mills, which have been linked to herring mortality, particularly in Southeast Alaska (Woodby and others, 2005).

In Prince William Sound, the murrelet population has declined in tandem with the herring biomass (Kuletz, 2005), and the cause of the herring decline in this region is not clear. The Prince William Sound herring population has fluctuated widely, with a peak estimated adult biomass in 1988 of about 100,000 metric tons. The herring stock collapsed in 1993, declining from an estimated 16,082 metric tons in 1993 to a low of 6,384 metric tons in 2001 (Thomas and Thorne, 2003). There is no agreement on the cause of the collapse. In addition to the hypothesized competition with hatchery-raised salmon smolts, other perturbations include overharvest when stocks were low (Thomas and Thorne, 2003) and the 1989 EVOS (Paine and others, 1996; Spies and others, 1996).

Murrelets will feed on salmon smolt (Carter and Sealy, 1986), and murrelet numbers increased at a fish hatchery in Prince William Sound for 4 days after release of smolts (Scheel and Hough, 1997). Salmon are not likely to be an important prey, at least for chick-rearing, because they are not an energetically high quality food (Van Pelt and others, 1997). Further, at least in Prince William Sound, salmon smolts have only a brief period of availability in bays and nearshore waters (Willette and others, 2001). The instigation of salmon hatcheries in Prince William Sound may have exacerbated the apparent decline of natural prey species such as herring and sand lance (Pearson and others, 1999). Beginning in 1977 and increasing throughout the 1980s, hatchery-reared pink salmon smolts were released in April to coincide with the spring plankton bloom. Since 1988, more than 500 million smolts have been released annually (Thomas and Thorne, 2003). Hatchery-reared salmon could potentially compete with other forage fish that feed on zooplankton, such as juvenile herring, and juvenile and adult sand lance (Pearson and others, 1999; Purcell and Sturdevant, 2001).

Juvenile pollock are not often fed to murrelet chicks in Alaska (Kuletz, 2005), likely because of their low caloric value (Van Pelt and others, 1997). However, they are a common prey species consumed by adults (this volume). Pollock adults may reduce survival of juvenile pollock because of their cannibalistic feeding habits (National Oceanic and Atmospheric Administration, 2004). The largest fishery in Alaska is the pollock fishery, primarily in the Bering Sea, but they also are harvested in the Gulf of Alaska. Because adult pollock consume juvenile pollock as well as other forage species, and because adult pollock are a large proportion of the biomass in Alaska's waters, one hypothesis is that harvesting pollock could reduce competition with other predators for forage species. This hypothesis was suggested by Hunt and Stabeno (2002), who found a positive relationship between Black-legged Kittiwake productivity and pollock catch levels in the Pribilof Islands. Energetic models for the Bering Sea suggested that reduction of the adult pollock biomass by 10 percent could result in increased populations of many other species, including murres (National Oceanic and Atmospheric Administration, 2006). Such an effect would be less likely to have a noticeable impact on murrelet populations, since areas of pollock harvest generally are not frequented by murrelets.

Bottom trawling is one of the gear types used in Alaska groundfisheries, and has the potential to damage benthic habitats (Heifetz, 1997). Damage of benthic substrates could impact nearshore forage fishes, particularly sand lance, which burrow into sandy substrates (Robards and others, 1999b). However, bottom trawling does not occur in most state waters (within 3 nmi of shore), and no-trawl restrictions apply to haul-outs sites used by Steller's sea lions, as well as areas near selected seamounts (Woodby and others, 2002). In addition, in July 2006, the Aleutian Islands Habitat Conservation Area, covering 279,114 mi^2, was established (71 FR 36694, June 28, 2006). This area (fig. 26) will be managed to protect benthic habitats, with sections closed to certain types of bottom-contact fishing. Together, these measures could be beneficial to murrelets in the Aleutian Island regions, and potentially other nearshore habitats throughout Alaska.

British Columbia

Of the common prey items taken by Marbled Murrelets, only Pacific herring are commercially exploited on a large scale in British Columbia. Herring populations were seriously depleted through over-fishing in the 1960s in many parts of British Columbia, but the impacts on bird populations were not studied. Herring stocks have recovered in some areas but remain low in other areas, and the effects of herring availability on Marbled Murrelets should be assessed in more detail. Quotas for the roe herring fishery (gillnets and seine) in 1997–2005 ranged from 26,200 to 30,497 tons (Department of Fisheries and Oceans Canada, 2006a). Most of this fishery occurs in the Strait of Georgia with smaller amounts off the west coast of Vancouver Island, the Prince Rupert area, the central coast, and Haida Gwaii (Queen Charlotte Islands) (Department of Fisheries and Oceans Canada, 2006a). A further 1,050 metric tons are harvested in the food and bait herring fishery in the Prince Rupert and Strait of Georgia areas (Department of Fisheries and Oceans Canada, 2006b). Herring eggs also are harvested by First Nations as spawn-on-kelp.

Small baitfish, First Nations, and recreational fisheries also occur for anchovy, eulachon, and surf smelt (*H. pretiosus*), which are known to be taken as prey by murrelets (Burkett, 1995). There are no stock assessment programs for some of these species (e.g., surf smelt) and it is unclear how large the stocks are in British Columbia.

One of the most important prey species for murrelets in British Columbia is Pacific sand lance. There is no commercial fishery for this species in British Columbia, but *Ammodytes* spp. are fished to produce fish-meal in many other parts of the world, and demand for fish-meal used in finfish aquaculture might lead to a fishery in British Columbia. There is currently no restriction on exploitation of forage species in British Columbia.

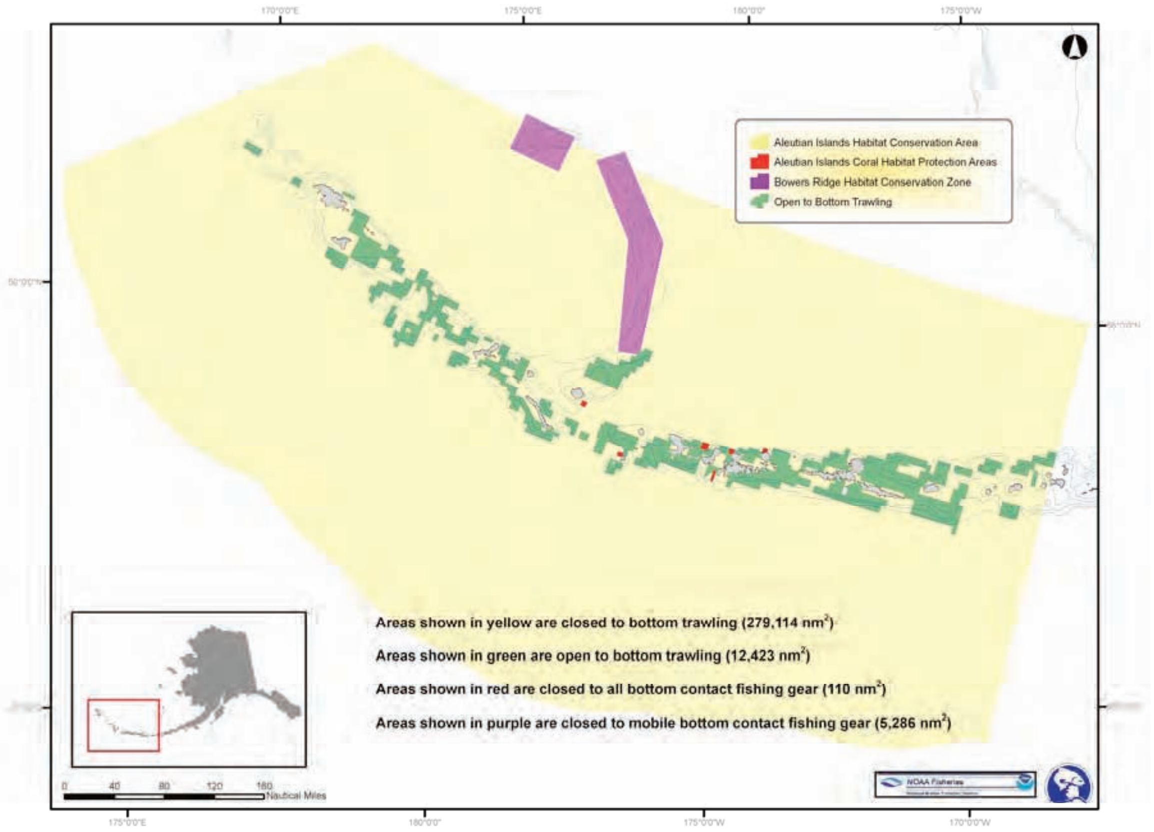


Figure 26. Outline of the Aleutian Islands Habitat Conservation Area and other areas with trawl restrictions.

Murrelets also take euphausiids (krill) and there is a small krill fishery in British Columbia taking five species, but dominated by *Euphausia pacifica* (Department of Fisheries and Oceans Canada, 2004). The krill are frozen and used primarily in the manufacture of fish food. The fishery is centered in the Strait of Georgia and nearby coastal inlets (e.g., Bute, Knight, Toba Inlet, Howe Sound) and usually involved seven to eleven vessels (Department of Fisheries and Oceans Canada, 2004). The quota and landings have been stable around 500 tons for many years (fig. 27). Given the increase in salmon-pen aquaculture in British Columbia, and the support given to this industry by the provincial government, there are likely to be pressures to expand the krill fishery and increase quotas. An intensive euphausiid fishery might affect murrelets directly, because they eat large euphausiids, or it could disrupt the food webs on which they depend.

Effects of Vessel Disturbance

Kuletz (1994) and Piatt and Naslund (1995) first raised concern about the potential effects of vessel disturbance on Marbled Murrelets in Alaska. This issue was not addressed in the Marbled Murrelet Recovery Plan for Washington, Oregon, and California (U.S. Fish and Wildlife Service, 1997), but was briefly mentioned in other recent status reviews (Burger, 2002; McShane and others, 2004). Concerns about the effects of vessel disturbance have developed in recent years, due to increases in vessel traffic in many remote areas of Alaska and British Columbia. However, it has been difficult to determine rates and degree of potential impacts to seabirds, including Marbled Murrelets. Preliminary studies have documented limited effects (see below) but more work is needed to study this problem. Because boat traffic is inevitable in many areas frequented by murrelets, it will be useful to determine to what degree murrelets can habituate to boat traffic. Anecdotal reports suggest that murrelets may habituate in some locations (McAllister, unpub. data; cited by Strachan and others, 1995). However, other species have shown only limited ability to habituate to disturbances (Burger and Gochfeld, 1990; Bleich and others, 1994).

Studies on a variety of birds indicate that disturbance from motorized vessels can result in decreased reproductive success (e.g., brooding waterfowl; Keller, 1991; Mikola and others, 1994), behavior changes with consequent energetic impacts (e.g., shorebirds; Burger and Gochfeld, 1991; or waterbirds; Schummer and Eddleman, 2003), habitat loss (e.g.,

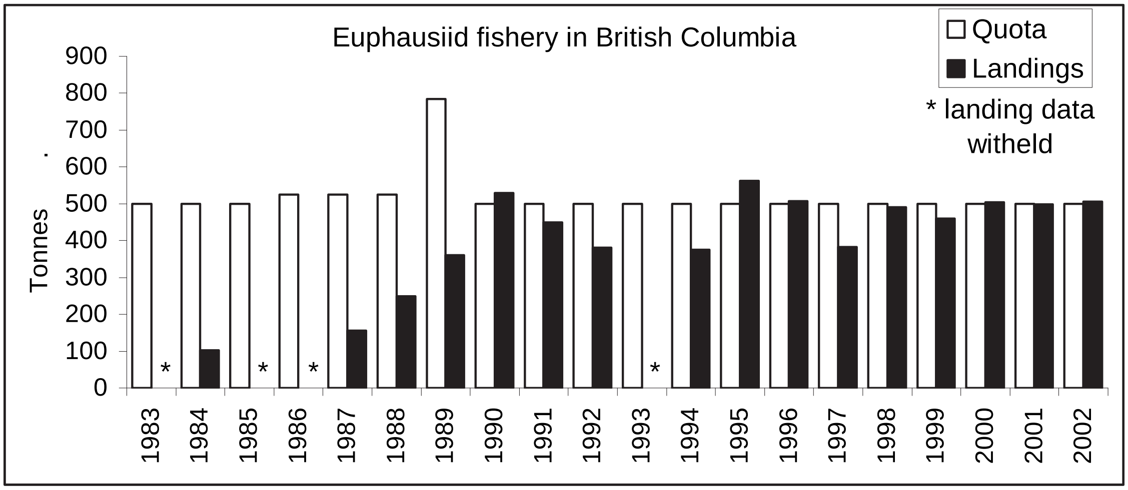


Figure 27. Statistics on the fishery for euphausiids (krill) in British Columbia (data from Department of Fisheries and Oceans Canada, 2004).

stop-over sites associated with waterfowl migration; Kaiser and Fritzell, 1984), or reduced access to favored foraging areas (Ronconi and Cassady St. Clair, 2002). However, some marine and waterbird species eventually habituate to the operations of vessels and noise (e.g., gulls; Burger and Galli, 1987, or wading birds; Stolen, 2003). Some studies which reported boating impacts to marine and waterbird species were located in areas with high levels or rates of boat traffic (e.g. Mississippi River; Korschgen and others, 1985; or Great Lakes; Knapton and others, 2000). In general, large, loud, or fast boats have been shown to have greater impacts than smaller, quieter, or slower boats. Responses to disturbance also vary with environmental factors such as habitat type, tides, time of day, and weather (review in Agness, 2006).

Studies of Vessel Disturbance and Murrelets

Responses to vessel disturbance are species-specific, and there is little empirical data on the influence of vessels on Marbled Murrelets. Several studies reviewed below indicate that *Brachyramphus* murrelets are displaced by vessel traffic, and possibly impacted energetically. However, the long-term, population-level, or regional implications of this immediate impact remain unknown.

During USFWS boat-based surveys in south-central Alaska, 93–95 percent of murrelets were initially observed on the water (Kuletz and others, 2003a; U.S. Fish and Wildlife Service, unpub. data, 1989–2004), indicative of the diving and surface-resting behavior that make murrelets susceptible to disturbance from vessel traffic. For 2 years following the 1989 EVOS, areas which previously had little vessel activity saw relatively high vessel traffic during response operations and damage assessment studies. Within the spill zone, Kuletz (1996) found significant, negative relationships between numbers of boats and Marbled Murrelet densities at Naked Island in Prince William Sound and Kachemak Bay in Cook Inlet. Low-flying aircraft also were negatively correlated with murrelet counts in two bays frequented by float planes and helicopters participating in the spill response (Kuletz, 1996). In Southeast Alaska, Speckman and others (2004) observed that the approach of small boats caused Marbled Murrelets holding fish (presumably meant for their chicks) to dive and then swallow the fish. This behavioral response has implications for reproductive success as well as energetic cost of chick-rearing for murrelets.

In Alaska, recent studies of vessel disturbance on murrelets have focused on Kittlitz's Murrelets because this species is a candidate for listing under the ESA (71 FR 53755). Kittlitz's are physically and behaviorally similar to Marbled Murrelets, thus study results provide insights into possible disturbance effects on both species. For example, in Prince William Sound, a 2001 pilot study found that Kittlitz's Murrelets were at least temporarily displaced by boat traffic. When boats were present, fewer birds made foraging dives and more birds flew off the water compared to undisturbed focal groups (Kuletz and others, 2003a).

In Prince William Sound, S. Stephensen (U.S. Fish and Wildlife Service, unpub. data, 2005) tested the effects of small boat transit on *Brachyramphus* murrelet density (93 percent Marbled Murrelets). Stephensen conducted paired comparison counts of murrelets from a 25-ft vessel in Harriman Fjord, Prince William Sound, Alaska, in July 2004. Each pair of murrelet counts consisted of an initial and return transits (n = 23 pairs). For all paired transects, there was a significant decrease (t = 2.58, df = 22, P = 0.02) in the number of murrelets between initial ($\bar{x}$ = 27.7 ± se 5.0 murrelets) and return ($\bar{x}$ = 18.9 ± 3.0) runs, suggesting that murrelets had left the immediate area. In Washington, Hamer and Thompson (1997) also found displacement of Marbled Murrelets during vessel activity, with 68 percent (*n* = 50 birds) of murrelets moving a short distance as a vessel approached. Of these, 11 percent of the birds moved more than 30 m.

A more extensive study was conducted in Glacier Bay National Park and Preserve (GBNPP; Agness, 2006). Agness found that vessel activity overlapped spatially and temporally with Kittlitz's Murrelets in Glacier Bay; since Marbled Murrelets coincide with Kittlitz's, they would face the same influences in those areas, as well as other areas not occupied by Kittlitz's. Declines in nearshore density of murrelets attributed to vessel disturbance, though significant, were temporary, typically recovering within the day. Behavioral changes of Kittlitz's Murrelets during vessel activity included increased flight, with a mean of 30 percent of birds taking flight. On days with high vessel traffic, birds showed an increase in diving behavior, which Agness (2006) suggested was due to lower energetic costs of diving compared to flying from disturbance. Based on models of murrelet behavior and energetics, Agness (2006) concluded that Kittlitz's had a net energy loss due to vessel disturbance, but the impact may only be significant under 'maximal vessel conditions.' In her models, maximal vessel conditions were based on the 2004 daily vessel limit imposed by the USNPS in Glacier Bay (see below). Birds not holding fish for their chicks were more likely to fly in response to vessels, and thus the model indicated significant energetic costs (equivalent to 6.5 Pacific sand lance per day) to most Kittlitz's Murrelets during maximal vessel activity.

A recent study (Hentze, 2006) off southwestern Vancouver Island, British Columbia, an area with high volumes of recreational fishing activity, examined the impacts of vessel disturbance on four seabird species, including the Marbled Murrelet. Marbled Murrelets tended to react (dive or take flight) more readily to approaching boats than Common Murres and Rhinoceros Auklets, but less so than Pelagic Cormorants. Murrelets showed a rapid increase in the proportion of birds reacting as the boat approached starting at 40 m, until almost 90 percent of the birds reacted when the boat was within 5 m. Overall, at all passing distances 59.8 percent of murrelets showed no reaction, 31.0 percent dived and 0.2 percent took flight (*n* = 3,080 observations from a moving boat). From a small sample of six birds flushed by a boat and tracked with a surveyor's theodolite, Hentze (2006) showed that the mean flight distance was 116 m (range = 51–208 m), mean flight time was 40 s (range = 8–130 s), and the time to resume foraging after landing was 65 s (range = 24–171 s). In this study, the tendency of murrelets to leave a site when disturbed by boats depended on sea state, group size, and average bird density. Rougher seas and higher densities of murrelets in the surrounding area increased departure rates for murrelets, whereas larger group sizes reduced departures following disturbances. Because single birds were more likely to flush, and single birds may be more likely to be breeding individuals (Mack and others, 2002), Hentze suggested that boat disturbance would disproportionately affect breeding birds. Hentze (2006) concluded that 150 m buffer zones might be sufficient to reduce boat disturbance effects on Marbled Murrelets.

In an overlapping study made in the same place and time as Hentze's (2006) study, Bellefleur and others (2005) showed that boat speed had a significant effect on the reactions by Marbled Murrelets. On average, murrelets flushed at 40 m when approaching boats were traveling at speeds greater than 29 km/h (16 knots) but flushed at 28 m at speeds of less than 12 km/h (7 knots). Size of boat (7 m vs. 5 m hull length) had no significant effect at the speeds tested.

Vessel Activity in Alaska

Boat traffic in Alaska varies seasonally, regionally, and in vessel size and activity (i.e., commercial fishing, oil rig support, cargo, recreational, cruise ships). In National Parks, some restrictions on vessel activity have been established to minimize impact to wildlife. Areas with relatively high vessel activity that overlap with relatively high murrelet densities include Kachemak Bay–lower Cook Inlet, areas of Kodiak Island, Kenai Fjords National Park and Preserve (KFNPP), Prince William Sound, GBNPP, and areas adjacent to coastal cities in Southeast Alaska. In addition to commercial shipping patterns at industrial ports (see section, "Oil Spills", above), specific information on vessel activity is available for Prince William Sound, KFNPP, and GBNPP.

Prince William Sound

Both fishing and tourism-related vessel activity increases during the summer months in Prince William Sound, and thus coincides with peak murrelet densities in Prince William Sound during their breeding season. Fishing vessel activity in Prince William Sound increased during the 1980s with the establishment of salmon hatcheries. In addition, tourism has increased since the 1980s, with related vessel traffic heaviest in the fjords with tidewater glaciers (Murphy and others, 2004). During summer 2001, Kuletz and others (2003a) examined boat traffic and murrelet density in five fjords of Prince William Sound. During their surveys, they found three times more boats in shoreline waters ($\leq$200 m from shore) than in mid-inlet waters (>200 m offshore), but relative to kilometer traveled (because of highly convoluted shoreline routes), boat density (boats per km) was actually slightly higher in mid-inlet waters. Boat activity increased after May and peaked in July. Boat traffic patterns were similar in a USFS study in 2001 (U.S. Fish and Wildlife Service, unpub., data, available in Kuletz and others, 2003a), and corroborate the USFS results from earlier 1996–98 studies (Murphy and others, 2004). Vessel traffic leaving Whittier is heaviest in Passage Canal and Port Wells, and generally decreased with distance from ports such as Whittier (fig. 28).

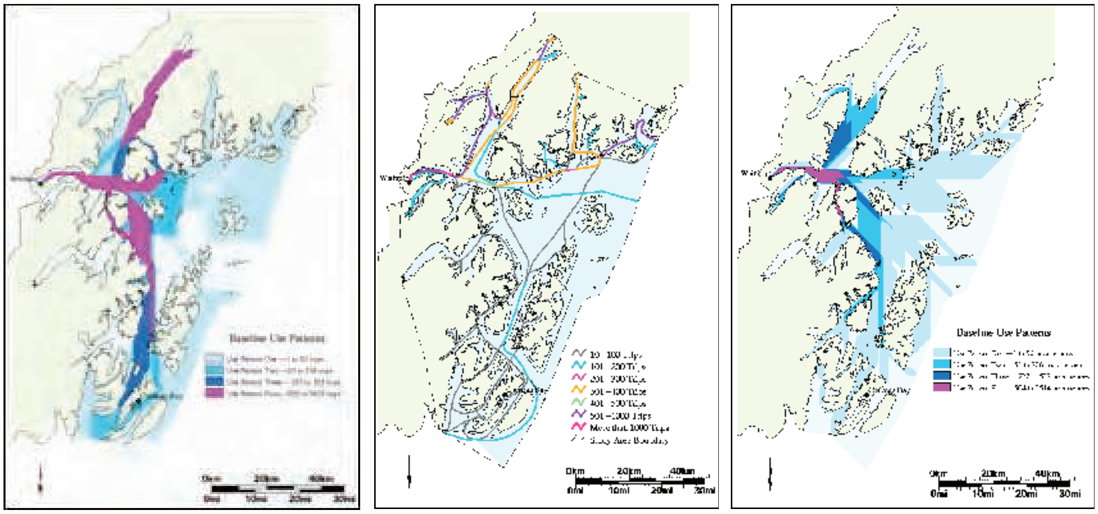


Figure 28. Vessel traffic in western Prince William Sound, based on studies by the U.S. Forest Service and the U.S. Fish and Wildlife Service.

Between 1996 and 1998, cruise ship and State ferry activity was highest in Passage Canal, but also was heavy (769–1,151 trips between May–September) in College Fjord, and Long, Columbia, and Heather bays (Murphy and others, 2004). Harriman Fjord cruise ship and ferry traffic was slightly lower at 385–768 trips during the same time period. Most commercial fishing trips departing from Whittier traveled to College Fjord (526–2,623 trips between June and September; Murphy and others, 2004).

National Parks

In Alaska, bays and fjords with tidewater glaciers are popular tourist destinations. Two such sites occur in the KFNPP and GBNPP. The southern Kenai Peninsula is difficult to access, but KFNPP was established in 1980, and at least two of the park's fjords, Aialik Bay and Northwestern Fjord, have become primary destinations for park visitors. Vessel traffic from Seward to these bays has increased to more than 75,000 people per annum, with travel modes ranging from kayak to 100-ft tour-vessels to cruise ships.

In 1979 and 1980, studies documented one to two vessels per day in upper Aialik Bay. By 1996, multiple vessels visited Aialik Bay daily (U.S. National Park Service, 2004). Concerns about disturbance of harbor seals (*Phoca vitulina*) prompted study of the potential impacts of vessel traffic on seals in KFNPP (Tetreau, 1998). Voluntary operating guidelines for tour vessels were adopted based on study results. Viewing guidelines for marine mammals were adopted in 2001, and following further study, more stringent guidelines were established in 2003 (U.S. National Park Service, 2004). These guidelines reduced vessel speed in the upper portions of bays, benefiting all marine wildlife.

Glacier Bay became a National Monument in 1925 and a National Park in 1965. Glacier Bay was designated a Biosphere Reserve in 1986, which supported efforts to regulate activities in the park. Visitation in Glacier Bay grew to more than 100,000 people annually by the 1970s. Most tourists visit GBNPP by cruise ship. Commercial fishing also increased during the 1980s, but was phased out in the late 1990s (Catton, 1995). Currently, GBNPP regulates the numbers of boats allowed into the park and restricts entrance to designated areas. In 2004, the daily limit into GBNPP between May and September was 2 cruise ships, 9 large tour boats, and 25 private recreational motor vessels (Agness, 2006). In 1999, a tour boat accident resulted in a multi-agency response that involved a large number of boats in the affected bay for several weeks (K. Kuletz, U.S. Fish and Wildlife Service, personal observation, 1999).

State Ferry System

The Alaska State Marine Highway provides ferry service to remote communities throughout southeast and south-central Alaska, typically operating eight ferries. Two new high-speed ferries were recently added to the fleet, and both have operated in Southeast Alaska. The *M/V Fairweather* started service in 2004, and the *M/V Chenega*, launched in 2005. Four high speed ferries were originally designed, but as of February 2006, plans for completion the remaining two were on hold.

Effects of Research Activities

Studies of Marbled Murrelets typically are conducted in the marine environment. Studies involve surveys from boats, but also more intrusive activities, involving collections, and capture and handling. The total murrelet mortality attributed to research activities is small, but is reviewed here for the record.

Marbled Murrelets have been collected by shotgun for diet and contamination studies in Alaska, for a total of 346 birds collected between 1969 and 2001 (this volume). Capture and banding of murrelets is a potentially disruptive activity to individual birds and their breeding success (Bradley and others, 2004). In Alaska, capture of murrelets has been attempted with dip-nets and spotlights (Quinlan and Hughes, 1992; Whitworth and others, 2000; Newman and others, 2006), mist-nets set above the water (Burns and others, 1994; Kuletz and others, 1995a), gillnets set below the water's surface (Quinlan and Hughes, 1992), and net guns (Quinlan and Hughes, 1992). Some known and suspected mortality occurred from these studies.

The first radio-telemetry study in Alaska was in Southeast Alaska, in 1983 and 1984, when 17 Marbled Murrelets were captured and fitted with radio tags (Quinlan and Hughes, 1992). During this study, only seven birds survived beyond release. Attempts at surgically implanting radios or use of external harnesses were unsuccessful. Excessive preening after release also may have led to predation by Bald Eagles immediately after release. During radio-telemetry studies in 1993 (Burns and others, 1994) and 1994 (Kuletz and others, 1995a), 60 birds were captured and fitted with radio transmitters. No birds were lost during capture and handling, but the remains of three were found, and predation by Bald Eagles was suspected. During the 1999 study, at least one radio-tagged murrelet death was associated with Bald Eagle predation or scavenging (Whitworth and others, 2000).

In 2005, in Port Snettisham, Southeast Alaska (Newman and others, 2006), 45 Marbled Murrelets were captured and fitted with radio transmitters and another 11 were sampled for blood-health assessments. At least one tagged bird was believed to be killed by predation. During the continuation of this study in 2006, another 40 birds were captured. At least 15 were found dead, again with predation by Bald Eagles suspected or documented (K. Nelson, OSU Wildlife Cooperative Research Unit, oral commun., 2006). This level of mortality was unusual for murrelet telemetry studies, and similar efforts have successfully tagged hundreds of murrelets from British Columbia to California. The researchers speculated that murrelets were compromised by the unusually high numbers of Bald Eagles present in the capture area, and a late, cold spring (K. Nelson, oral commun., 2006).

The total number of murrelets known or potentially affected by capture and tagging is not significant relative to the Alaska population. However, the large population of avian predators in Alaska may make radio-telemetry more risky than farther south, where predation has not been reported as a frequent problem (Bradley and others, 2004; Peery and others, 2004a). Future research in Alaska may need to consider ways to mitigate the apparently high predation rate of radio-tagged murrelets in Alaska. Another consideration is that the predation of radio-tagged murrelets reflects a generally higher avian predation on murrelets in Alaska.

Nesting Habitat: Characteristics, Threats, and Trends

Marbled Murrelets' dependence on large, old-growth coniferous trees for nesting habitat has been well-documented (Ralph and others, 1995; Burger, 2002; McShane and others, 2004). In this section, we review what is known about the use of terrestrial habitats by Marbled Murrelets in Alaska and British Columbia. We briefly review the methods by which terrestrial habitat use patterns of Marbled Murrelets have been studied. We then describe how our understanding of nesting habitat characteristics has grown, as more nests have been found, and more sophisticated modeling studies have been undertaken. We then synthesize existing information about the amount and distribution of habitats suitable for nesting. We consider threats to nesting habitats from anthropogenic sources, and briefly address natural ecological processes. Finally, we address the general land management practices that may affect the future of Marbled Murrelet nesting habitat.

Defining nest habitat for murrelets in Alaska has proven challenging. There is little information available compared to what is known for murrelets in the southern portion of their range. Although few murrelet nests have been found and documented in Alaska, Marbled Murrelets appear to use a broader range of habitats in Alaska than at lower latitudes. For example, ground-nesting birds occur in both forested and unforested areas, and tree-nests have been found within a greater range in tree sizes. Because ground nests of the Kittlitz's Murrelet can be mistaken for those of Marbled Murrelets, the relative occurrence of ground nesting for Marbled Murrelets may have been underestimated (Day and others, 1983).

Within Alaska, offshore surveys of murrelets suggest that about 97 percent of the population occurs near lands with at least some old-growth forest cover, and thus Piatt and Ford (1993) estimated that about 3 percent of the Marbled Murrelet population nests on the ground. The northernmost extension of the north temperate rain forest extends from Southeast Alaska, north along the Gulf of Alaska, and throughout south-central Alaska. However, the extent of forested habitat is highly variable in the more northern and western edges of this biome. Areas considered "forested" include unforested habitat, and tree line may extend only 200 m above sea level and a few kilometers inland (Kuletz and others, 1995a). The coastal areas of the northern Gulf of Alaska, including Prince William Sound, the Kenai Peninsula, and Kodiak Island, appear to be zones where both tree- and ground-nesting occur, although evidence suggests that forested habitat is preferred (Kuletz and others, 1995a; Marks and Kuletz, 2001). The remainder of the murrelet population in southwestern Alaska including the Alaska Peninsula and the Aleutian Islands, have only ground-nesting opportunities because most of the area is unforested (see section "Habitat Amount and Distribution" below), and murrelet densities are comparatively low in these regions (Piatt and Ford, 1993).

Methods for Surveying Use of Terrestrial Habitats by Marbled Murrelets

Two methods have been used to systematically study terrestrial habitat use of Marbled Murrelets: (1) audio-visual dusk/dawn watches; and (2) radar surveys. The audio-visual surveys are useful for providing a stand-scale presence/absence determination (Kuletz and others, 1995b), however, they may underestimate the number of birds using an area by 75 percent or more (Cooper and Blaha, 2002; Lank and others, 2003). Furthermore, they are biased towards landscapes easily accessible to observers (Lank and others, 2003) and this may be important in remote Alaska. Radar surveys, although not yet widely used in Alaska, have been used to assess movement between marine and terrestrial sites at the landscape-scale (reviewed in Burger, 2002). Radar counts of murrelets indicate the value of each watershed as nesting habitat and show watershed-level habitat associations (Burger, 2001b). However, the steep and rugged topography in Alaska has caused problems with using the radar method. Both methods are reviewed below.

Audio-visual surveys used to assess inland activity at dusk or dawn has been a standard method used to determine if murrelets were 'occupying' an area for nesting (Rodway and others, 1993; Nelson, 1997). During their inland flights, murrelets often vocalize, allowing aural detection, or they may be visually identified flying above or below the canopy (each observation is termed a 'detection'). Murrelets usually exchange incubation duties with their mate before dawn, but also make inland flights to nesting areas prior to breeding and post-breeding (Nelson, 1997), or even during winter (Naslund, 1993).

Dawn watches for murrelet activity have been conducted sporadically in Alaska, partly because lack of roads and remote, difficult terrain make large-scale studies expensive and logistically complicated. Two major efforts have occurred. The first concerted effort to monitor dawn murrelet activity occurred from 1990 to 1993. This study was implemented following the EVOS to identify lands for possible purchase as a means of protecting habitats used by injured species, such as the Marbled Murrelet (Kuletz, 1997). The goals of the study were to define murrelet nesting habitat in south-central Alaska, and to identify specific tracts of land of high value to murrelets (see section, "General Nesting Habitat Characteristics"). The other major effort was in the 1990s by the USFS in the Tongass National Forest. The USFS conducted dawn watches as part of an effort to categorize forest lands for management and planning purposes.

In Southeast Alaska, four sites were surveyed over the course of 2-3 years to detect seasonal patterns of Marbled Murrelet activity and to assess the efficiency of survey protocols (Brown and others, 1999). They detected Marbled Murrelets throughout the year, however, detection rates were highest in July, which corresponded with the breeding season, and there were no detections in September and October, which corresponds with the molting period. Their analysis showed that a revised survey protocol for Southeast Alaska would optimize detection rates for the amount of effort spent. They also found that winter surveys were hardest to perform accurately because birds were more likely to be absent from the forest and because surveys are harder to conduct in harsh weather.

Smith and Harke (2001) conducted point count surveys along forested sections of road in Southeast Alaska to quantify spatial and temporal variability in Murrelet detections and to estimate the effort required to detect changes in detections over time. They observed a high degree of spatial and temporal variability in Murrelet detections. They found there was a 90 percent probability of documenting a 10 percent annual decline in detections in 6 years by making 12 annual visits to 22 dawn survey stations spaced ≥1.6 km apart. The authors suggested that sampling effort could be reduced without reducing power by sampling every second or third year.

The second method used to study inland murrelet activity has been radar surveys. Marine radar has proven more accurate than dawn watches to monitor inland flights of murrelets. Audio or visual observations can drastically underestimate the numbers of murrelets flying into a watershed (Cooper, 1993; Burger, 2001b; Cooper and others, 2001; Cooper and Blaha, 2002). Radar surveys also are more accurate at detecting changes in murrelet abundance among years, and thereby may indicate changes in the proportion of birds attempting to breed (Burger, 2001b; Cooper and others, 2001). Cooper and others (2006) found that small annual declines in murrelet populations were harder to detect with certainty using radar surveys. A sampling period of 11–15 years would be needed to detect an annual decline of 2–4 percent with ≥80 percent power.

In Alaska, Cooper (1993) used marine radar in July 1993, at six bays in the KFNPP. In paired comparisons with standard visual observers, radar detected as much as 1.7 times as many murrelets as the human observer (Cooper, 1993). The radar was limited, however, in detecting murrelets once they flew past the shoreline. Because of the area's steep topography, conditions were not ideal for using radar. Typically, marine radar is used where a wide river mouth creates an open viewing area at the base of a watershed (Cooper and others, 2001). Because the sites in Kenai Fjords were randomly selected, the radar operator, based on an anchored vessel, could not select the optimum site from which to conduct surveys (Cooper, 1993). With improved radar units and proper selection of sites (Burger, 2001b), marine radar could be a useful and cost effective tool in the remote coastal areas of Alaska.

Five radar studies in British Columbia (reviewed by Burger and others, 2004a) showed significant positive correlations between numbers of murrelets and areas of suitable habitat per watershed, although the measures of habitat differed among the studies. These data provided the first strong evidence that the watershed populations of Marbled Murrelets are directly proportional to the areas of old-growth forest available. There was no evidence that murrelets pack into remnant old-growth patches in higher densities as areas of old growth are reduced by logging. Breeding populations of murrelets were therefore predicted to decline as areas of old-growth decrease. Densities (murrelets per area of habitat) derived from the radar counts were significantly higher on the west of Vancouver Island (0.090 ± 0.060 SD birds per ha of likely habitat) than on the British Columbia mainland coast (0.045 ± 0.039 birds per ha) when the habitat classified as good was considered in each study (Burger and others, 2004a). These density estimates are useful for management, either for estimating areas of habitat needed for specific populations of murrelets, or conversely for estimating the numbers of birds a specific area can support.

General Nesting Habitat Characteristics

Prior to the early 1980s, only eight Marbled Murrelet nests had been found throughout its range, and all but two were ground nests (Day and others, 1983). As of 1996, well documented nests in Alaska include 19 tree nests (table 26) and 15 ground nests (table 27; DeGange, 1996). The relatively high number of ground nests was likely due to the greater possibility of finding a ground nest opportunistically. A few nests have been on or under large tree roots, with mossy substrates, and near a cliff ledge (Ford and Brown, 1995). Between 1991 and 1993, 15 murrelet nests were found in Prince William Sound, Kenai Fjords, Kodiak, and Afognak Island using dawn watch methods (Naslund and others, 1995; Marks and Kuletz, 2001). Between 1983 and 2006, radio telemetry was used to locate 6 nests and 10 suspected nest sites (Quinlan and Hughes, 1990; Kuletz and others, 1995b; Whitworth and others, 2000; K. Nelson, oral commun., 2006). In addition, DeGange (1996) compiled 30 records of potential nest sites (summarized in table 28). Of these, five were unconfirmed ground nests and 11 were unconfirmed tree nests; the remaining observations had no supporting information as to nest type.

The most recent effort to locate Marbled Murrelet nests in Alaska has been in the Snettisham area of Southeast Alaska, using radio telemetry (Newman and others, 2006). In 2005, this study found one potential nest site in a forested area. In 2006, two potential nest sites were found on cliffs near forested habitat, but the nests could not be reached because of terrain (K. Nelson, Oregon State University, oral commun., 2006).

The most geographically extensive examination of potential nesting habitat in Alaska relied on dawn activity levels of murrelets as an index of habitat suitability (Kuletz and others, 1995a). Between 1991 and 1993, dawn watches were conducted in Prince William Sound, Kenai Fjords National Park and Afognak Island, Alaska (*n* = 262 sites). The highest activity levels were associated with the heads of bays where there were large trees with high epiphyte cover. The best model predicting nesting behavior (circling above or flying below canopy) included location relative to the head of a bay, tree diameter and number of potential nesting platforms per tree.

Among the three subregions, Prince William Sound sites had the lowest detection level, with 23.8 ± 3.11 detections/survey (± SE); followed by Kenai Fjords, with 29.9 ± 5.78 detections/survey (± SE); while Afognak Island had exceptionally high detection levels, with 38.4 ± 5.27 detections/survey (± SE) (Kuletz and others, 1995a). The lower inland detections in Prince William Sound were attributed to the greater amount of available habitat there, compared to Kenai Fjords. Trees on Afognak Island had the largest number of mossy potential nest platforms. The surrounding waters also had relatively high numbers of Marbled Murrelets; 1992 boat surveys on the northern and western sides of Afognak Island estimated more than 5,000 Marbled Murrelets were present on the water (Fadely and others, 1993).

Analysis of a subset of the above data (*n* = 72 sites), from three islands in the Naked Island group in central Prince William Sound, showed that murrelet activity was significantly higher in stands of large trees and moderate to high volume classes, with 0.50 (± 0.22) to 1.00 (± 0.34) subcanopy behaviors/site at moderate volume classes compared to 0.06 (± 0.06) and 0.32 (± 0.22) subcanopy behaviors/site at low and high volume classes, respectively (Kuletz and others, 1995c). Occupied behaviors were in forests with average tree diameter greater than 46 cm. Although these trees were not large compared to trees in regions farther south (McShane and others, 2004), the trees were more than 200 years old (U.S. Forest Service, Glacier Ranger District, Anchorage, Alaska, unpub. data, 2006), and typically were the largest in the forest stand. Analysis of another subset of the data, encompassing 84 sites throughout the entirety of Prince William Sound, found that murrelet activity levels were highest in forests with trees greater than 28 cm diameter (the cut-off size in a timber type land coverage). Murrelet activity levels were significantly higher at the heads of bays, with the exception of glaciated or recently deglaciated bays (Marks and others, 1995).

In Kenai Fjords, which is undergoing recent and rapid deglaciation, more of the coastal land base is unforested. Thus, the randomly selected dawn watch sites in Kenai Fjords occurred more frequently in non-forested habitats. Unlike in Prince William Sound and Afognak, murrelet detection levels in Kenai Fjords were highest near the outer promontories and lowest in the inner bays (Marks and Kuletz, 2001). This was likely because more forests and larger trees occur near the promontories, whereas the inner bays were often treeless, having been glaciated until after 1900 (Marks and Kuletz, 2001). Among the non-forested sites, murrelet activity was higher in areas that had been ice-free since 1900, where there was more ground cover such as lichen and alder (*Alnus* spp).

Table 26. Summary of Marbled Murrelet tree nests in Alaska.

[Adapted from data in DeGange, 1996. Range of values in parentheses]

Nest characteristics	Regions					
	Prince William Sound			Kodiak	Southeast Alaska	
	Mountain Hemlock	Western Hemlock	Sitka Spruce	Sitka Spruce	Mountain Hemlock	Western Hemlock
Number of nests	8	2	1	4	1	3
Average tree diameter (cm)	56 (45-71)	53 (30-76)	72	80 (61-104)	120	74 (69-79)
Average tree height (m)	22 (16-30)	21.5 (21-22)	30	25 (21-27)	25	29.7 (26-34)
Average branch diameter (cm)	15.9 (10.5-27.1)	15.4 (14.6-16.2)	12.7	80 (61-104)	19	19.2 (17.5-24)
Average distance to coast (km)	0.52 (0.25-1.04)	0.38	0.1	0.8 (0.4-1.2)	1.2	2.6 (0.5-6.4)
Average canopy closure (percent)	63 (40-75)	85	75	40	na	70 (60-80)
Average elevation (m)	143 (75-305)	95 (75-115)	70	60 (100-305)	348	121 (30-274)

Table 27. Characteristics of Marbled Murrelet ground nests in Alaska.

[Adapted from data in DeGange, 1996. Range of values in parentheses]

Characteristics	Southeast	Prince William Sound	Kenai Peninsula	Cook Inlet and Kodiak
Number of nests	2	3	5	5
Slope (°)	54 (38-70)	49 (25-85)	44 (19-90)	10
Elevation (m)	198 (195-200)	62 (7-180)	238 (20-710)	239 (68-690)
Aspect	W,SW	SW,W,NW	N,NW,S,SE	N,NE,SE,SE/S
Distance to coast (km)	7.8 (2.5-13.0)	0.47 (0-1.0)	0.33 (0-1.0)	1.6 (0.08-6.2)
Located near forest	Yes	1-Yes, 2-No	1-Yes, 4-No	1-Yes, 4-No

Table 28. Additional evidence of Marbled Murrelet nests in Alaska.

[Summarized from DeGange, 1996. Reports did not always include information on forest cover. Of the 30 reports of possible nesting, 24 had information on forest type or cover]

Summary of suspected nest site characteristics		Southeast	Prince William Sound	Kenai Peninsula	Kodiak-Afognak
	Total number of reports	9	10	2	9
Nest type	Unconfirmed ground nest[1]	0	4	1	0
	Unconfirmed tree nest[2]	3	5	0	3
Evidence	Adult observed[3]	1	5	0	3
	Chick found[4]	2	3	1	6
	Egg or eggshell fragments found	7	2	0	1
Records where information on forest cover was available					
General cover type	Area was forested	4	5	1	9
	Not forested (grass or shrub)		4	1	
Tree types (where noted)	Sitka spruce tree				7
	Western red cedar	1			
	Spruce-hemlock forest		1		
	Conifer forest		3		

[1] Found by flushing adult, or eggs found, and one via telemetry.

[2] Found by radio-tagged birds flying into area or tree, bird on ground below trees, or fallen from felled tree.

[3] Following radio-tagged adult, or adult on ground, or fallen to ground after tree felled.

[4] Chick found on the ground (foreseted and non-foreseted areas), or found dead.

Presumably, the distance between nesting and foraging area is a factor in defining potential murrelet nesting habitat, at least in a general way (Bradley and others, 2004; Kuletz, 2005). Murrelets may nest as much as 75 km inland (Nelson, 1997), suggesting that "commuting" is not a critical factor. Although the sample size was small, Bradley and others (2004) study of radio-tagged birds showed no significant relationship between distance to foraging areas and reproductive success. In Prince William Sound, birds radio-tagged in different marine habitat types had similar foraging distances, and birds nesting above a deep-water fjord did not fly farther to forage in shallow habitat, but rather foraged primarily in the fjord in areas of upwelling (Kuletz and others, 1995b; Kuletz, 2005).

In Prince William Sound, the distances from the coast for 15 confirmed nests (DeGange, 1996) were all <1 km and for six potential nest sites discovered through radio telemetry, all were <6 km from water. Mean over-water distance from suspected nest to forage site was 20 km. This was considerably less than distances recorded in SEAK (75 km, and as much as 100 km; Whitworth and others, 2000) or British Columbia (39 km; Hull and others, 2001). Kuletz (2005) suggested that the steep topography and low tree-line in Prince William Sound may restrict murrelets to near shore nest sites, greatly reducing flight distances to the water, compared to sites farther south. In contrast, potential nest locations in SEAK were 4–9 km from the sea (Whitworth and others, 2000), and in British Columbia were on average 4–15 km inland although some nests have been found farther inland (Hull and others, 2001). In Oregon, mean distance inland for nests was 17 km, with a maximum of 40 km (Nelson, 1997).

Ground Nests

The number of documented ground nests includes two in SEAK to five in the Cook Inlet–Kodiak region (table 27). The two ground nests SEAK were on steeper slopes than farther north, and distance to the coast was greater. In total, 5 of the 15 ground nests were located near a forest (table 27). Most ground nests included some form of vegetative cover, such as alder or willow (Kuletz and Marks, 1997; Marks and Kuletz, 2001).

Ground nesting is rare in British Columbia. Bradley and Cooke (2001) report one confirmed and two probable nest sites on cliffs used by radio-tagged birds on the central mainland (Desolation Sound and Mussel Inlet). All three were on steep slopes (70–90°) offering open flyways, at relatively high elevations (800–1,300 m), within 15–21 km of the ocean, and were confirmed or suspected of being on moss-covered platforms surrounded by shrubby vegetation. At all three sites, the mossy ledges and crevices provided many more potential nest platforms than available in adjacent trees. The high elevation and position on cliffs suggested that risk of ground predators was low. Bradley and Cooke (2001) suggested that ground/cliff nests were relatively rare in their study area, and comprised 3 percent (1/30) of confirmed nests, and 3 percent (2/78) of suspected nest sites. Additional ground nests were found in Desolation Sound and on Vancouver Island in 2001, but details are not available. Rodway and others (1991, 1993) searched alpine areas in Haida Gwaii (Queen Charlotte Islands) but found no evidence of nests or near-nest activity. No ground or cliff nests have been found south of British Columbia (Nelson, 1997; McShane and others, 2004).

Tree Nests

Of the 19 documented tree nests in Alaska, 4 were in SEAK, 2 were on Kodiak Island, 2 were on Afognak Island, and 11 were in Prince William Sound (table 26). In SEAK and Prince William Sound, nest tree species were primarily in mountain hemlock (*Tsuga mertensiana*) or western hemlock (*T. heterophylla*). The four nests found on Kodiak Island and one nest from Prince William Sound were in Sitka spruce (*Picea sitchensis*). Nest tree diameter and height generally decreased on average at the higher latitudes (table 26), which would be expected because tree size decreases with increasing latitude (Viereck and Little, 1972). Elevation of tree nests was highest in SEAK. Naslund and others (1995) found that the 14 tree nests in south-central Alaska were all on large moss-covered platforms in trees >30 cm in diameter. Nest trees were among the largest trees in the immediate area.

The moss platforms of the tree nests found in Alaska have been composed of the hanging moss, *Antitrichia curtipendula* (Quinlan and Hughes, 1990; Kuletz and others, 1994b; appendix C). This moss also was the most common epiphyte found on five of six nest branches used by Marbled Murrelets in British Columbia (Burger, 1995a). Recent studies of epiphyte distribution and biomass in canopies of old-growth coastal forests in B.C., Washington, Oregon show that *A. curtipendula* typically is the dominant moss species, found on branches (axes) primarily in the sheltered lower to mid crowns (Peck and others, 1995; McCune and others, 1997; McCune and others, 2000; Sillett and Rambo, 2000). McCune (1997) found that bryophyte biomass was greatest in old-growth stands, and he hypothesized that bryophytes encroached gradually upward from the forest floor. Similarly, Sillett (1995) found that bryophyte biomass increased with increasing stand age. These observations reinforce that the nest platforms of Marbled Murrelets are dependent on the old-growth nature of the forests, which allows development of a thick moss layer in mid-canopy over long periods of time—i.e., centuries.

Burger (2002b) reviewed the inland breeding habitats of Marbled Murrelets in British Columbia at three spatial scales: nest sites (microhabitat), stand-level, and landscape-level. Based on the British Columbia review, Burger (2002b) concluded that, given a choice, murrelets will select nest sites on boughs with the following five characteristics:

- Sufficient height to allow stall-landings and jump-off departures;
- Openings in the canopy for unobstructed flight access;
- Sufficient diameter to provide a nest site and landing platform;
- Some soft substrate to support a nest cup; and
- Overhead foliage cover.

The first four conditions are almost always found in old-growth trees, which explains why the overwhelming majority of nests are in such trees, although the birds are obviously adaptable and might nest in suboptimal sites, which do not meet these conditions. The proximal cues used by the birds to select nest sites are not known, but seem likely to be a combination of these five features. Murrelets frequently land in trees in which no nests are found, indicating that several sites are considered by prospecting birds before deciding on a nest site. One consistent pattern is that murrelets tend to nest in trees with many suitable platforms even though only one is needed for a nest site. They might be attracted to trees offering several possible nest sites.

At the nest site level, most nests were on large limbs (15–75 cm diameter) in older conifers (Burger, 2002). Tree species preference varied among study areas in British Columbia and was not a reliable indicator of suitable habitat. In a sample of 123 nests from British Columbia, all were in old conifers except one (0.8 percent) found in a red alder (*A. rubra*). Most nests have been found in yellow cedar (*Chamaecyparis nootkatensis*; 50 percent), western hemlock (15 percent), Douglas fir (11 percent), western red-cedar (*Thuja plicata*; 10 percent), and Sitka spruce (9 percent), with fewer in mountain hemlock (2 percent) and amabilis (silver) fir (*Abies amabilis*; 2 percent; Burger, 2002). The high proportions of yellow cedar and Douglas fir among nest trees are artifacts of the large number of nests found in the Sunshine Coast on the southern mainland, where these species are common. These tree species tend to be less common or absent in many other parts of the murrelet's range in British Columbia.

With the exception of the single alder mentioned above, all trees containing nests in British Columbia were old-growth conifers, based on their size, structure, epiphyte loads and, in many cases, evidence of senescence. All were likely more than140 years old, and most were less than 200 years old (Burger, 2002). Nest trees typically were larger and often provided more platform limbs than other trees nearby (Manley, 1999).

Estimates of nest density were made from three studies in British Columbia (Burger, 2002). In fragmented and heavily logged habitat on the Sunshine Coast, Manley (1999) estimated the nest density as 0.3–0.7 nests per ha, which apparently included nests active in previous years. In Clayoquot Sound, western Vancouver Island, Conroy and others (2002) reported density as 0.66 ± 0.29 (SD) visible nests per ha. Considering only nests active in the year they were found, the density was 0.11 ± 0.12 nests per ha. In valley-bottom habitat in Carmanah and Walbran valleys on southwest Vancouver Island, A.E. Burger and V. Bahn (University of Victoria, unpub. data, 2002) estimated densities of 0.60 ± 0.35 (SD) nests per ha, which was equivalent to 0.15 ± 0.09 active nests per ha per year. All three of these studies appear to have sampled areas with higher nest densities than expected across the British Columbia range, because the mean densities recorded with radar (birds per ha), which might sometimes include both members of a breeding pair plus an unknown proportion of non-breeding birds, were much lower (0.090 and 0.045 birds per ha for west Vancouver Island and Desolation Sound, respectively; Burger and others, 2004a; see also below).

Stand-Level Habitat Characteristics

Burger (2002b) reviewed many studies of stand level habitat associations in British Columbia, either comparing stands with nests with randomly selected stands, comparing occupied stands with those showing no occupancy, or using audio-visual detections as indicators of relative abundance. There was considerable variability among these studies but murrelet nesting, occupancy and high levels of activity were frequently positively associated with:

- Tree diameter at breast height (DBH);
- Density of large trees (DBH >80 cm) per ha;
- Variation in tree size (DBH or height);
- Epiphyte (moss, ferns and lichens) cover on branches and thickness;
- Density of potential platforms per ha; and
- Density of trees with platforms;

and generally negatively associated with:

- Elevation (below 600–900 m preferred);
- Forests on the coastal fringe (within ca. 500 m of exposed coasts); and
- Slope and aspect showed variable effects—positive in some areas and neutral or negative in other areas.

An analysis of 45 nests located by telemetry in Desolation Sound indicated some important stand-level features (Bradley, 2002; Burger, 2002). Forest polygons containing nests were compared with randomly selected bordering polygons with trees (treed) or with platform limbs. Polygons with nests were found in older stands of trees, in areas with larger mean basal area of trees, and in areas with greater vertical complexity in canopy structure.

Models of these data indicated that, relative to random polygons (treed or with potential platforms), nest polygons tended to be less uniform with more canopy gaps, and greater vertical complexity in the canopy. These habitat models gave similar results to other models derived from audio-visual and forest structure data.

Landscape-Level Habitat Characteristics

Burger (2002b) reviewed studies which had considered habitat associations at the landscape scale (considering entire watersheds or larger land units). Data came from studies using audio-visual surveys, nest sites located by telemetry, radar counts, and vegetation mapping. In most cases, studies compared measures of murrelet occupancy, nest sites or relative abundance with GIS habitat features derived from the interpretation of forest cover data, satellite imagery, or aerial photography.

At the landscape level, areas with evidence of occupancy tended to have higher proportions of large, old-growth forest, larger stands and greater habitat complexity, but distance to the ocean (as much as about 60 km) did not seem important, apart from some avoidance of coastal fringes. Elevation had significant negative effects in some studies but not all.

There is considerable interest in British Columbia on whether and how elevation and slope affect the probability of nesting by murrelets. Burger (2002b) therefore reviewed these in detail and found optimal nesting conditions in British Columbia are likely to be found at 0–900 m elevation (perhaps 0–600 in watersheds with more intact old-growth stands), less suitable conditions are found at 900–1,500 m, and areas above 1,500 m are unlikely to be used. In all cases, elevation should not be the sole criterion for establishing suitability, and evidence of nesting, occupancy and/or suitable habitat (e.g., potential nest platforms) is needed for establishing habitat suitability. Furthermore, given the inconsistency in data on slope, it seems prudent to avoid including slope as a strong predictor (+ve or –ve) of suitable habitat in British Columbia. Instead, management and mapping should focus on forest structure, measures of canopy accessibility, and nest site attributes known to be reliable indicators (e.g., presence of platform limbs and epiphyte cover). Additionally, aspect does not appear to have a strong effect on the placement or success of nests, although south-facing slopes in drier areas appear to have fewer mossy platforms than other aspects.

Zharikov and others (2006) compared habitats at known nest sites located with telemetry in Desolation Sound (heavily logged; 121 nests) and Clayoquot Sound (relatively intact; 36 nests) with randomly located points in these same areas. Using logistic and multiple regression models, they examined which landscape features best predicted the occurrence of nest sites. Murrelets tended to occur in patch sizes proportional to their occurrence in Clayoquot Sound but in smaller patches than expected in Desolation Sound. Streams, steeper slopes, and lower elevation were identified as features more likely to be associated with nest sites. They also reported that nests were closer to clearcut edges than expected, but this cannot be interpreted that the murrelets had an affinity to forest edges or clearcuts, because the distances that were reported (mean distance to forest edge was 1.9 and 2.4 km at nest sites and randomly chosen points, respectively), were far greater than the distances that forest edge-effects are normally found (about 50–100 m). Their conclusion that murrelets show no ill effects from breeding in old-growth forests fragmented by logging is somewhat in conflict with results of several other studies from British Columbia and elsewhere (Burger, 2002; see below).

Amount and Distribution of Nesting Habitat in Alaska and British Columbia

Even with the increased effort to study murrelet nesting biology in recent years, it continues to be a challenge to characterize nesting habitat. During the last decade, several landscape-scale models have been developed that use a variety of techniques to assess the importance of habitat characteristics to nesting Marbled Murrelets (Lank and others, 2003). In some areas within the breeding range, occupancy was most related to the availability of low-elevation, unfragmented old-growth forests that were near productive marine areas (Meyer and others, 2002). However, given the variability in vegetation characteristics, biogeoclimatic influences and landscape conditions, individual models likely can only be used at the regional level (McShane and others, 2004). In this section, we review the amount and distribution of potential nesting habitat within the breeding range of Marbled Murrelets within major regions of Alaska and British Columbia.

Three general areas of coastal Alaska are important to breeding Marbled Murrelets: SEAK, south-central Alaska and part of southwest Alaska including the Alaska Peninsula and the Aleutian Islands. The region was strongly influenced by the Pleistocene glaciation. Within these areas, nearly 29 million ha fall within 60 km of shore (fig. 29), the typical maximum range for murrelets flying inland from the ocean

(Lank and others, 2003). The Tongass National Forest in SEAK may be the single most important forest habitat for Marbled Murrelets as it encompasses the center of distribution for the species and the majority of the old growth western hemlock and Sitka spruce forests in the State. In the wake of EVOS, however, Prince William Sound in south-central Alaska has been the focus of most of the Marbled Murrelet research in the State. Much less is known about nesting habitat and nesting ecology in the Alaska Peninsula and the Aleutian Islands regions as little work has been done to examine distribution or habitat use.

Attempts to evaluate the amount and distribution of murrelet nesting habitat in Alaska are confounded by the fact that an unknown proportion of the Murrelet population nests on the ground. Piatt and Ford (1993) estimated that 3 percent of the population in Alaska nests on the ground on the basis of marine distribution and at-sea densities relative to unforested regions. Lank and others (2003) suggest there may be a larger fraction of ground-nesters (20–30 percent) at some sites based on inland detections at unforested sites (Marks and Kuletz, 2001). DeGange's (1996) review of 34 nests in Alaska identified 15 as ground nests and 19 as tree nests. However, the high proportion of ground to tree nests was likely an artifact of the higher probability of finding ground nests compared to tree nests (DeGange, 1996). Further confusing the situation, an overlap in ground-nesting and tree-nesting Marbled Murrelets occurs between Kodiak and Prince of Wales Islands (Nelson, 1997). Marks and Kuletz (2001) suggest that limited forest cover and/or limited prey availability near forested areas could play a role in the selection of ground nests. Bradley and Cooke (2001) believe that large-scale removal of original old growth forests is a

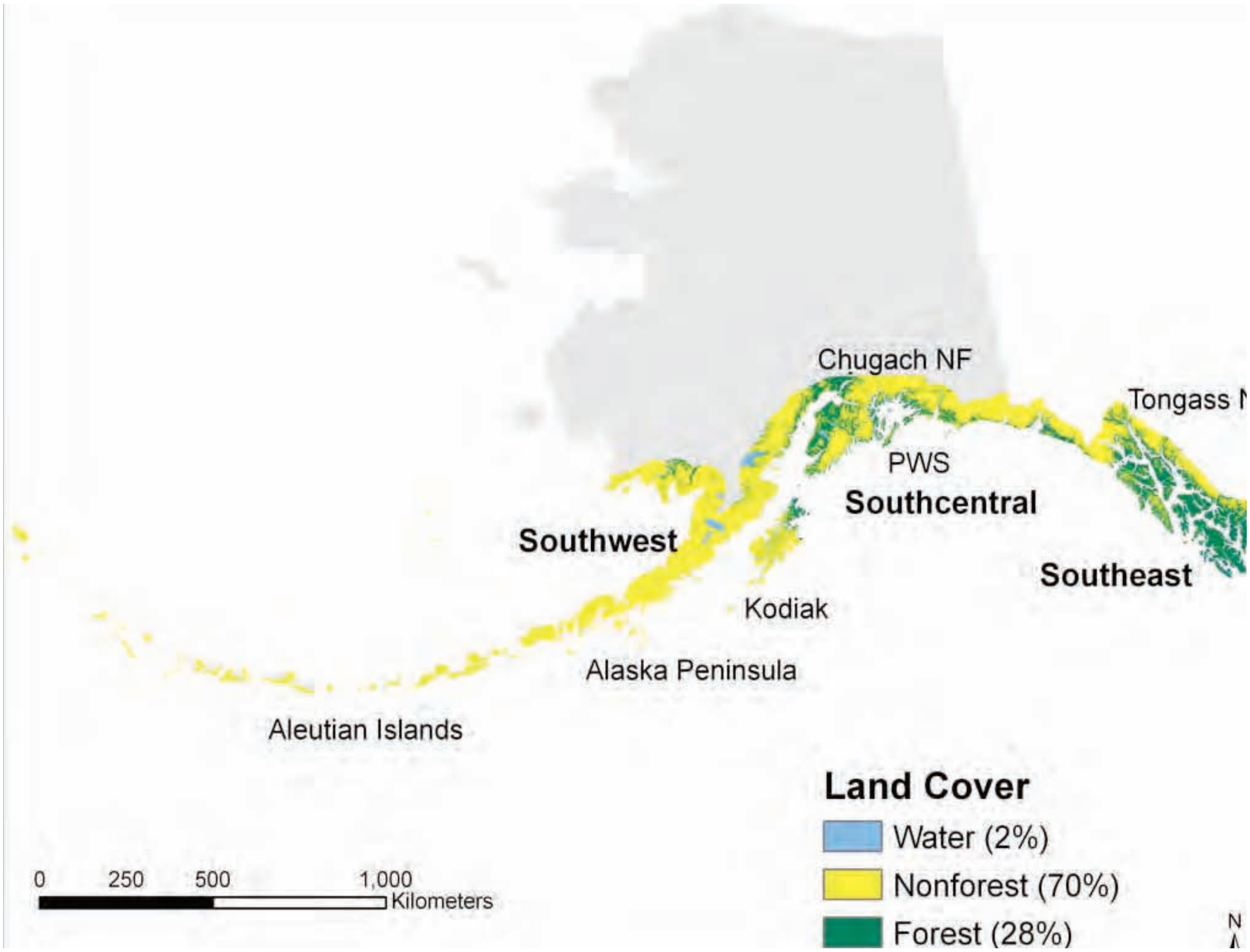


Figure 29. Forested and nonforested areas within the breeding range of Marbled Murrelets in coastal Alaska.

factor in the selection of ground nest sites in British Columbia. In any case, the vast majority of Marbled Murrelets nest in trees within old-growth forests are found within 60 km of the coast (Lank and others, 2003; McShane and others, 2004), and therefore we focus here on forested habitat except in areas where murrelets occur in wholly unforested regions.

Common approaches for evaluating nesting habitat suitability include assessing landscape, stand or tree-scale characteristics relative to use or non-use of a particular habitat (Burger, 2002; Lank and others, 2003; McShane and others, 2004; Raphael and others, 2006). Compared to British Columbia and the western U.S. coastal states, very little work has been done to assess occupancy and habitat use on a regional scale in Alaska. Inaccurate habitat maps and ever-changing knowledge of nesting habitat requirements at the site, tree, plot and landscape scales makes it difficult to determine habitat suitability (McShane and others, 2004). Although information on habitat classification is available for much of the Tongass and Chugach National Forests, current and comprehensive information for other parts of coastal Alaska, including private and locally owned lands, is scarce or nonexistent.

The CMMRT (Bertram and others, 2003) outlined a recommended sequence of analytical methods for predicting stand and landscape-level habitat features as follows:

1. Identify areas under consideration using GIS and habitat maps;
2. Assess and rank habitat suitability using habitat algorithms and habitat indicators;
3. Assess evidence of suitable nesting habitat with interpretation of aerial photography;
4. Select potential polygons to be considered as suitable nesting habitat; and
5. Confirm that potential polygons are suitable habitat using a variety of ground-truthing techniques.

Albert and Schoen (2006) have recently begun the development of a Marbled Murrelet habitat suitability index (HSI) for Alaska. In their conservation assessment for SEAK, they employed the first steps for assessing habitat suitability by modeling vegetation and topographic characteristics such as stand age, tree size, slope and distance from shore (see section, "Southeast Alaska"). A modeling effort for Prince William Sound (R. DeVelice, U.S. Forest Service, oral commun., 2006) went further to select the best habitat suitability model by ground-truthing habitat characteristics and incorporating known occupancy. Still, nesting habitat requirements are debated among experts and regional variation in habitat quality requires that each area be considered separately. As ground-nesting habitat requirements are not well understood, there have been no attempts to assess occupancy or habitat suitability for ground-nesting Marbled Murrelets in unforested regions of Alaska such as the Alaska Peninsula and Aleutian Islands.

Forest Inventory and Analysis (FIA) data provide high-quality forest data for much of the forested area in southern Alaska. As part of a nationwide census, the USFS conducts annual and periodic surveys to determine the extent, condition, volume, growth and depletions of timber on forest land across all ownerships. We obtained FIA plot data collected in 1995–2003 for south-central and SEAK. FIA sampling used a systematic-grid sample with a grid spacing of 4.8 km. They used high resolution orthophotographs and satellite imagery to classify land cover and vegetation type, and to determine plot locations. Sampling intensity was chosen to meet sampling error guidelines of ±3 percent per million acres for productive forest area and ±10 percent per billion ft^3 for net volume. Unforested areas or those within reserved areas were not ground-truthed (van Hees and Mead, 2005).

We used general land cover and land-status datasets available the State of Alaska to estimate the amount and distribution of nesting habitat in Alaska when plot data or published material were not available. Land-cover data were digitized by the USGS Earth Resources Observation and Science (EROS) program using AVHRR satellite imagery (1-km resolution). Land status coverages were compiled by the BLM and ADNR and are current as of March 2006.

British Columbia has made more progress towards identifying suitable habitat compared to Alaska. Several models or algorithms have been developed that combine habitat measures to classify and map large areas in British Columbia (reviewed by Tripp, 2001; Burger, 2002). Some algorithms combined measures derived from canopy structure, elevation, distance from ocean and from forest edges. Others used biogeoclimatic units (e.g., Broad Ecosystem Units) and forest cover maps, either separately or in combinations. Several studies have done ground-truthing to assess the validity of their algorithms and found them to be reasonably reliable in predicting suitable nesting habitat. The reviews concluded habitat classification was most reliable using regionally specific algorithms, combined with confirmation of habitat suitability using helicopter and/or ground surveys.

Southeast Alaska

SEAK is approximately 840 km long by 190 km wide spanning from the Yakutat Bay to the north and Dixon Entrance to the south. The area includes coastal mountain peaks reaching 3,000 m on a narrow strip of mainland and the island chain that makes up the Alexander Archipelago.

The upland forests in SEAK are dominated by western hemlock and mixed hemlock-Sitka spruce stands. Alaskan yellow cedar, western red cedar, shore pine and mountain hemlock also are present. Western hemlock trees average 37–75 cm in DBH and 27–36 m in height. In contrast, Sitka spruce trees in mature stands average 75–100 cm in DBH and 36–67 m in height. Mountain hemlock trees usually occur near tree line and average 38–50 cm in DBH and 18–25 m in height. Well developed moss layers are characteristic of these stands (Viereck and others, 1992). Rainfall, moderate temperature and relatively low levels of disturbance contribute to the maintenance of the productive old growth characteristics of southeast forests.

The Federal government holds 8.3 million ha of land in SEAK, of which 6.8 million ha are within the Tongass National Forest (fig. 30). Other major landholders include Glacier Bay National Park and Preserve (1.1 million ha), the State of Alaska, who manages the Haines State Forest (216,000 ha) and other smaller holdings, and the Alaska Native Corporations (274,000 ha; table 29).

SEAK covers about 9.3 million ha of land area. Recent forest inventory work found that 48 percent of the land area is forested (van Hees and Mead, 2005), while the rest is comprised of fen, sphagnum bogs, rock, glaciers, ice fields and water. Timberland, or the forested area that can produce

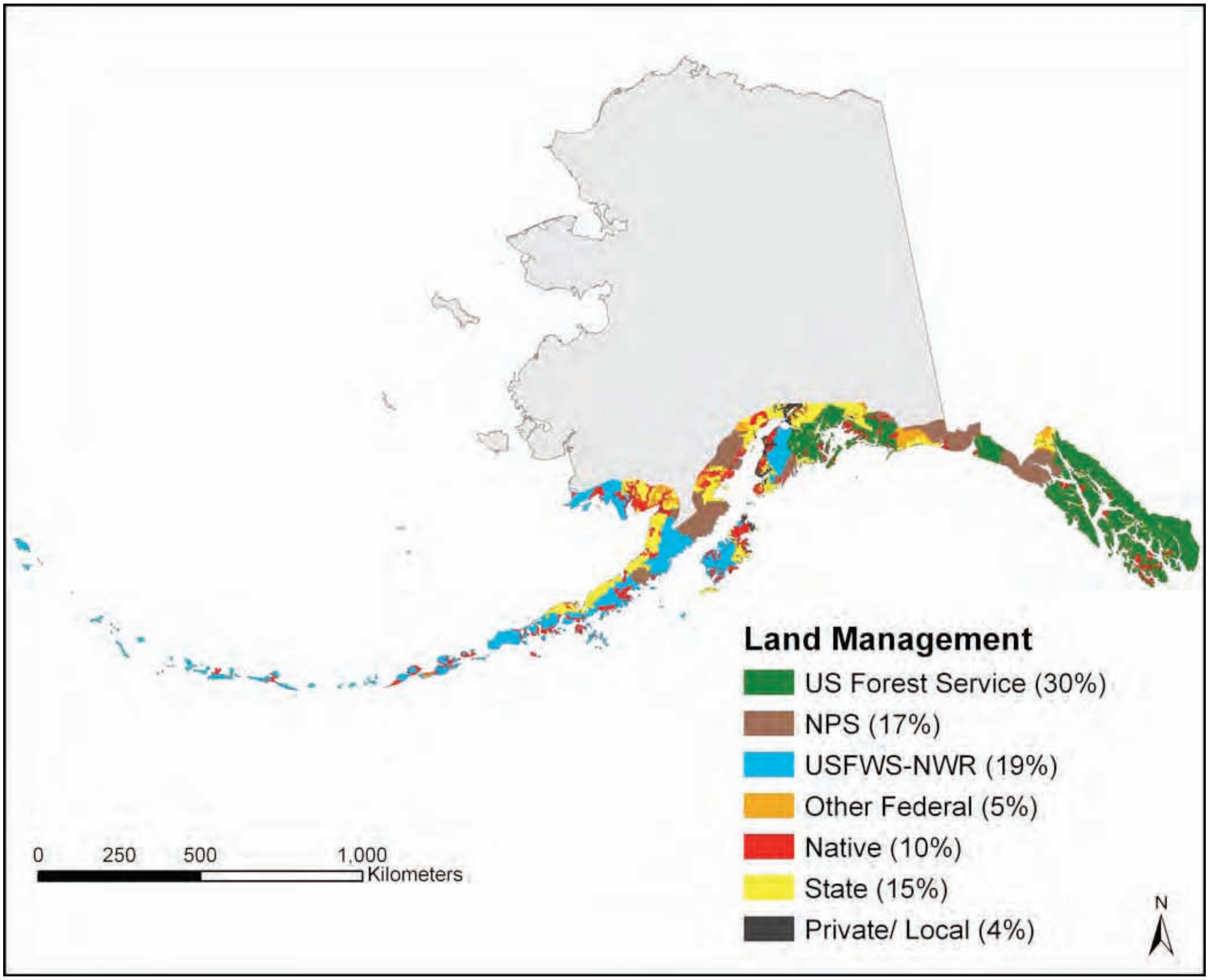


Figure 30. Land management within the breeding range of Marbled Murrelets in coastal Alaska. Data are based on 2006 BLM and ADNR sources.

Table 29. Area (thousands of ha) and land ownership for areas within 60 km of of the shore in southeast (SEAK), south-central (SCAK) and southwest (SWAK) Alaska.

[Data are based on 2006 land-status estimates compiled by the Bureau of Land Management and State of Alaska Department of Natural Resources]

Landowner	SEAK	SCAK	SWAK	All areas
U.S.Forest Service	6,609 (72%)	2,087 (27%)	0 (0%)	8,697 (30%)
National Park Service	1,626 (18%)	875 (11%)	2,308 (19%)	4,810 (17%)
National Wildlife Refuge	0 (0%)	1,313 (17%)	4,333 (36%)	5,645 (19%)
Other Federal	149 (2%)	557 (7%)	714 (6%)	1,420 (5%)
Native	274 (3%)	876 (11%)	1,794 (15%)	2,943 (10%)
State	346 (4%)	1,501 (19%)	2,540 (21%)	4,387 (15%)
Private, local, other	231 (3%)	608 (7%)	244 (2%)	1,083 (4%)
Total	9,235	7,817	11,933	28,985

1.4 m^3 of wood per ha per year and is accessible and available for production of wood products, comprises about 1.6 million ha (18 percent) of land area in all SEAK. Most forested areas are considered old-growth and are limited to elevations less than 750–900 m (Everest, 2005). Seventy-three percent of the timberland in SEAK is 150 years or older (van Hees and Mead, 2005). Of 2,463 plots visited in SEAK, 995 (40 percent) had a stand age greater than 150 years covering an estimated 2.1 million ha of land area (fig. 31).

As discussed above, Albert and Schoen (2006) have recently completed a comprehensive analysis of productive old growth stands in Southeast Alaska. They used a combination of Forest Service data, Landsat ETM and orthophotographs to classify vegetation and land cover. They assessed the amount of productive old growth using a classification system developed by Caouette and DeGayner (2005), based on tree size and stand density to categorize large tree (>53 cm), medium tree (43–53 cm) and small tree stands (<43 cm). Using these guidelines, they estimated that there are roughly 2.3 million ha of productive old growth forest in SEAK (table 30). Productive old-growth stands make up about 52 percent of the forest. Large, medium, and small tree stands comprise 10, 75, and 15 percent, respectively, of old-growth forest in SEAK. Northern Prince of Wales Island contains nearly 24 percent of all large-tree forests in SEAK. Other areas that contain considerable amounts of large-tree old-growth include Admiralty Island, South Prince of Wales, East Chichagof, Kuiu, and Yakutat Forelands (table 31).

A nesting habitat capability model for several focal species including the Marbled Murrelet in SEAK (Albert and Schoen, 2006) was based on several factors that contribute to nesting habitat including stand age, forest structure, slope, and distance from shore (table 32). Although the model was based on a team of Murrelet experts' professional judgment on important habitat requirements, and they used the best

Table 30. Generalized classification of vegetation and land cover in Southeast Alaska.

[From Albert and Schoen, 2006. **Abbreviations:** ha, hectare; POG, productive old growth; <, less than]

Land cover	Area (ha)	Percent of total
Productive Old Growth		
POG-Large Tree	238,308	2.69
POG-Medium Tree	1,754,073	18.91
POG-Small Tree	357,691	4.04
Other Forest		
Clear-cut and 2nd growth	318,198	3.60
Conifer < 150 yrs	119,931	1.36
Conifer forest (other)	183,162	2.07
Deciduous forest	27,540	0.31
Mixed forest	6,187	0.07
Muskeg forest	477,633	5.40
Muskeg woodland	522,375	5.90
Sub-alpine forest	483,749	5.47
Non-forest vegetation		
Alpine tundra	220,268	2.49
Slide zone	326,990	3.69
Shrubland	389,298	4.40
Herbaceous nonforest	428,703	4.84
Freshwater wetlands		
Muskeg meadow	105,857	1.20
Emergent wetlands	19,275	0.22
River bar	22,219	0.25
Lake	82,777	0.94
River channel	58,347	0.66
Coastal wetlands		
Algal bed	33,334	0.38
Rocky shore	15,663	0.18
Salt marsh	13,540	0.15
Sand and gravel beach	2,345	0.03
Tideflat	5,090	0.06
Unconsolidated sediments	45,254	0.51
Unvegetated lands		
Ice and snow	1,455,348	16.44
Unvegetated	1,213,659	13.71
Urban	3,978	0.04
Total[1]	8,930,793	100.00

[1] Discrepancies between FIA and Albert and Schoen (2006) area estimates are because FIA plots covered the area north of Yakutat to Icy Bay, but excluded reserves and unforested lands.

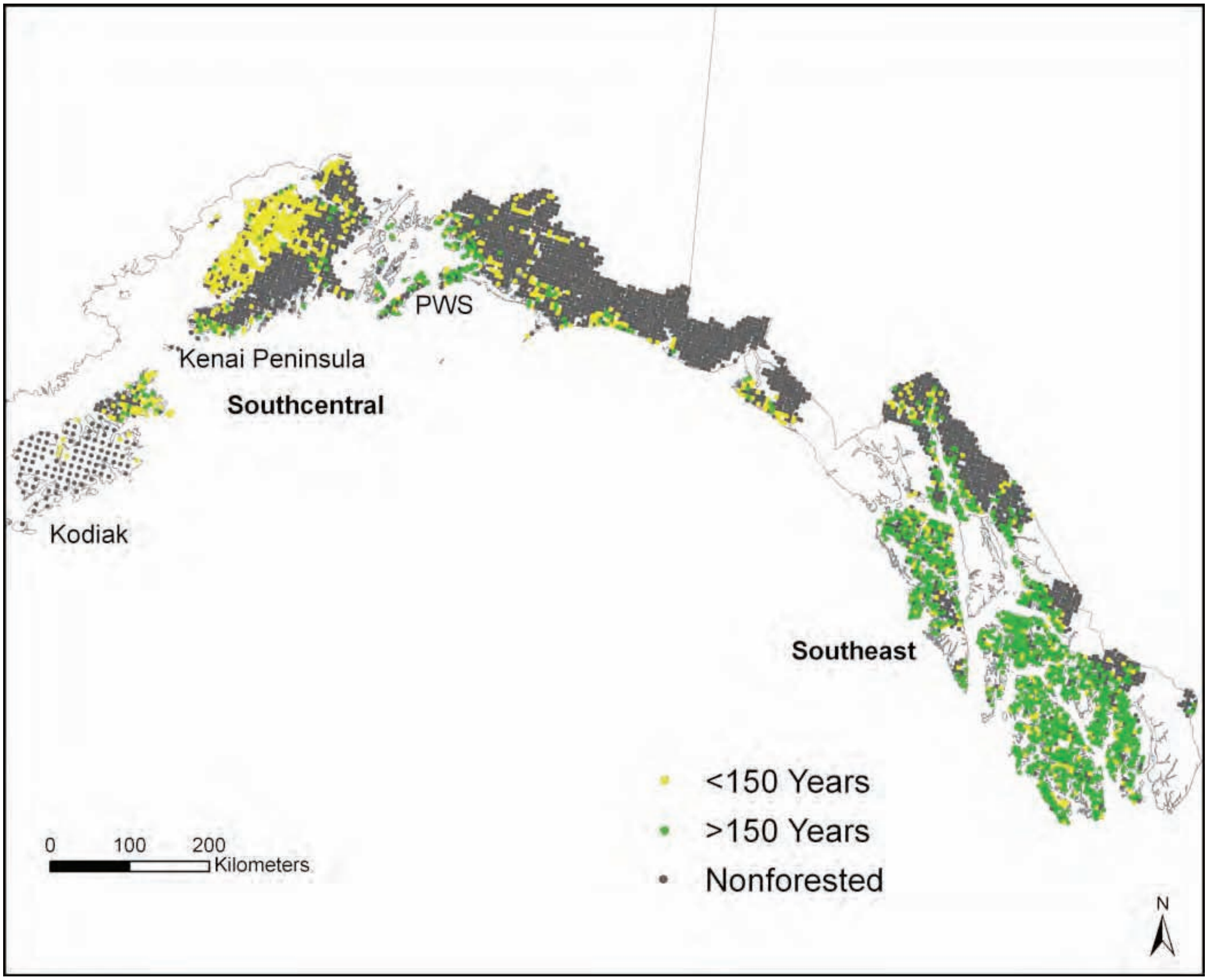


Figure 31. Forest Inventory and Analysis (FIA) plot data from south-central (n = 2,533) and Southeast Alaska (n = 2,463).

forest cover data available, the authors recognized that further research will help refine the model parameters. For example, the model did not differentiate among small, medium, and large tree old-growth, and it therefore may be an overestimate of suitable habitat. Likewise, the optimum value for slope also is disputed among experts. Moreover, the model lacks occupancy data, which are required to better assess the actual extent of nesting habitat (Lank and others, 2003). We caution that the model should be tested when occupancy data are available, however, to date, it is the best attempt to quantify habitat suitability for Marbled Murrelets.

Albert and Schoen's (2006) modeling efforts found that 413,900 ha (4.7 percent) in SEAK have high potential (suitability index ≥ 75), 409,879 ha (4.7 percent) have medium potential (suitability index = 50–74), 1,220,640 ha (13.9 percent) have low potential (suitability index = 1-49) and 6,755,785 ha (76.8 percent) are unsuitable (suitability index = 0) for nesting Marbled Murrelets (table 33). The areas with the highest nesting habitat suitability are Revilla Island/ Cleveland Peninsula, Admiralty Island, North Prince of Wales and E. Chichagof Island (fig. 32). Areas of high marine density include the area near Admiralty Island, the northeast end of Chichagof Island and the area near Northern Prince of Wales Island including Zarembo and Kupreanof Islands. In contrast, the areas with the lowest potential for suitable habitat are the Fairweather Ice fields, Yakutat Forelands, and W. Chichagof

Table 31. Land area and management status (percent of current distribution) of large-tree old growth forests among provinces in southeast Alaska.

[Adapted from Albert and Schoen, 2006. Watershed-scale reserves includes areas where non-development land-use designations encompass the entire watershed. Sub-watershed scale reserves are areas that include a portion of entire watersheds within non-development land-use designations. Buffers include stand-level protections under the Alaska State Forest Practices Act as well as the Tongass Land Management Plan standards for riparian, estuary, and beach fringe forests]

Province	Land area (ha)	Management status (percent of current distribution)			
		Watershed-scale reserves	Sub-watershed reserves	Buffers	Timberbase
E. Baranof Island	816	43.9	8.0	25.1	23.1
W. Baranof Island	1,940	59.1	15.9	6.0	19.0
Etolin/ Zarembo Island	4,908	23.6	24.2	12.1	40.1
Kupreanof/ Mitkof Island	8,621	15.1	25.0	14.7	45.2
Dall Island Complex	3,907	42.6	43.3	1.5	12.6
Revilla Island/ Cleveland	12,968	41.7	20.8	7.5	30.1
N. Prince of Wales	56,514	13.5	31.4	13.8	41.3
E. Chichagof Island	15,287	42.9	14.7	16.6	25.7
Outside Islands	5,493	41.9	17.7	12.0	28.4
Chilkat River Complex	8,492	0.9	9.6	0.0	89.5
Taku River/ Mainland	9,678	18.0	33.5	9.4	39.1
Kuiu Island	14,703	31.6	15.3	10.6	42.5
Stikine River/ Mainland	8,582	51.0	12.4	11.4	25.1
Yakutat Forelands	11,160	52.1	10.5	1.3	36.1
S. Prince of Wales Island	17,600	42.5	17.9	10.9	28.7
Lynn Canal/ Mainland	6,778	41.9	16.1	7.6	34.5
Admiralty Island	40,443	88.1	7.7	0.1	4.1
N. Misty Fjords	6,657	90.1	2.6	2.7	4.6
S. Misty Fjords	5,735	99.7	0.0	0.0	0.3
W. Chichagof Island	819	99.3	0.0	0.0	0.7
Grand total[1]	241,098	43.0	18.5	8.4	30.0

[1] Does not include Glacier Bay or the Fairweather Icefields.

Table 32. Habitat variables and suitability factors used to estimate the relative value of Marbled Murrelet nesting stands in Southeast Alaska.

[From Albert and Schoen, 2006. Abbreviations: POG, productive old growth; <, less than; >, greater than; ≥, equal to or greater than; m, meter]

Variable	Habitat type	Habitat suitability index
Age class	<150 years	0.00
	≥150 years	1.00
Tree size	Small POG	0.50
	Medium POG	0.75
	Large POG	1.00
Slope (degrees)	0-5	0.20
	5-10	0.40
	10-15	0.60
	15-20	0.80
	>20	1.00
Distance from shore (m)	<300	0.30
	>300	1.00

Table 33. Habitat suitability for Southeast Alaska, based on forest cover and topology.

[From Albert and Schoen, 2006. ha, hectare]

Habitat potential	Habitat suitability index	Area (ha)	Percent of total
Unsuitable	0	6,755,785	76.8
Low	1-49	1,220,640	13.9
Medium	50-74	409,879	4.7
High	75-100	413,900	4.7

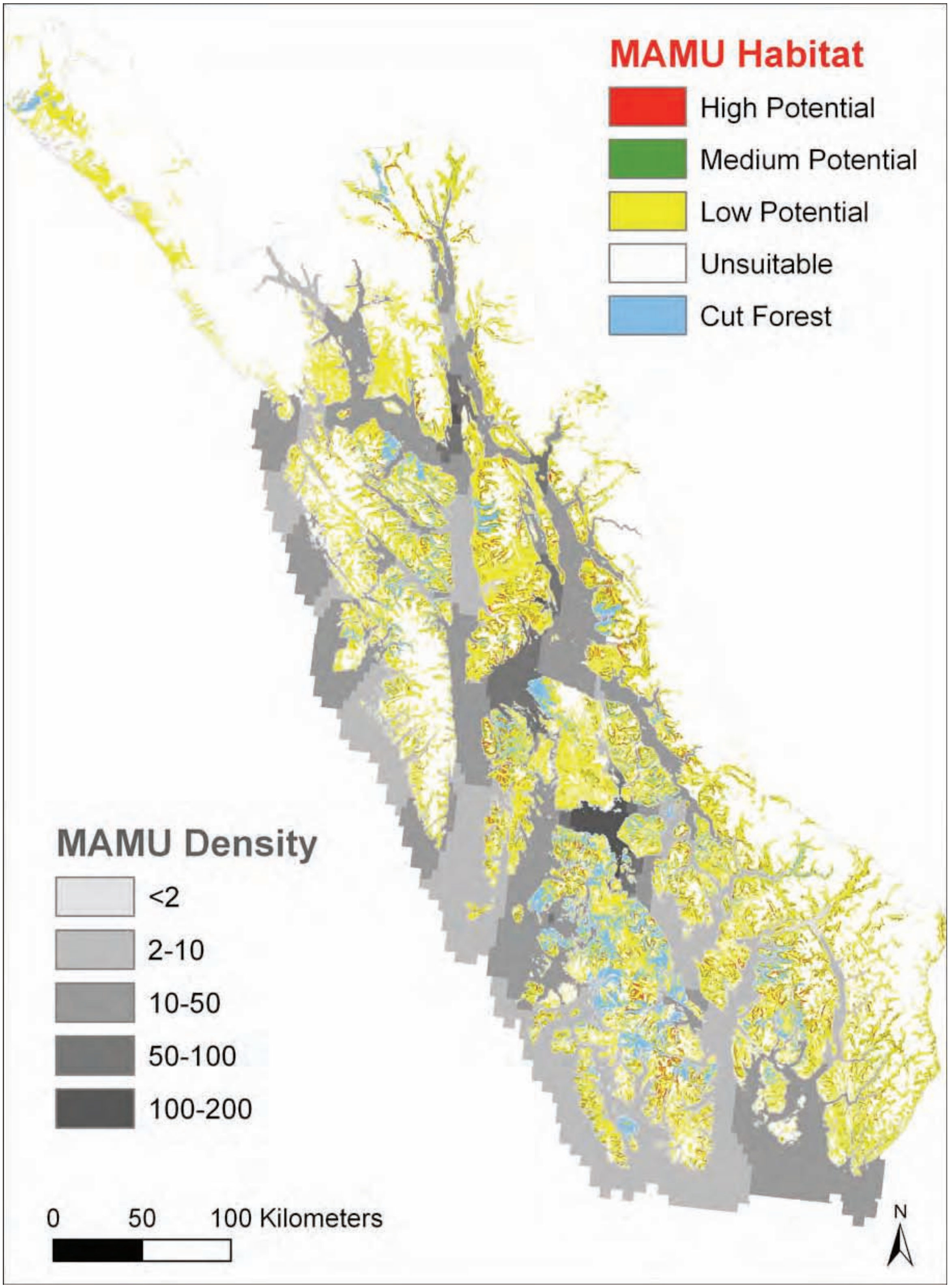


Figure 32. Marbled Murrelet habitat suitability and marine density for southeast Alaska. Data are based on the Albert and Schoen (2006) habitat suitability model. Densities at sea in birds per square kilometer.

Island. An analysis of the change in habitat suitability from 1954, when industrial logging began in the region, to the present found a 14-percent degradation of murrelet habitat relative suitability scores for the region. Furthermore, about 30 percent of currently existing suitable habitat (based on the sum of habitat suitability index scores within the region) occurs on managed state, federal or private lands with potential for harvest (table 34).

South-Central Alaska

The south-central Alaska region includes Kodiak, the Kenai Peninsula, Chugach National Forest, and Icy Bay. A part of the Kenai Peninsula and all of Prince William Sound are located within the Chugach National Forest.

The Kodiak Island Archipelago is located in the Gulf of Alaska approximately 30 mi across Shelikof Strait from the Alaska Peninsula. The island group is an extension of the Chugach-St. Elias Mountains and was nearly completely

Table 34. Current condition and management status of nesting habitat for Marbled Murrelets in southeast Alaska.

[From Albert and Schoen, 2006. Watershed-scale reserves include areas where legal or administrative protections encompass the entire watershed (VCU). Sub-watershed scale reserves are areas that include a portion of entire watersheds (VCU) within legal or administratively protected status. Buffers include stand-level protections under the Alaska State Forest Practices Act as well as the Tongass Land Management Plan standards for riparian, estuary, and beach fringe forests. Managed lands include U.S. Forest Service timber base as well as all State, private, and Federal lands lacking explicit legal of administrative protection]

Province	Habitat capability index		Current condition	Management status and scale (percent of current habitat value)			
	Original (1954)	Current (2002)	Percent of original habitat value	Watershed-scale reserves	Sub-watershed reserves	Buffers	Managed lands
N. Prince of Wales	229,309	138,269	60.3	17.7	28.0	7.3	47.0
Kupreanof/ Mitkof Island	96,196	76,516	79.5	14.6	21.4	4.8	59.2
E. Chichagof Island	131,045	104,324	79.6	33.4	16.6	6.0	44.0
Etolin/ Zarembo Island	69,743	55,968	80.2	20.7	24.2	6.6	48.5
E. Baranof Island	26,185	21,216	81.0	38.8	14.1	6.4	40.7
Yakutat Forelands	10,788	9,008	83.5	65.4	15.4	1.1	18.0
Outside Island	30,343	26,016	85.7	67.2	11.2	4.4	17.2
Dall Island Complex	30,233	25,995	86.0	33.7	34.1	2.3	29.8
Revilla Island / Cleveland Pen.	177,284	153,666	86.7	48.8	14.5	3.6	33.1
S. Prince of Wales	51,442	45,145	87.8	46.8	15.9	5.9	31.3
W. Baranof Island	54,306	48,136	88.6	64.9	15.0	1.7	18.4
Kuiu Island	81,973	72,720	88.7	55.3	10.4	4.4	30.0
Chilkat River Complex	46,220	41,653	90.1	1.4	8.5	0.4	89.7
Taku River/ Mainland	103,942	96,974	93.3	41.5	18.6	4.4	35.5
Admiralty Island	160,117	151,858	94.8	89.3	8.4	0.0	2.3
Stikine River/ Mainland	96,527	92,493	95.8	54.8	11.6	3.8	29.7
Lynn Canal/ Mainland	56,045	54,238	96.8	53.5	15.4	3.2	27.9
Glacier Bay	26,789	26,693	99.6	92.9	6.5	0.0	0.5
S. Misty Fjords	82,636	82,636	100.0	99.8	0.0	0.0	0.2
N. Misty Fjords	62,528	62,528	100.0	94.0	2.9	0.3	2.8
W. Chichagof Island	15,939	15,943	100.0	98.7	0.0	0.0	1.3
Fairweather Icefields	8,047	8,051	100.0	99.9	0.0	0.0	0.1
All provinces	1,647,637	1,410,046	85.6	52.2	14.4	3.5	29.9

ice scoured during the Pleistocene glaciation. This region is characterized by alpine tundra at the higher elevations, forb/grass meadows with willow and alder at lower elevations and the northern area, including Afognak and Shuyak Islands, is forested with Sitka spruce and black cottonwood (Nowacki and others, 2001).

The Kenai Peninsula is an ecologically diverse region and includes the Cook Inlet Basin, Chugach-St. Elias Mountains and Gulf of Alaska coast. Forest type in the Cook Inlet Basin area generally is composed of black spruce, paper birch, and quaking aspen. The forests on the Gulf coast of the Kenai Peninsula are dominated by mountain hemlock and Sitka Spruce, while the lowland areas are characterized by boreal forests of white spruce, paper birch, and black spruce. The Kenai Peninsula has recently (late 1990s) been devastated by a Spruce Bark Beetle infestation that resulted in the loss of mature spruce trees on about 429,000 ha, or more than 50 percent of the forested land in the region (Boucher and Mead, 2006).

The Chugach National forest is the Nation's second largest national forest covering approximately 2.1 million ha. It is situated between the Kenai Peninsula and the Copper River Delta and it includes Prince William Sound. Old-growth forests in the region provide important fish and wildlife habitat, due to the unique structural attributes such as multilayered canopies, diverse forb and shrub layers, coarse woody debris, and large diameter trees (Ricketts and others, 1999). For this region, these attributes begin to appear when a forest reaches 150 years, although this may vary by plant association (Capp and others, 1992).

Collectively, non-forested cover types dominate the landscape of the Chugach Forest, accounting for about 78 percent of the gross area. The amount of forested land is about 22 percent (483,200 ha). Within the forested component, conifer forest types dominate, accounting for about 91 percent of forested lands, followed by unclassified forest (about 4 percent), hardwood forest (about 3 percent) and mixed hardwood-conifer forest (about 1 percent; U.S. Forest Service, 2002a).

The distribution of forested land on the Chugach National Forest differs greatly between the three geographic landscapes which make up the forest. Prince William Sound has 63 percent of the total forested land on the Forest (304,790 ha) with the remainder almost evenly split between the Copper River Delta (19 percent or 90,720 ha) and the Kenai Peninsula (18 percent or 87,690 ha). Of the forest structure classes available, Prince William Sound has the majority of old mature stands (47.44 percent) on the Forest with the remainder found on the Copper River Delta (11.44 percent) and the Kenai Peninsula (7.61 percent; table 35).

For the south-central FIA area, more than 1.6 million ha (22 percent) are forested (van Hees, 2005). Of the forested lands, more than 750,000 ha (47 percent) were classified as timberland (unreserved productive forest land; Campbell and others, 2005). The volume of timber on timberland was estimated at 5,087 million ft^3; with most of the volume on State and local government lands (44 percent), with the remaining volume primarily on private lands (28 percent) and National forest lands (23 percent). The study found that the Sitka spruce forest type was the dominant forest type in the region. They also reported that most timberland in south-central Alaska was of relatively low productivity, producing less than 50 ft^3 per acre per year. For timberland acres on State and private lands, average annual mortality and harvest exceeded average annual growth (Campbell and others, 2005).

FIA researchers visited 2,533 plots in south-central Alaska and 148 plots (6 percent) contained stands more than 150 years old. Plots containing old growth stand (>150 years) conditions covered an estimated 281,000 ha of land within the study area. Prince William Sound has the most abundant old growth forest stands in south-central Alaska, although forested areas of Afognak and Shuyak Islands, just north of Kodiak, the Gulf coast of the Kenai Peninsula, and scattered coastal areas between Prince William Sound and Icy Bay also contain old-growth stand conditions (fig. 31).

Marbled Murrelet nesting habitat suitability was assessed for the 245,000 ha of forest (32 percent of the total land area) in the Northern Gulf section of Prince William Sound and a portion of the Kenai Peninsula north of Seward (R. DeVelice, U.S. Forest Service, unpub. data, 2006). This approach used a combination of field sampling to validate vegetation classification and predictive modeling for suitable habitat based on existing geographic databases and landform characteristics. At each ground site, they recorded detailed information including landform, vegetation type, elevation, slope and aspect, and information about individual trees including number of mossy platforms present, and tree diameter. Vegetation types were classified within 1 km radius of field sites using interpretation of aerial photography, and

Table 35. Percent forest structural classes for the Chugach National Forest.

[From U.S. Forest Service, 2002b. Does not include ANILCA additions and forest stands with no structural attributes.

Structural class	Percent of forest structural classes			
	Copper River Delta	Kenai Peninsula	Prince William Sound	Total
Seed/sap	0.09	2.82	0.51	3.42
Pole timber	1.75	18.9	1.63	22.28
Young mature	5.12	1.69	1.01	7.8
Old mature	11.44	7.61	47.44	66.49
Total	18.4	31.02	50.58	100

these classifications also were compared to classifications made from satellite images. Nesting potential was assigned for six scenarios (i.e., different modeling exercises) using mossy platform abundance, which was inversely related to elevation (*P*<0.0001), tree size, which was related to aspect and landform (*P*<0.02 and *P*<0.0005, respectively), forest patch size, distance to shore, proximity to foraging areas (based on bathymetry) and slope. Each modeling scenario increased in habitat complexity with each variable added (table 36). They found that land-cover characterization based on satellite imagery was very effective for distinguishing forests from other vegetation, and interpretation of aerial photography differed from satellite image interpretation by only 3 percent. Six scenarios found high nesting potential more than 20–83 percent of the available forest (fig. 33). Scenario III, which included mossy platform abundance, tree size, and forest patch size, was selected as the best model because sites of 12 of 14 known nests were classified correctly under this model scenario. Scenario III included 133,000 ha of high potential nesting habitat and 104,200 ha of lower potential nesting habitat.

Southwest Alaska

The Alaska Peninsula is formed by the Aleutian Range, which contains some of the most active volcanoes on the continent. The north side, which includes Bristol Bay, is characterized by smooth glacial moraines that act as dams for lakes that have filled in behind them. The south side has rugged, deep fjordlands. Low shrub lands of willow, birch, and alder dominate, with heath and lichen communities interspersed. Alpine tundra and glaciers characterize the highlands (Nowacki and others, 2001).

The Aleutian Archipelago reaches from the Alaska Peninsula to the Kamchatka Peninsula and spans approximately 2,000 km. There are 12 relatively large islands and about 50 smaller islands, with summits reaching 2,800 m near the Alaska Peninsula and 1,000 m on Attu. The islands are treeless with lowland shrubs and inland meadow communities. Exposed upland areas between 125 and 270 m are characterized by mats of heath as a result of frost and high wind, and above 270 m sparse plants are scattered among boulder fields and barren ground. Heterogeneity in the plant community is maintained through disturbance caused by the harsh climate and volcanic activity (Heusser, 1990).

Table 36. Nesting habitat variables used in the Prince William Sound Marbled Murrelet habitat suitability model.

[From DeVelice, U.S. Forest Service, unpub. data, 2006. Higher suitability index values indicate higher nesting potential. Model complexity increased with each scenario, i.e., scenario I included only mossy platforms and model VI included all variables]

Variable	Habitat type	Suitability index	Scenario
Mossy platform[1]	Elevation >200 m	1	I-VI
	Elevation 50-200 m	5	
	Elevation ≤50 m	10	
Tree size[2]	Flat portions of rolling hills	3	II-VI
	Mountain sideslopes, valley bottoms or rolling hills not on southerly aspect	5	
	Mountain sideslopes and rolling hills with southerly aspects, valley bottoms not on southerly aspect	7	
	Valley bottoms with southerly aspects	10	
Forest patch size	<3 ha	1	III-VI
	3-100 ha	7	
	>100 ha	10	
Distance to shoreline	<300 m	5	IV-VI
	≥300 m	10	
Slope	<15, or >35	5	V-VI
	15-35	10	
Proximity to foraging area	Outside grid	5	VI
	Within grid	10	

[1] Mossy platforms were inversely related to elevation.

[2] Tree size was related to aspect and landform.

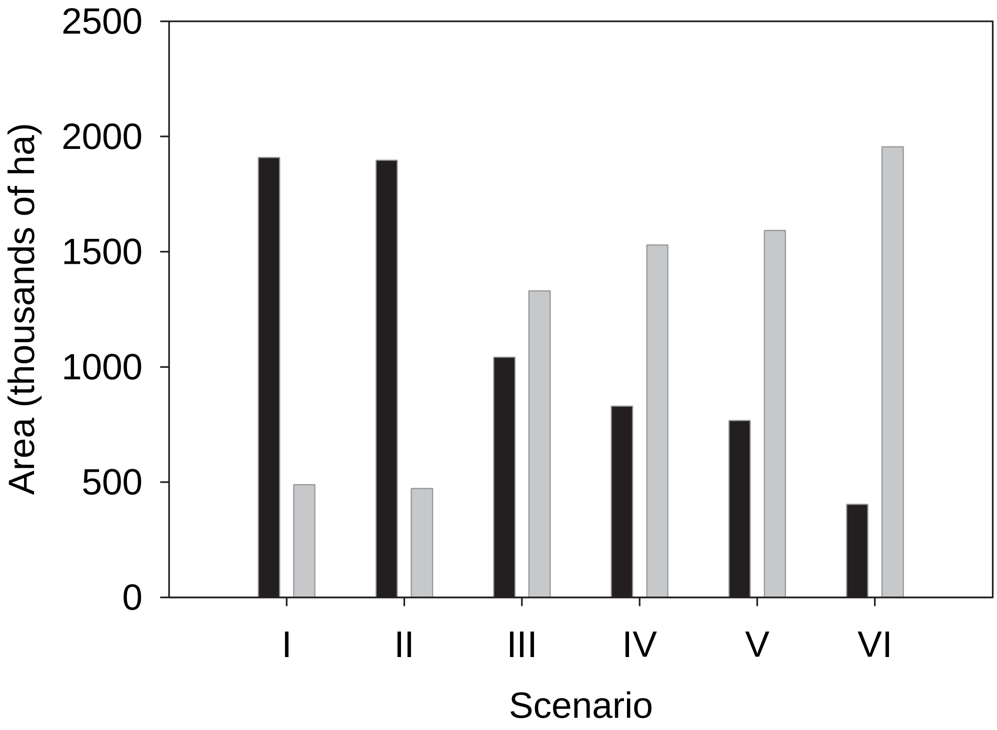


Figure 33. Area of low nesting potential habitat (black) and high nesting potential habitat (gray) for six habitat modeling scenarios in Prince William Sound (DeVelice, U.S. Forest Service, unpub. data, 2006).

The Alaska Peninsula and Aleutian Islands together comprise 41 percent of the entire southern coastal Alaska study area covering about 12 million ha of land area (fig. 29). The Federal government manages 61 percent of the land and more than one-half of Federal holdings are National Wildlife Refuge lands. The State of Alaska manages 21 percent of the land, Native allotments comprise another 15 percent while private, local and other owners make up the remainder (table 29).

FIA data for the southwest Alaska inventory area were not available because they are not comparable to south-central Alaska and SEAK inventory data (B. van Hees, U.S. Forest Service, oral commun., 2006). Only 8 percent of the area is forested, all of which occurs on the Alaska Peninsula. Although Marbled Murrelets undoubtedly breed in the Aleutians, based on their abundance, no nests have been documented there so far.

British Columbia

Based on a synthesis of available evidence and mapping trials, the CMMRT (Bertram and others, 2003) derived regionally specific algorithms to assist the mapping of terrestrial murrelet habitat throughout the British Columbia range (table 37). These algorithms also were adopted as the method for identifying likely nesting habitat by the provincial IWMS (Burger, 2004). The table also summarizes current knowledge of mappable features thought to be important for murrelets in British Columbia (critical microhabitat features such as platform limbs and moss development are not shown on forestry maps or other GIS databases). Some of the parameters shown in table 37 are not available in some regions in British Columbia; consequently province-wide mapping was done using a simpler algorithm based largely on stand age, tree height, and distance from the sea (see table 37). Mapping of the British Columbia-wide habitat using variations of these algorithms is nearing completion but no maps or data are available yet (T. Chatwin and M. Mather, British Columbia Ministry of Environment).

The general CMMRT algorithms and regional variations thereof have been tested using interpretation of aerial photography to assess tree and canopy features, and low-level helicopter surveys to assess availability of potential nesting platforms, mossy mats, large trees, canopy openings and other features deemed necessary for murrelets to nest (Bertram and others, 2003). Following field trials, provincial standards were introduced for both interpretation of aerial photography and low-level helicopter assessments of murrelet habitat (Burger,

Table 37. Definition of polygon features that provide suitable nesting habitat for Marbled Murrelet in British Columbia, as recommended by the Canadian Marbled Murrelet Recovery Team.

[From Bertram and others, 2003; see also Burger, 2004. The features are grouped by the likelihood that polygons with these features will contain a large proportion of suitable nesting habitat. Additional features are described in the text, p. 116-117. No feature should be used in isolation but in combination with other features in developing algorithms. Symbols: >, greater than; <, less than]

Feature	Most likely	Moderately likely	Least likely
Distance from saltwater (km): all regions	0.5–30	0–0.5 and 30–50	>50
Elevation (m)			
Central & Northern Mainland Coast	0–600	600–900	>900
Haida Gwaii (Queen Charlotte Islands)	0–500	500–800	>800
All other regions	0–900	900–1500	>1500
Stand age class: all regions	9 (>250 yr)	8 (140–250 yr)	<8 (<140 yr)
Site index productivity classes: all regions[1]	Class I and II (site index 20+)	Class III (site index 15-19)	Class IV (site index <15)
Tree height class: all regions[2]	4–7 (>28.5 m)	3 (19.5–28.4 m)	<3 (<19.5 m)
Vertical canopy complexity: all regions[3]	MU	NU and U	VU (VNU)

[1] Productivity classes as defined in Green and Klinka (1994, p. 197); approximate 50-year site index values also given—application of these indices might vary with different tree species and across regions.

[2] Nests have been found in polygons ranked height class 1 or 2 but the nests were in larger trees than the polygon average.

[3] Vertical complexity ranked from least to highest (see Waterhouse and others, 2002). VU = very uniform (<11 percent height difference leading trees and average canopy, no evidence of canopy gaps or recent disturbance). U = uniform (11–20 percent height difference, few canopy gaps visible, little or no evidence of disturbance. MU = moderately uniform (21–30 percent height difference, some canopy gaps visible, evidence of past disturbance, stocking may be patchy or irrigular. NU = non-uniform (31–40 percent height difference, canopy gaps often visible due to past disturbance, stocking typically patchy or irregular). VNU = very non-uniform (>40 percent difference, very irregular canopy, stocking very patchy or irregular)—has not been tested.

2004). Waterhouse and others (2004) used a sample of 274 nest sites from several parts of British Columbia to confirm the applicability of interpretation of aerial photography for classifying likely murrelet nesting habitat.

Waterhouse and others (2002) used forest attributes available from interpretation of aerial photography to analyze 45 nest sites found by radio-telemetry on the Sunshine Coast, southern mainland of British Columbia. Five attributes (tree height, basal area of trees, stand age, crown closure, and vertical complexity of the forest canopy) best predicted which forest polygons were more likely to be used for nest sites and also which nest sites were more likely to be successful.

Several studies have used observers surveying from helicopters flying at low altitudes to gather data for testing habitat algorithms and to identify polygons where the canopies contain platforms and other essential elements for murrelet nesting (e.g., Leigh-Spencer and others, 2002; Hobbs, 2003; Burger and others, 2005; Donald, 2005). In British Columbia, many forest companies are now using a combination of forest cover GIS mapping (sometimes also using interpretation of aerial photography) and low-level helicopter assessments, to map and rank forest polygons on their potential as nest habitat (e.g., Deal and Harper, 2004).

The area of suitable nesting habitat currently found in British Columbia is not accurately known. Estimates of habitat areas vary greatly depending on which algorithm is used and how reliable the mapping and GIS data are. The first estimate, based on Baseline Thematic Mapping (a coarse-scale GIS mapping used for forestry in British Columbia) by Marven Eng (British Columbia Ministry of Forests, unpub. data, 2006) suggested that there were 3.9 million hectares of habitat in 2000 (table 38). This is almost certainly an overestimate, made before detailed algorithms of habitat had been developed in

Table 38. Estimates of areas of likely nesting habitat for Marbled Murrelets in British Columbia, 2000.

[Estimates from M. Eng, British Columbia Ministry of Forests]

Habitat available	Area (ha)	Percent of original	Percent of 1973 amount
Original	7,670,923	100	-
1973	5,163,830	67	100
2000	3,933,715	51	76
2030	3,161,372	41	61

British Columbia (Burger, 2002). A province-wide mapping program that applies an algorithm proposed by the CMMRT (Bertram and others, 2003) is nearing completion (T. Chatwin and M. Mather, British Columbia Ministry of Environment). Preliminary results from such analyses indicate areas of habitat ranging from 1.5 to 2 million hectares of likely suitable habitat in British Columbia. This is approximately distributed in the six Marbled Murrelet Conservation Regions (Bertram and others, 2003; see also fig. 7) as follows: Southeast Vancouver Island: 4 percent; West and North Vancouver Island: 25 percent; Southern Mainland Coast: 10 percent; Central Mainland Coast: 28 percent; Northern Mainland Coast: 19 percent; Haida Gwaii (Queen Charlotte Islands): 14 percent.

Threats to Nesting Habitats

The principal threats to Marbled Murrelets in their use of the terrestrial environment for nesting are related to losses or changes in nesting habitat. When using inland habitats for nesting, adult murrelets also are exposed to increased risk of predation. Nests also can be lost to terrestrial predators. Many of the threats to murrelets in the terrestrial environment are anthropogenic. Here we consider the main threats to Marbled Murrelets related to nesting, focusing on:

1. Direct loss of suitable nesting habitat from timber harvest;
2. Fragmentation and edge effects;
3. Increased predation risk;
4. Effects of human disturbances at nest sites on adults and chicks; and
5. Changes in nesting habitat from natural forest processes such as wildfire, insect/disease, and windthrow.

These factors are discussed in the following sections as they pertain to the recent past, current, and projected future nesting habitat conditions for the Marbled Murrelet in Alaska and British Columbia.

Losses of Suitable Nesting Habitat from Timber Harvest

Timber harvest has occurred at some level throughout the entire old-growth forest nesting range of the Marbled Murrelet in Alaska and British Columbia. Industrial-scale logging has occurred primarily in SEAK and British Columbia. Timber harvest from south-central Alaska makes up only 1–3 percent of the total harvest for Alaska (U.S. Forest Service, 2002b). Logging levels also have varied through time. In this section, we review available information about losses of old-growth forest suitable (or known to be used) for murrelet nesting in Alaska and British Columbia.

Southeast Alaska

Industrial-scale logging began in SEAK in the 1950s. The exact number of hectares logged is not known, but the available estimates range from 267,400 to 364,500 ha. Albert and Schoen (2006) estimate that about 318,000 ha of forested land have been harvested, with 188,800 ha on Federal land and 129,500 ha on private or other lands. Their analysis also found that 12 percent of old-growth forests, and 28 percent of large-tree forest types have been harvested since industrial logging began in 1954. Barbour and others (2005) determined that by 2001, 267,400 ha in SEAK had been harvested with 175,400 ha on National Forest land; 79,600 ha on native corporation lands; and 12,400 ha on State and other lands. Of this, about 162,000 ha of high-volume old growth forest has been clearcut (Szaro and others, 2005). DeGange's (1996) review found that 184,856 ha of Tongass National Forest lands were cut by 1995, and an additional 303,750 ha had been conveyed to the State of Alaska or to Alaska Native corporations. Iverson and others (1996) suggest that perhaps 60 percent of those conveyed lands were harvested by 1995, bringing the total harvested forest estimate to 364,500 ha (DeGange, 1996).

Historically, timber in the Tongass National Forest was not harvested equally across all volumes of productive forest. Early harvest practices were more focused on logging the very large trees, and less restricted by regulations that were enacted later, such as the Tongass Land Management Plan (TLMP) and Tongass Timber Reform Act (TTRA; see section, 'General Forest Management Practices'; Albert and Schoen, 2006). The pattern of harvesting the most productive and structurally most complex forest was consistent through 1994 (Iverson and others, 1996). Areas logged after 1986 were 29 percent large-tree, 65 percent medium-tree, and 6 percent small-tree productive old growth types. Furthermore, large-tree forests were logged at a rate that exceeded their proportional abundance by 2.89 times (table 39). Logging also focused disproportionately on the most productive landforms, such as low-elevation karst and riparian forests (Albert and Schoen, 2006). These are among the most productive terrestrial habitats of SEAK and are likely to contain the forest types most preferred by the Marbled Murrelet.

In recent years, demand and harvest of timber in the Tongass has decreased significantly (Hanley and others, 2005). From 1990 to 2004, timber harvest decreased by 67 percent primarily due to changes in the International market (Brackley and others, 2006). The two pulp mills awarded long-term contracts in the 1950s have closed, and harvests on Native lands decreased dramatically in the early 1990s because much of the best timber has already been cut (see section, "Effects of Forest Management Practices on Nesting Habitat"; Knapp, 1992).

Table 39. Rate of logging for forest types potentially suitable for Marbled Murrelets on the Tongass National Forest in Southeast Alaska.

[Figures are based on logging since 1986 to 2000 for which data on previous forest structure was available (n = 242,221 acres; Albert and Schoen, 2006).Index of selectivity = percent use / percent availability]

Forest types	Forest types logged		Availability of forest types		Index of selectivity
	acres	percent use	acres	percent available	
Large-tree	70,839	29.3	588,871	10.1	2.89
Medium-tree	156,572	64.6	4,334,410	74.6	0.87
Small-tree	14,810	6.1	883,874	15.2	0.40
Total	242,221	100	5,807,155	100	

At the regional-scale, harvests within eight regions (E. Baranof, W. Baranof, Etolin/Zarembo, Kupreanof/Mitkof, Dall Island Complex, Revilla/Cleveland Peninsula, North Prince of Wales, and E. Chichagof) have removed 35–70 percent of the original large-tree forests (table 40). Four of those regions (Etolin/Zarembo, Kupreanof/Mitkof, Revilla/Cleveland Peninsula, and North Prince of Wales) have 30 percent or more of the large-tree old-growth stands in the timber base.

South-Central Alaska

The total amount of land area harvested in south-central Alaska is not known, however, van Hees (2005) estimated that 2062.9 MMBF (scaled post harvest) were harvested from 1988 to 2001 (table 41). About 97 percent of the harvest occurred on private land, 2 percent on State land, and 1 percent on National Forest land. For the Chugach National Forest section of Southcentral, less than 1 percent of the forested land has been harvested in the last 30 years (U.S. Forest Service, 2002b). The amount of forest harvested on 6,642 ha of private lands within the Chugach National Forest boundary is unknown but expected to be minimal. Although the total amount of forest harvested on 168,500 ha of Native Corporations' land within the Chugach boundary is unknown, forest managers speculate that several thousand acres have been harvested in the last 15 years. Most native harvests have occurred in eastern Prince William Sound, Montague Island, east of Cordova and the Kenai Peninsula. The State owns about 154,400 ha of land within the Chugach boundary and less than 404 ha have been harvested (U.S. Forest Service, 2002b). Timber harvest levels in south-central Alaska have declined in recent years (table 41).

The amount of mature and old-growth forest decreased by 3,110 ha (17 percent) over a 25-year period between 1974 and 1999 on Chugach National Forest lands portion of the Kenai Peninsula (table 42; U.S. Forest Service, 2002b). From 1980 to 1999, 35.4 MMBF were harvested from the Chugach National Forest at an average annual rate of 1.8 MMBF per year. The rate of loss of old-growth and mature forest cover classes on the Kenai Peninsula averaged 0.72 percent per year. The rate of loss on other portions of the forest is unknown, but likely less than this (DeLapp and others, 2000).

Kodiak Archipelago

The land cover/vegetation classification of the Kodiak Archipelago is the result of the digital image analysis of a three date series of Landsat ETM + scenes acquired between September 1999 and September 2000 (M.D. Fleming and P. Spencer, U.S. Geological Survey, unpub data, 1999–2000). There are 107,129 ha of old growth forest within the Kodiak Archipelago, with 92,867 ha (87 percent) located on Shugak and Afognak Island (M.D. Fleming and P. Spencer, U.S. Geological Survey, unpub data, 1999–2000).

Afognak land is largely private, with the exception of the Kodiak National Wildlife Refuge and the Afognak Island State Park (fig. 34). Most of the logging has been done on private land since the 1980s. The vegetation survey of 1999–2000 (M.D. Fleming and P. Spencer,U.S. Geological Survey, unpub data, 1999–2000) allows us to quantify both the area of existing old growth forest and the area of logged land on Afognak and Shuyak islands (fig. 35, table 43). Old growth forest is described as Dense Sitka Spruce Forest—areas of dense stands of 60–100 percent crown closure. However, it generally is not known how suitable the old-growth on Afognak Island is for Marbled Murrelet nesting. Four tree nests of Marbled Murrelets are known from the Kodiak Archipelago (table 26) and Kuletz and others (1995a) found the highest numbers of detections on Afognak Island compared to sites in Prince William Sound and in the Kenai Fjords. However, Three categories of vegetation fall under

Table 40. Distribution of productive old-growth forest types and percent of timber harvest within 20 biogeographic provinces in Southeast Alaska.

[Albert and Schoen, 2006. Glacier Bay and Fairweather Icefield provinces are not included. Percent of original large-tree forest harvested was estimated by extrapolating the rate of logging of large-tree forests after 1986 from areas with known forest structure (29.3 percent) to all areas logged. Index of selectivity equals the percentage of timber harvested divided by the percentage of original distribution of productive forests among provinces]

Province	Large-tree forests (acres)	Productive old growth (POG)		Timber harvest		Percent of original POG harvested	Percent of original large-tree forest harvested	Index of selectivity
		(acres)	(percent)	(acres)	(percent)			
N. Prince of Wales	130,649	632,303	11.33	295,782	37.8	31.9	39.8	2.59
Dall IslandComplex	9,654	108,864	1.95	26,885	3.4	19.8	44.9	1.61
Yakutat Forelands	27,576	82,841	1.48	18,290	2.3	18.1	16.3	1.47
Kupreanof/ Mitkof Islands	21,302	357,721	6.41	67,619	8.6	15.9	48.1	1.29
Etolin/ Zarembo Island	12,128	230,651	4.13	41,300	5.3	15.2	49.9	1.23
E. Chichagof Island	37,775	438,249	7.85	71,483	9.1	14.0	35.6	1.14
Outside Islands	13,573	118,490	2.12	18,404	2.4	13.4	28.4	1.09
E. Baranof Island	2,016	91,309	1.64	13,797	1.8	13.1	66.7	1.07
Chilkat River Complex	20,984	138,538	2.48	19,940	2.6	12.6	21.8	1.02
Revilla Is./ Cleveland Pen.	32,045	580,282	10.40	72,838	9.3	11.2	39.9	0.91
South Prince of Wales	43,490	168,570	3.02	17,881	2.3	9.6	10.7	0.78
Kuiu Island	36,331	290,855	5.21	29,670	3.8	9.3	19.3	0.75
W. Baranof Island	4,795	236,137	4.23	19,445	2.5	7.6	54.3	0.62
Taku River/ Mainland	23,914	344,340	6.17	21,540	2.8	5.9	20.8	0.48
Stikine River/ Mainland	21,207	334,943	6.00	15,031	1.9	4.3	17.2	0.35
Admiralty Island	99,937	606,438	10.87	27,103	3.5	4.3	7.4	0.35
Lynn Canal/ Mainland	16,748	212,334	3.80	6,282	0.8	2.9	9.9	0.23
North Misty Fjords	16,449	217,164	3.89	0	0.0	0.0	0.0	0.00
South Misty Fjords	14,171	316,370	5.67	0	0.0	0.0	0.0	0.00
W. Chichagof Island	2,023	74,397	1.33	0	0.0	0.0	0.0	0.00
All provinces	586,766	5,580,795	100.00	783,288	100.0	12.3	28.1	

'Logged land': (1) Sitka Spruce Regeneration—areas that have been logged within the past 15–30 years and are re-vegetating with spruce saplings; (2) Salmonberry-Devil's Club-Elderberry—areas exclusive to recently logged stands which were dense Sitka spruce, and (3) Sand and Gravel Roads. As of 1999–2000, there were 92,867 ha of existing old growth forest, and 17,348 ha of logged land (table 43; M.D. Fleming and P. Spencer, U.S. Geological Survey, unpub data, 1999–2000).

British Columbia

There have been three attempts to quantify the loss of likely murrelet nesting habitat in British Columbia. The first, in 2000 by M. Eng (British Columbia Ministry of Forests) involved fairly broad assumptions and used relatively crude estimates of likely habitat applied to coarse-scale biogeoclimatic mapping (see above). This analysis suggested that throughout coastal British Columbia, 33 percent of nesting habitat was removed by 1973 and 49 percent by 2000 (table 38). This analysis was undertaken during the review of the murrelet's Canadian status by COSEWIC (Hull, 1999), and was followed by confirmation of the species' Threatened status in Canada.

The second attempt by Demarchi and Button (2001a, 2001b) was reviewed in Burger (2002b). Habitat ratings were based on the standard six-class system for wildlife in British Columbia (Resource Inventory Committee [RIC], 1999), and were developed by Demarchi (2001) in collaboration with government wildlife biologists familiar with murrelets. These were then applied to habitat polygons derived from 1:250,000 Broad Ecosystem Inventory mapping. This scale

Table 41. Estimated timber harvest volume (million board feet, scaled post harvest) by year and owner group, south-central Alaska, 1988 to 2001.

[Adapted from van Hees, 2005. Source: U.S. Department of Agriculture, Forest Service, Alaska Region. Data on file with Ecosystems Planning, U.S. Department of Agriculture, Forest Service, P.O. Box 21628, Juneau, Alaska 99802-1628]

Year	Estimated timber harvest volume (million board feet)			
	National Forest	State	Private	All owners
1988	1.0	2.1	85.6	88.7
1989	1.5	2.1	120.0	123.6
1990	1.5	1.0	105.1	107.6
1991	1.5	2.5	134.5	138.5
1992	0.5	1.0	123.5	125.0
1993	1.7	0.0	127.2	128.9
1994	6.5	0.0	186.0	192.5
1995	1.9	2.6	230.1	234.6
1996	3.3	8.1	207.6	219.0
1997	2.2	8.6	237.1	247.9
1998	1.5	5.0	172.2	178.7
1999	0.4	5.4	139.9	145.7
2000	0.3	1.8	56.3	58.4
2001	0.4	2.1	71.3	73.8
Total	24.2	42.3	1,996.4	2,062.9

allows only a coarse analysis of habitat availability. Two maps were produced: the first showed habitat *capability* (see Demarchi and Button, 2001a), indicating the likely pre-industrial distribution of suitable inland habitat in the past, based on biogeoclimatic conditions; the second map showed habitat *suitability* indicating the likely distribution and ranking of inland nesting habitat in 2001. Comparisons between the capability mapping (predicted historical) and suitability mapping (present status) showed considerable changes in many areas, primarily due to industrial logging, urbanization and agriculture (Burger, 2002, fig. 4.10). Taking into consideration the top three habitat rankings (those most likely to be used by murrelets; Burger, 2002), this analysis indicated an overall loss of habitat by 34.6 percent, with particularly high habitat reduction on Vancouver Island, the southern Mainland, and Haida Gwaii (Queen Charlotte Islands) (table 44). Demarchi (2001) stressed that comparisons of habitat suitability and capability provide a meaningful expression of the loss of habitat potential but do not provide a measure of absolute habitat loss (i.e., square kilometer lost).

The relative changes suggested by the Demarchi and Button (2001a, 2001b) analysis match the losses of old seral forests shown in a series of satellite images collated by the

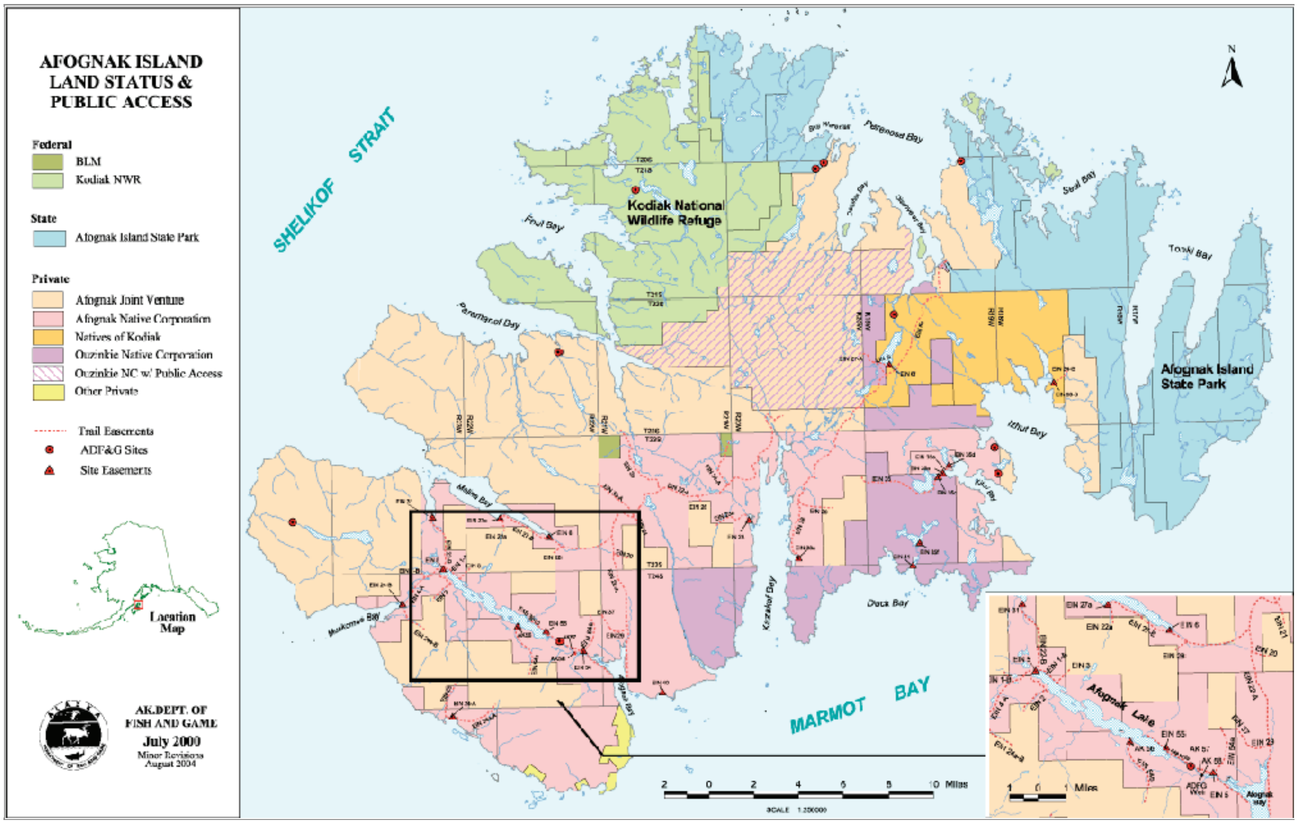


Figure 34. Land use of Afognak Island.

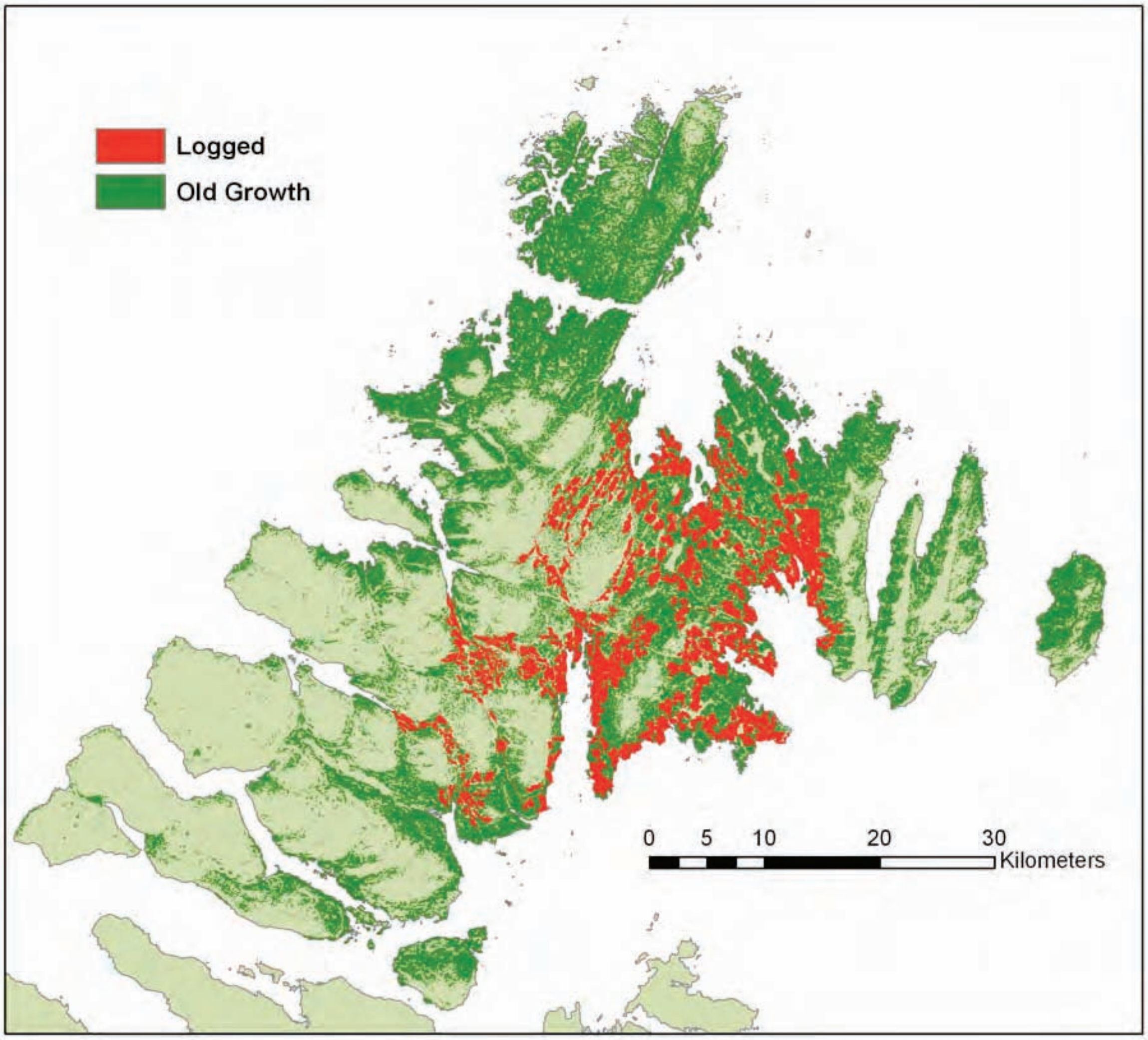


Figure 35. Areas of logged and old growth forest on Afognak and Shuyak Islands, Kodiak Archipelago as of 2000 (M.D. Fleming and P. Spencer, U.S. Geological Survey, unpub. data, 2000).

Table 42. Changes in forest size class distribution of the Chugach National Forest portion of the Kenai Peninsula from 1974–99 (National forest lands only).

[Source: Chugach National Forest GIS corporate database and Kenai Forest Successional Model (DeLapp and others, 2000)]

Structure class	Acreage in 1974	Percent forest acreage in 1974	Acreage in 1999	Percent forest acreage in 1999	Acreage change	Percent change
None	42,233	19.2	39,676	18.0	-2,557	-6
Seed/sapling	14,494	6.6	18,795	8.5	(+) 4,301	(+) 29.7
Pole	111,010	50.5	103,311	47.0	-7,701	-6.9
Young saw	9,254	4.2	8,334	3.8	-920	-9.9
Old saw	42,997	19.5	35,298	16.0	-7,699	-17.9
Standing dead	0	0	14,574	16.6	(+) 14,574	

Table 43. Area of old growth forest and logged land on Shuyak and Afognak Islands as of 1999–2000.

[From M.D. Fleming and P. Spencer, U.S. Geological Survey, unpub. data, 2000]

	Vegetation category	Hectares
Old growth forest	Dense Sitka Spruce forest	92,867
Logged land	Sitka Spruce regeneration	3,149
Logged land	Salmonberry-Devil's Club-Elderberry	10,034
Logged land	Sand and gravel roads	4,165
Logged land	Total logged	17,348

Table 44. Likely changes in the availability of moderate to very high quality nesting habitat (habitat classes 1-3 combined; see Burger, 2002) for Marbled Murrelets in each forest district, and for the entire British Columbia coast.

[Data from Demarchi and Button, 2001a, 2001b. Capability represents the ability of the land base to produce habitat in which murrelets could nest, and suitability represents the current availability of such habitat. In this table the combined percent area within the top three habitat classes is shown, along with the percent change from capability to suitability. Forest districts are ranged from highest to lowest percent capability]

Forest district	Percentage of area in classes 1-3		
	Capability	Suitability	Percent change
Port Alberni[1]	64	34	46.9
Campbell River[1]	61	36	41
Haida Gwaii (Queen Charlotte Islands)	53	45	15.1
Duncan[1]	53	12	77.4
Port McNeil[1]	46	30	34.8
Mid-Coast	29	26	10.3
Sunshine Coast	27	8	70.4
North Coast	26	24	7.7
Squamish	13	7	46.2
Chilliwack	13	6	53.8
Kalum	10	8	20
Cassiar	3	0	100
Chilcotin	3	0	100
Whole BC Coast	26	17	34.6

[1] Forest Districts on Vancouver Island.

Sierra Club of Canada for coastal British Columbia (fig. 36) and Vancouver Island (fig. 37). A high proportion of the "old rainforest" mapped from these satellite images would have been suitable nesting habitat for Marbled Murrelets, because the pre-1999 logging was concentrated in low-elevation, accessible forests with the largest trees. Recent GIS analysis has confirmed that the Sierra Club of Canada's selection of "old rainforest" was a reasonably good measure of likely habitat on southern Vancouver Island (Dr. R. Page, University of Victoria, unpub. data, 2006).

The third attempt to analyze habitat loss was by Holt (2004) for Haida Gwaii (Queen Charlotte Islands), using a refined version of a GIS habitat algorithm originally developed for this archipelago by McLennan and others (2000). This analysis indicated a 42 percent decrease in likely nesting habitat due to industrial logging (fig. 38). This estimate of loss is considerably higher than the 15 percent decrease suggested for this region by Demarchi and Button (see table 44). The discrepancy is in part due to the coarse-scale nature of the Demarchi and Button (2001a, 2001b) analysis. The Holt (2004) estimate, based on a local habitat algorithm and more detailed GIS mapping, is likely closer to reality.

A more detailed analysis of currently available and past decreases of nesting habitat throughout British Columbia by the British Columbia Ministry of Environment is nearing completion (December 2006), but the results are not yet available.

In summary, several independent analyses show significant reductions in nesting habitat for Marbled Murrelet in British Columbia. It is likely that 33–49 percent of habitat area has been lost due to industrial logging. The uncertainty in estimating habitat loss arises primarily from problems in reliably predicting habitat suitability from GIS databases (i.e., satellite imagery, interpretation of aerial photography, or forest cover mapping; see Tripp, 2001; Burger, 2002). Losses have been disproportionately high in regions known to support a high proportion of the British Columbia nesting population (i.e., Vancouver Island, Haida [Queen Charlotte Islands] Gwaii I). Radar studies in British Columbia have consistently shown significant correlations between the areas of available habitat and numbers of murrelets (Burger, 2001a; Burger and others, 2005), suggesting that murrelet populations in British Columbia are likely to have declined by a similar proportion to the habitat reductions.

Fragmentation and Edge Effects

Fragmentation of forested habitat occurs when contiguous areas of forest are reduced to smaller isolated fragments through logging or other forms of habitat modification. The ecological consequences of fragmentation include effects on population viability and size, local or regional extinctions, displacement, fewer nesting attempts, failure to breed, reduced number of nests, lower nest success, increased predation, crowding in remaining patches and overall reduction of adult survival (Andrén, 1995; Raphael and others, 2002b; McShane and others, 2004). The effects of distance to the edge habitats can vary with the structure of the adjacent forested habitat and with distance to human activity (Raphael and others, 2002b), however, higher nest success has been found farther from the forest edge in some studies (Nelson and Hamer, 1995; Manly and Nelson, 1999). In this section, we discuss relevant information on the effects of fragmentation and edge habitats based on recent reviews (Burger, 2002; McShane and others, 2004).

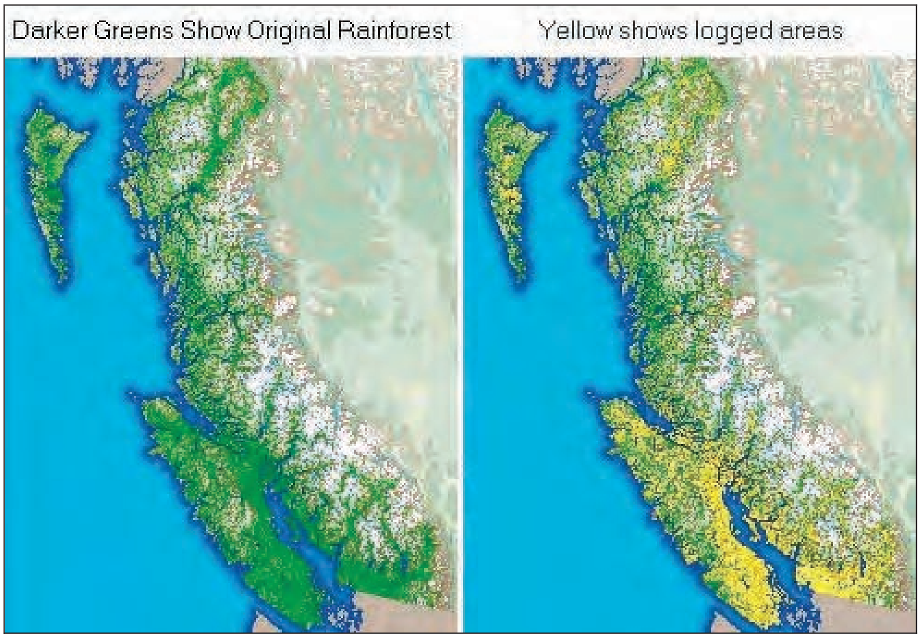


Figure 36. Satellite imagery showing loss of old seral rainforest in coastal British Columbia by 1999 (Sierra Club of Canada).

Figure 37. Satellite imagery showing loss of old seral rainforest on Vancouver Island (Sierra Club of Canada).

Most of the available information on the effects of habitat fragmentation and edge on Marbled Murrelets has come from studies conducted in WOC, and British Columbia (McShane and others, 2004). Therefore, some caution should be taken when applying the results of these studies to tree nesting murrelets in Alaska. Although forest habitat in SEAK may be more similar to British Columbia habitats due to the contiguous nature of the forest in these areas, the forest landscape is very different in south-central Alaska. Here, it has been estimated that only 10 percent of all south-central Alaska timberland were capable of producing large tree stands (van Hees, 2005). In addition, the stands in south-central containing the greatest tree volume generally are found near tidewater along shorelines, at the lowest elevations, or often occur as long narrow stringers between extensive open wetlands or non-forest habitat types. Therefore, the forest habitat in south-central may be naturally fragmented more often.

The effects on murrelets of fragmentation of forests and the creation of artificial forest edges (e.g. at clearcuts and roads) were reviewed (Burger, 2002). Important points are as follows:

- Many nests were near natural and man-made forest edges. It is not clear whether murrelets consistently prefer to nest near edges in all habitats, or whether they are attracted to edge habitat by ease of access.

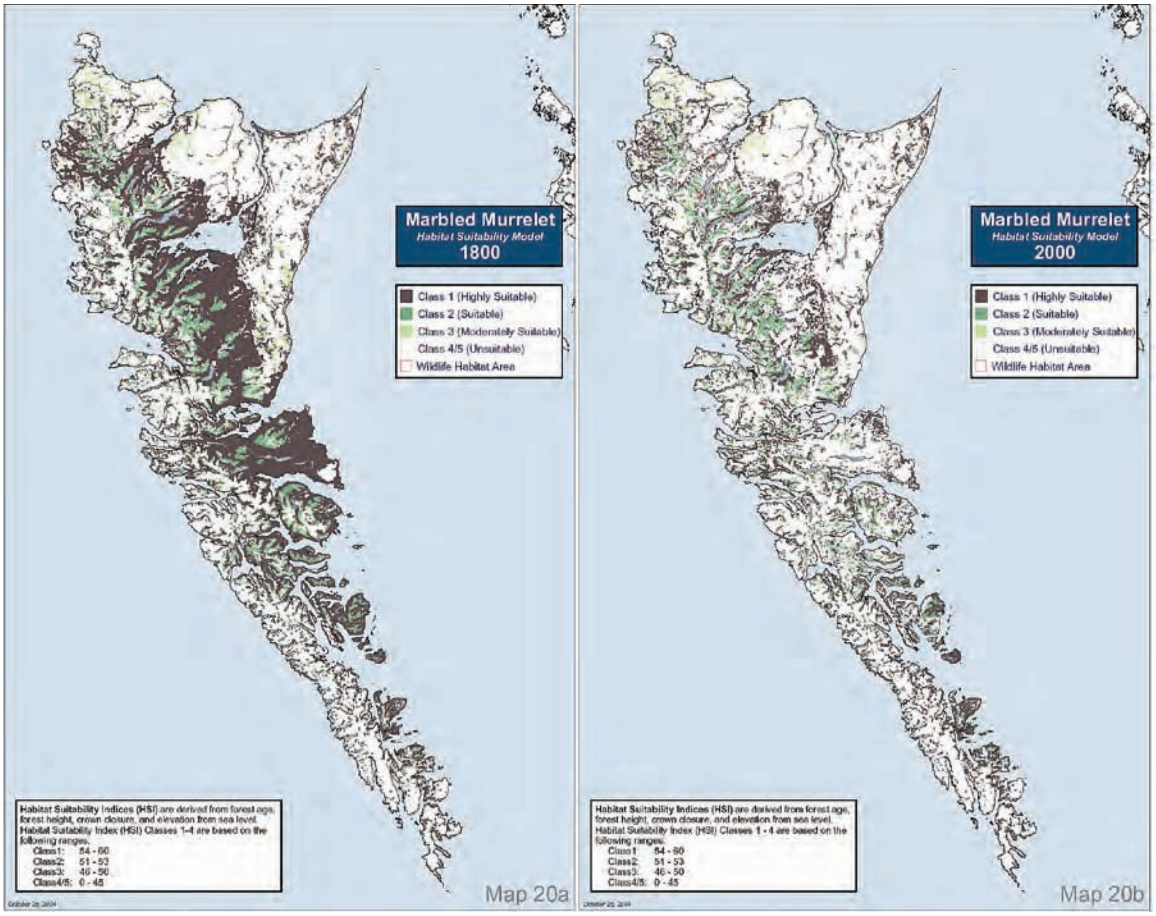


Figure 38. Estimated areas of suitable nesting habitat for Marbled Murrelet on Haida Gwaii (Queen Charlotte Islands), showing the likely changes between 1800 and 2000 (from Holt, 2004). Overall, this analysis showed a 42 percent decrease in suitable habitat by 2000.

- Clearcut logging changes the microclimate near abrupt forest edges. This may affect nest microhabitats (e.g., moss cover on branches), and is currently being studied in British Columbia (D. Lank, Simon Fraser University, oral commun., 2006).
- Edges affect predation risk. Fragmentation and creation of abrupt forest edges is likely to increase predation risk from corvids, especially Steller's Jay. Several studies showed that this jay is most often found close to forest edges bordering clearcuts, and is more abundant in fragmented forest than in contiguous forest. The effects of forest fragmentation on other predators, such as squirrels and raptors, are less obvious or not significant. Murrelets sympatric with Northern Goshawks might suffer greater predation if both species are forced to share remaining patches of old-growth in heavily logged areas. Proximity to human activities, and the age and structure of forests bordering old-growth also affect abundance of predators.
- Nest success relative to forest edges shows inconsistent trends. In a sample of murrelet nests from across the Pacific Northwest, nests within 50 m of a forest edge had lower success than those greater than 50 m from an edge (38 and 55 percent, respectively, n = 29 in each sample), although this was not statistically significant. Successful nests were significantly farther from edges (mean 141 m) than failed nests (mean 56 m). In contrast, analysis of 98 nest sites in Desolation Sound showed that sites adjacent to natural edges appeared to have higher success than those in the forest interior, and there were no significant differences between nest sites adjacent to artificial versus natural edges, and artificial edges versus interior forest. The differences among the studies with regard to edge effects are likely due to variations in predation pressure, edge type, and local habitat availability (Lank and others, 2003). Many of the Desolation Sound nests were in small, high elevation forest patches where there were few predators, whereas many of the other studies

were in low elevation sites with high predation risk. In addition, none of the Desolation Sound sites involved forest edges near human settlements or other sites of human activity likely to attract corvid predators, which are known to affect predation risk for murrelets (Luginbuhl and others, 2001; Raphael and others, 2002b).

- Simple geometric models of the possible effects of edges, relative to forest patch area, suggest that effects restricted to 50 m of artificial edges would affect a progressively larger portion of the forest as patch areas declined below 200 ha. Likely effects on breeding success would increase most rapidly as patch areas declined below about 50 ha. The shape of the forest patch also affects the proportion of edge habitat, and the proportion of the patch bounded by natural edges would modify edge effects.
- The type of edge (natural versus man-made) and the habitat bordering an old-growth patch (e.g., recent clearcut or maturing forest) appear to affect nesting success and predation risk, and need to be considered in planning protected habitats for murrelets. Natural edges (e.g., bordering avalanche chutes or bogs) seem to produce fewer negative effects than hard man-made edges bordering recent clearcuts and roads.

Predation Effects

The life history and behavior of the Marbled Murrelet has been shaped by predation pressure. Despite secretive behaviors and cryptic plumage, the Marbled Murrelet is still highly susceptible to predation, especially during nesting. In this section, we present the potential changes in predation pressure based on an analysis of Christmas Bird Count (CBritish Columbia) data and we briefly discuss what is known about predation on murrelets in Alaska.

To explore potential changes in recent predation pressure on murrelets, we evaluated trends in abundance of seven confirmed or suspected murrelet predators in coastal (<25 km from shoreline) regions of Alaska and British Columbia. Using Christmas Bird Count (CBritish Columbia) data, we calculated the normalized deviation in abundance for each species from 1970 to 2006 (fig. 39) after adjusting for count effort (Sauer and others, 1996).

Over the 36-year period in Southeast Alaska, there was a marked increase in abundance of Bald Eagles (*Haliaeetus leucocephalus*) during the late 1980s (ca. 3-fold increase) but numbers apparently decreased again during the late 1990s (fig. 39). Periodic Bald Eagle surveys conducted during summer by the FWS between 1967 and 2002 revealed a similar marked increase during the late 1980s, but much less of a decline in the 1990s (Jacobson and Hodges, 1999; P. Schempf, U.S. Fish and Wildlife Service, oral commun., 2006). Eagle populations in Prince William Sound during summer also increased by about 60 percent between 1982 and 1995, but declined about one-third by 2005 (P. Schempf, U.S. Fish and Wildlife Service, oral commun., 2006). In SEAK, numbers of Steller's Jays observed on CBritish Columbias about tripled up until about the mid-1990s, but counts returned to average after that time. Sharp-shinned Hawks (*Accipiter striatus*) and Common Raven (*Corvus corax*) counts increased steadily and significantly during the 36 years (fig. 39), with numbers about doubling over that time-span.

In British Columbia, four of seven predators increased significantly in abundance on CBritish Columbias (fig. 39), and some of these changes were quite large: Bald Eagles increased about 8-fold, Peregrine Falcons (*Falco peregrine*) tripled, and populations of Steller's Jays and Common Ravens about doubled. Northwestern Crow (*Corvus caurinus*) populations changed little, while Northern Goshawks (*Accipiter gentilis*) exhibited a significant decrease to about one-half of historic count numbers. These striking changes in British Columbia may be a direct result of forest fragmentation and urban development in the Georgia Basin during the past 30 years.

Studies have clearly shown that an increase in abundance of native predators can cause declines in bird populations (Cote and Sutherland, 1997, Parrish and others, 2001) but it is difficult to quantify those impacts. Experiments in which changes in both vertebrate predator and prey populations are manipulated and monitored in temperate forest systems are rare. Once such study (Marcstrom and others, 1989) showed that an approximate doubling or tripling of the population of predators— i.e., similar to that noted in the CBritish Columbia data— caused a rate of decline in prey as great as that observed for Marbled Murrelets in Alaska and British Columbia (see section, "Population Status and Trends"). Predation pressure can have multiple indirect effects on prey species including alteration of foraging behavior (Sinclair and others, 1998) and timing of breeding (Lima, 1998). An increase in predators can exacerbate existing effects of habitat degradation, fragmentation, and destruction (Cote and Sutherland, 1997). Predation pressure can directly slow or prevent the recovery of a population (Sinclair and others, 1998) and a stable but reduced population increases the risk of extinction through random events (Cote and Sutherland, 1997).

Other evidence suggests predation may be a factor in adult survival. Marbled Murrelets were found to be an important prey item for Northern Goshawks in SEAK (Lewis and others, 2006). Eleven Marbled Murrelets were delivered to six different goshawk nests, based on video recordings at nests, and a total of 31 Marbled Murrelets were delivered to 21 different goshawk nests, based on prey remains and deliveries combined.

Figure 39. Trends in numbers of murrelet predators observed on Christmas Bird Counts in southern coastal British Columbia (Campbell River, Comox, Deep Bay, Duncan, Ladner, Nanaimo, Pender Islands, Squamish, Sunshine Coast, Vancouver, Victoria, White Rock) and in Southeast Alaska (Craig, Glacier Bay, Haines, Juneau, Sitka). Plotted are normalized annual deviations from long-term average (1970–2006) of the total number of birds seen per party-hour of effort.

In an ongoing study in SEAK, 32 Marbled Murrelets were radio-tagged over 3 nights between June 28–29 to June 30–July 1 (Newman and others, 2006). One bird (3 percent) was repeatedly detected on land on Admiralty Island soon after marking and was presumed to have been eaten by a Bald Eagle (*Haliaeetus leucocephalus*)—a species which nested in relatively high densities on the island. Similarly, of 15 Kittlitz's Murrelets radio-tagged in Icy Bay during 2006, 2 were killed by Peregrine Falcons, and 2 were killed by Bald Eagles (M. Kissling, U.S. Fish and Wildlife Service, oral commun., 2005).

A naturalist aboard a 720-feet long cruse ship in Glacier Bay National Park, Bruce Whittington (Victoria Natural History Association, oral commun., 2005) observed a peregrine falcon prey upon at least four seabirds in a few short hours in a single day. These birds appeared to be Kittlitz's Murrelets. He observed the falcon use the various masts and other boat structures as perches and, as the cruise boat approached adult murrelets on the water, the boat would flush these birds from the surface of the water. The falcon was then observed to take off and stoop on the fleeing seabirds, catching them within seconds and returning to the ship to consume them. He also reported talking with other shipboard naturalists and Alaska marine pilots and learned that several had seen Peregrines landing on ships, and some had seen the falcons taking seabirds near the vessels.

Effects of Natural Forest Processes

Disturbances such as disease, insect infestations, and windstorms are natural processes within the old-growth forests used by Marbled Murrelets for nesting in Alaska and British Columbia. These disturbances have the potential to affect the amount and quality of inland habitat for the Marbled Murrelet, particularly at the local and watershed scales. Fire and insect damage are uncommon throughout much of the coastal areas of British Columbia (Burger, 2002). Likewise, the wet climate in SEAK causes the threat of wildfires in coastal forests to be low (Snyder, 2006). A detailed review of disturbance to forest resources is beyond the scope of this report. However, in this section, we briefly review what is known about natural forest processes that may affect Marbled Murrelet nesting habitat.

Long-lived trees become infested with heart-rot fungi, hemlock dwarf mistletoe, and root rot fungi as they age. Heart rot fungi affects nearly one-third the volume of trees in old-growth hemlock-spruce forests, causing them to be undesirable for commercial timber use. Small-scale disturbances such as heart rot fungi such as this may help to maintain the stability of old-growth stands when large old trees collapse and create a canopy opening that allows suppressed trees to grow. Decay fungi are essential for the productive stands in Southeast Alaska where wildfires are rare because they decompose branches, roots, and dead trees (Snyder, 2006).

Between 1987 and 2003, Spruce Beetle infestation affected 429,000 ha on the Kenai Peninsula (U.S. Forest Service, 2004; Boucher and Mead, 2006), and 240,000 ha in the Copper River Basin (Werner and others, 2006). On the Gulf Coast, mixed forests of mountain hemlock and Sitka spruce suffered the lowest regional mortality of spruce (22 percent reduction in Sitka spruce basal area) during the outbreak. Sitka spruce are poor hosts for supporting spruce beetle reproduction (Holsten and Werner, 1990) which likely influenced the low levels of spruce mortality during the outbreak and related vegetation change in this region. Although much of the spruce bark beetle infestations affected the boreal forest of the Kenai lowlands and regions farther inland, infestations also occurred in coastal areas near Kachemak Bay (Werner and others, 2006). Dawn watches and opportunistic observations (K. Kuletz, U.S. Fish and Wildlife Service, oral commun., 1997) indicated that Marbled Murrelets had nested in areas where trees later succumbed to beetle infestations. It is likely murrelet nesting habitat around Kachemak Bay was lost to beetle kill (Kuletz and others, 1997).

In SEAK, wind is an important natural disturbance agent that develops old-growth forest structure (Harris, 1989; Nowacki and Kramer, 1998). The topology in SEAK, including extensive icefields, steep mountains and narrow channels, makes the region particularly susceptible to frequent maritime windstorms. Productive western hemlock and western hemlock – Sitka spruce forests are predisposed to blowdown because of their top-heavy nature (large and tall canopies) and shallow rooting (Harris, 1989). When the trees fall, uprooting and soil churning causes nutrient cycling and increased soil permeability (Snyder, 2006). Although windstorms can have a positive effect on unfragmented habitat by creating openings in the forest canopy, catastrophic storms can cause single-generation stands with uniform canopies to form. Large-scale wind disturbance (affecting 70–400 ha) has been documented on Chichagof, Kuiu, and Prince of Wales Islands (Nowacki and Kramer, 1998). In contrast, Hennon and McClellan (2003) found that frequent, small-scale disturbance helps to shape the forest structure in SEAK, with decay fungi and heart rot contributing the bole wounds and canopy breakage contributing to tree mortality. In some areas, wind disturbance and forest management practices have additive effects on old-growth loss because clearcuts are more prevalent in wind protected areas (Kramer and others, 2001).

The recent die off of Alaska yellow-cedar will likely impact future forest composition in Southeast Alaska and British Columbia forests. Alaska yellow-cedar trees have declined throughout a 200,000 ha band throughout SEAK to at least 150 km south of the Alaska-British Columbia border, and most concentrations of dead trees were found between 300–400 m elevation (Hennon and others, 2005). In SEAK, at least 202,500 ha of yellow cedar decline have been mapped to date (Snyder, 2006). Active tree mortality occurred in many southeast locations in 2005, indicating an intensification of the problem on previously impacted lands. Although still not completely understood, the cause appears to be related to spring freezing injury in open canopy forests characterized by reduced snowpack, and is currently hypothesized to be a result of climate change (Hennon and Shaw, 1994; Snyder, 2006).

General Land Management Practices

The USDA Forest Service manages the majority of old-growth forests in southeast and south-central Alaska, therefore it is important to also consider the relevant land-management practices in these regions. In this section, we will discuss the historical and current land-management issues as it relates to timber harvest and Marbled Murrelet nesting habitat. We then discuss habitat reserves in the context of land management practices. Finally, we consider how nesting habitat for Marbled Murrelets in Alaska and British Columbia could change in the near future.

Industrial-scale logging in the Tongass began in the 1950s when two pulp mills were awarded long-term contracts. Although logging began in the late 1800s in the Chugach, most of the harvest occurred in Prince William Sound and Afognak Island during the late 1960s and 1970s (U.S. Forest Service, 2002b). In 1971, the Alaska Native Claims Settlement Act (ANCSA) transferred about 223,000 ha from the Tongass and 168,500 ha from the Chugach to Alaska Natives. Logging began shortly after the acquisition and although harvest data are limited on Native lands, Knapp (1992) estimated that 3 billion board feet of timber were harvested on native lands in southeast from 1979 to 1989. Today, most timberland on native lands in SEAK has already been harvested (Nie, 2006).

Later, several acts of legislation were put into place to govern the way National forests were managed. The National Forest Management Act of 1976 (NFMA; 16 U.S.C. 1604) required the USFS to develop management plans that provide for the diversity of plant and animal communities within National forests. This requirement was interpreted as "maintaining habitat to support viable and well-distributed populations of existing native and desired nonnative species in the planning area," where viable referred to "the likelihood that habitat conditions will support persistent and well distributed fish and wildlife populations over time" and well distributed referred to the natural distribution and dispersal capabilities of individual species over their current and recent distribution in SEAK (Julin, 1997).

The Alaska National Interest Lands Conservation Act (ANILCA) of 1980 set aside 2.2 million ha of the Tongass and 638,000 ha of the Chugach (of 22.6 million ha in Alaska) as Federally designated wilderness. In addition, ANILCA set a priority for subsistence use, and it created a timber utilization plan that was interpreted for the Tongass as a provision to supply at least 450 MMBF of timber per year regardless of cost or market demand (Nie, 2006). Later, the TTRA of 1990 was put in place to correct the timber supply mandate in ANILCA with new language that required the USFS to meet market demand for timber.

The most recent versions of LMPs were adopted in 2002 and 1997 for the Chugach and Tongass National Forests, respectively. The plans set forest-wide goals and objectives, and management prescriptions, as well as land-use designations provided a framework for reserves, natural setting, and development areas. For the Tongass, roughly 2.4 million ha were classified as wilderness and national monument, 3 million ha were set aside as natural setting, and 1.5 million ha were slated for moderate to intensive development such as timber and mineral production (Nie, 2006).

Allowable sale quantities (ASQ) also were set by the LMPs. For the Chugach, the ASQ was set at 6.3 MMBF for the first 5 years, and 10.6 MMBF for the next 10 years. The TLMP set the ASQ at 267 MMBF. However, the Tongass ASQ was based on an inaccurate interpretation of market demand and in August 2005 the 9th Circuit Court of Appeals ruled the plan arbitrary and capricious because it failed to consider the impacts of logging high-volume old growth forests. A revised version of the TLMP is expected in 2007.

Habitat Reserves

In SEAK, an estimated 57 percent of the Tongass is protected under the TLMP (Szaro and others, 2005). Although the TLMP is currently in a state of flux, as of June 2006, the draft proposed forest plan amendment proposal sets aside 456,948 ha within the old-growth reserve LUD. Another 1.06 million ha are designated under the wilderness LUD. Additionally, 1.25 million ha of land, including most of Admiralty Island and Misty Fjords, are within the Wilderness National Monument LUD where timber harvest is prohibited. About 43 percent of large-tree old growth forests in SEAK are protected under watershed-scale reserves (table 31). However, some areas of southern SEAK have a lower proportion of the large-tree forests protected under watershed-scale reserves. For example, North Prince of Wales, Kupreanof/ Mitkof, and Etolin/ Zarembo Islands have 13.5, 15.1 and 23.6 percent, respectively, designated within watershed-scale reserves (Albert and Schoen, 2006).

In south-central Alaska, about 32 percent of the forest land (525,200 ha) was withdrawn from timber use through statute or administrative regulation (van Hees, 2005; USFS, 2002). Reserved lands include national parks, national forest wilderness study areas, and national wildlife refuges. In addition to lands officially designated as reserved, most of the forest land on the Chugach National Forest (75 percent) is not considered suitable for timber harvest under the revised Chugach LMP (Oja and others, 1999) because it is currently managed for other uses such as research natural areas, recreation areas, beach fringe, riparian areas, scenic viewsheds, and wild and scenic recreational rivers. Campbell and others (2005) estimate that 68 percent of this forest land in the south-central area is reserved from harvest; primarily on the Kenai National Wildlife Refuge, national parks, and the Chugach National Forest. The Chugach LMP manages as much as 75 percent of the forest for activities other than timber harvest with a focus on research, recreation, and wild and scenic rivers. Additionally, land acquisitions in the aftermath of the *Exxon Valdez* oil spill for injured species habitat restoration secured 331,362 acres of forested habitat in the Kodiak, Kenai Peninsula, and Prince William Sound areas (described if further detail in the section, "Ongoing Conservation Efforts").

In British Columbia, as of November 2006, about 590,000 ha of likely nesting habitat is contained within protected areas (estimated areas vary considerably according to which habitat algorithm is used, and the varying reliability of GIS source data and final estimates are not available; T. Chatwin and M. Mather, British Columbia Ministry Environment, oral commun., 2006). This represents between 25 and 30 percent of the estimated total habitat area within British Columbia. Most of the protected areas (about 456,000 ha) fall within large provincial and national parks (e.g., Carmanah-Walbran and Strathcona provincial parks, and Pacific Rim and Gwaii Haanas national park reserves) and areas proposed for protection under the 2006 North Coast and Central Coast land-use decisions (e.g., Kwinamass River, Upper Ecstall, Khutzemateen, and Kitlope watersheds on the North Coast, and Spirit Bear, Koeye, and the Ahnuhati drainage complexes on the Central Coast).

A further 115,000 ha (approximately) of likely habitat is maintained in OGMAs, riparian reserves, and other designations restricting forest development. Finally, about 18,400 ha are maintained within the 124 Marbled Murrelet WHAs.

The current total area of protected habitat constitutes less than one-half of the 70 percent of 2002 habitat areas recommended for long-term maintenance by the CMMRT (Bertram and others, 2003). It is unclear whether the IWMS and other land-use planning exercises currently underway are sufficient to produce the outcomes called for in the CMMRT recovery strategy.

Nesting Habitat Projections

Loss of habitat from timber harvest will continue throughout the forested regions of Alaska and British Columbia. It is likely that in young stands, suitable nesting habitat will not develop for 150 or more years (Albert and Schoen, 2006; U.S. Forest Service, 2002b). For regenerated habitat, a delay in the development and structural complexity required for nesting is expected because development of suitable nesting habitat is dependent on trees attaining a size that supports nest platforms. Furthermore, the use of new habitat may lag for a considerable period because high philopatry leads to low rates of immigration. (McShane and others, 2004). In this section, we will discuss the potential for timber harvest projections using past rates of harvest. These rates should be viewed with caution as they are dependent on continued demand for timber and ever changing land management practices.

Southeast Alaska

Annual harvest rates for Tongass old-growth forests were classified by type of old-growth forest. Large tree productive old growth (POG) had a 0.85 percent, medium tree POG a 0.25 percent, and small tree POG a 0.17 percent average annual rate of decline (Albert and Schoen, 2006). Using these past average rates of decline, over the next 50 years, large-tree POG stands, considered to be the most suitable for Marbled Murrelets, could possibly show an additional 42.5 percent decline with a loss of 92,003 ha from timber harvest activity. Over the next 50 years, medium and small-tree POG stands, could potentially decline by 12.5 percent (186,277 ha) and 8.5 percent (26,605 ha), respectively. These projections depend, of course, on demand for Tongass timber, which, as discussed above, has declined considerably since the late 1990s.

Over the next 50 years, it is unlikely that any significant new old-growth forests will develop in southeast. Forest lands in Tongass National Forest are currently on a 100-year timber rotation, which does not allow enough time for suitable nest tree characteristics to develop (DeGange, 1996). Forests on private lands in Southeast Alaska are being clearcut resulting in increased forest fragmentation and general loss of suitable nesting habitat for Marbled Murrelets.

The location of current Timber Management and Old-growth Reserve LUDs relative to one another in southern SEAK make nesting habitat in this area particularly susceptible to habitat fragmentation. Although old-growth reserves have been designated, the placement of both LUDs creates a patchwork of forested habitat, especially on Prince of Wales Island, where 40 percent of the large-tree old growth has already been harvested (table 40). This may be especially important for Marbled Murrelets given the area of high marine density near the northern end of the island (fig. 32; fig. 40).

South-Central Alaska

Although the land area statistics were not available, as of 2003, 18,933 MMBF of coniferous sawtimber (mature and old-growth trees) in south-central Alaska were available for future logging (van Hees, 2005). From 1988 to 2001, the rate of decline in mature and old-growth conifer forest stands averaged 0.8 percent annually. This 0.8 percent annual rate of decline represented a particularly volatile period of logging, where harvest rates greatly increased from 1993 to 1998 for all landowners. Harvest rates on private lands ranged from 56 to just under 230 million board feet from 1988 to 2001 (table 41). This large annual range in harvest rates makes it very difficult to predict future trends. However, if current average annual harvest rates were to continue, this would mean a 40 percent decline of mature and old-growth conifer forests, through removal of 7,573 million board feet in the next 50 years. Although this is a dramatic rate of decline for mature and old-growth coniferous forests in south-central Alaska, it is uncertain whether past harvest rates would likely continue over the next 50 years.

British Columbia

Logging and to a far lesser extent road-building, urbanization and agriculture will continue to erode nesting habitat in British Columbia. In contrast to the protection murrelets have had in the WOC area under the ESA, evidence of stand occupancy by murrelets does not prevent forest companies from logging old forests in British Columbia, either on private land or on public leased lands. The projected loss of habitat is not known. The rough estimates made in 2000 by M. Eng (British Columbia Ministry of Forests) included a projected 10 percent loss of original habitat between 2000 and 2030 (table 38), but this is not considered reliable. A project is underway to reliably estimate future losses in some

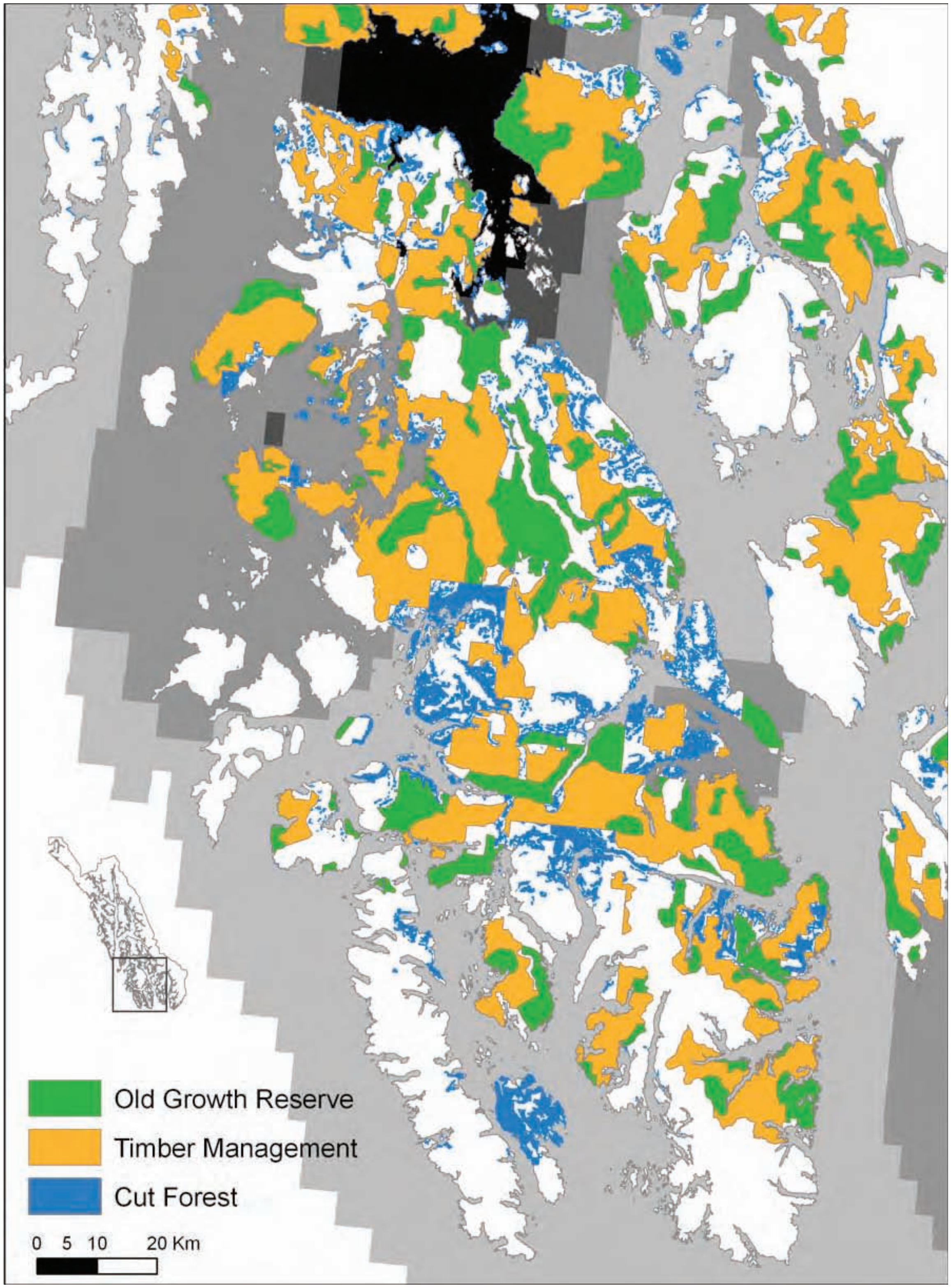


Figure 40. Timber management and old-growth reserve land use designations (LUD) in southern Southeast Alaska relative to density of murrelets at sea. Darker shades of grey represent higher marine density (relative scale)..

forest districts in British Columbia (Malcolm Gray, Integrated Land Management Bureau, British Columbia Ministry of Agriculture and Lands). The management guidelines published by the Canadian Marbled Murrelet Recovery Team (Bertram and others, 2003) recommend habitat loss no greater than 30 percent of the 2002 area by 2032 (approximately three murrelet generations) in order to down-list the murrelet from Threatened to Special Concern in Canada.

Loss of murrelet nesting habitat in the Sunshine Coast Forest District, southern mainland British Columbia was analyzed by Tomlins and Gray (2006). They used a combination of satellite imagery, land-use mapping (Baseline Thematic Mapping), forest inventory mapping (Vegetation Resources Inventory), and topographic data to identify murrelet habitat as defined by CMMRT (Bertram and others, 2003). Their report does not indicate the area of habitat lost prior to 1985, but does show that in that year 57.5 percent of the 764,954 ha of forest was classified as younger than 140 years (i.e., too young to be habitat), at which time likely murrelet habitat comprised 13.7 percent of the total forested area. Much of the forest lost to logging, and to a lesser extent fires and urbanization, prior to 1985 would have been in low-elevation forests with large trees (preferred by both murrelets and the timber industry), so the loss of murrelet habitat prior to 1985 would have been in the order of 50 percent. An earlier analysis using different habitat criteria suggested a 70 percent decline in murrelet habitat in this forest district (Demarchi and Button, 2001a, 2002b; Burger, 2002). Tomlins and Gray (2006) found that by 2005 murrelet habitat had declined by a further 12.0 percent of the 1985 area, and in 2005 likely murrelet habitat made up 12.1 percent of the total forested area (Tomlins and Gray, 2006). The annual rate of habitat loss had slowed considerably after 1993 (average <1 percent per year), as re-growth of forests into the 140+ age class partially balanced the loss of old growth.

Ongoing Conservation Efforts

In this section, we review ongoing efforts within Alaska and British Columbia that relate to conservation of the Marbled Murrelet. The Marbled Murrelet is not listed as Threatened or Endangered in Alaska under the ESA, thus there have been no federal efforts or directives aimed specifically at conservation of this species in Alaska. Region 7 (Alaska) of the USFWS considers Marbled Murrelets a species of management concern because of declining populations (U.S. Fish and Wildlife Service, 2002), but this designation does not confer legal status with respect to funding of studies or requirements related to resource extraction or development. Conservation efforts in Alaska, therefore, are largely indirect and tangential to larger programs with other conservation or management goals, such as management of State lands, management of National forests, oil spill prevention and response, and fisheries management. The only specific Marbled Murrelet conservation action we are aware of was the purchase of forested lands within the area affected by the EVOS to protect nesting habitat of the Marbled Murrelet (discussed in further detail below). In contrast, there are currently a variety of conservation efforts underway in British Columbia. Because the species is listed under both Federal and provincial statutes, there are imminent deadlines for recovery actions that are driving the current level of conservation effort. Although the level of conservation effort in British Columbia is currently greater than in Alaska, the British Columbia provincial government has been criticized for what many consider a slow response. Below, we describe the general protections being afforded in Alaska, and the more specific protections currently being implemented in British Columbia.

Alaska

State of Alaska Efforts

The Marbled Murrelet is currently a ‘featured species’ in the Non-Game Conservation Strategy of the Alaska Department of Fish and Game (2006), which has guided funding of several studies through the Federally funded State Wildlife Grant program. Studies funded by this program have included:

1. Decadal trends and current population estimates for Marbled and Kittlitz’s Murrelets in Kachemak Bay, Alaska, 2004–06;
2. Marbled Murrelet activity patterns in Port Snettisham, SEAK, 2004–06; and
3. Marbled Murrelet nesting habitat, activity patterns, and health in Port Snettisham, SEAK, 2005–07, using radio-telemetry.

These studies represent a recent renewal of study effort on the species in Alaska, after the pulse of EVOSTC-funded studies of Marbled Murrelets tapered off.

Efforts in the Tongass and Chugach National Forests

An interagency conservation assessment for Marbled Murrelets in SEAK (DeGange, 1996) concluded that a conservation strategy for murrelets in the Tongass National Forest should consider a reserve-based approach. DeGange (1996) recommended that old growth forests within 31 mi of the ocean and at lower elevations be targeted for preservation efforts. During the 1990s, the USFS conducted inland ‘dawn watches' to assess murrelet breeding activity in selected timber parcels of the Tongass National Forest (Brown and others, 1999). The USFS also conducted at-sea surveys in selected areas (see appendix M). To date, these data have not been analyzed, and have not been systematically used to manage selection of timber sales.

Farther north, the Chugach National Forest (U.S. Forest Service, 2002a) considered Marbled Murrelets a 'management indicator species' and a 'species of interest' in their Forest Plan revision process. The Chugach National Forest listed the Marbled Murrelet as an indicator species for late forest succession stands in the Kenai Peninsula and Prince William Sound, and for sheltered inshore waters in Prince William Sound and Copper River Delta (U.S. Forest Service, 2002a, tables 3–50 therein). Established standards and guidelines in the Chugach may provide some level of protection from forest management activities.

Oil Spill Prevention and Response

Oil spill prevention and response is organized around a Unified Command structure which includes the State and Federal on-scene coordinators (Berg, 2003). In the event of a spill, an inter-agency spill response team is mobilized to assess and mitigate the spill effects, including representatives from the USFWS as the trust agency for migratory birds. The USFWS may deploy damage assessment teams to monitor bird mortality and risk, and recommend ways to minimize impacts. Details on the organization and implementation of spill response relative to seabirds are available in Berg (2003). In Alaska, most spills have not been monitored for bird mortality beyond the immediate spill zone. Two citizen's groups active in monitoring oil spill prevention and response in areas with high murrelet populations are the Cook Inlet Citizens Advisory Group and the Prince William Sound Citizens Advisory Council.

Fisheries and Marine Habitat Conservation

There are no Federal or State directives to conserve Marbled Murrelets or their foraging habitats at-sea in Alaska. However, restriction of some fishing activities in designated areas may benefit conservation of murrelets indirectly. Presidential Executive Order 13158 (May 2000) directed Federal agencies to work with States and other entities to develop a National system of Marine Protected Areas (MPAs). A National MPA program was reaffirmed by President Bush in 2001. A similar program has been mandated from the Canadian Federal government for British Columbia under the 1997 Oceans Act. In November 2001, an ADFG Task Force was appointed to develop a strategy for developing a MPA program for the State. The Task Force prepared a report to provide background on MPAs, outline the strategy, and guide public input (Woodby and others, 2002). The report focuses on fisheries, but recognizes protection of other marine life, including seabirds. The task force was disbanded in 2003, and there is no further record of actions by the State on MPAs.

Woodby and others (2002) noted that, "Nationally, 17 pieces of federal legislation provide a basis for establishing and managing MPAs; these include: the Magnuson-Stevens Fishery Conservation and Management Act, ESA, Migratory Bird Conservation Act, Fish and Wildlife Act (1956), and the Alaska National Interest Lands Conservation Act." Alaska currently has semi- or protected areas that are considered MPAs under the State's definition, which differs from the national definition in that it may include fishing with some temporal or gear closures, or single-species closures. These protective measures were established primarily to reduce bycatch of non-target species and to protect fish habitats (Woodby and others, 2002). Areas with limited or no fishing include large offshore areas closed to trawling in the eastern Bering Sea shelf, in eastern Gulf of Alaska, and in state waters from Kodiak westward to Bristol Bay (Witherell and others, 2000).

In waters 3–200 mi offshore (the Exclusive Economic Zone), NOAA-Fisheries has jurisdiction. Waters managed by the State extend from shore to 3 nmi offshore. Woodby and others (2002) listed more than 200 individual MPAs in 18 categories in State and Federal waters in Alaska. These included "State critical habitat areas, State game refuges, State and Federal fisheries management zones, wildlife sanctuaries and refuges, and Alaska Coastal Zone Management Plan areas." Examples of protected areas include no-transit zones around Steller's sea lion (*Eumetopias jubatus*) rookeries (primarily in the Aleutian Islands and a few areas in the Kodiak Archipelago) and the Walrus Island State Game Sanctuary (in Bristol Bay), and no-trawl zones in the Aleutian Islands Habitat Conservation Area (71 FR 36694; June 28, 2006). However, many other "MPA's" listed in the report (e.g., the Kachemak Bay National Estuarine Research Reserve) do not carry any restrictions.

Exxon Valdez Oil Spill Trustee Council

The EVOSTC was established with oil spill settlement funds, and between 1990 and 1999, the Trustees funded nearly annual studies on either nesting habitat or foraging requirements of Marbled Murrelets. The EVOSTC funded 11 years of boat-based surveys of Prince William Sound through 2007 (9 July surveys, 1989–2005), which provided data on population trends in the Sound. Through 2006, the EVOSTC has funded nearly $3.9 million in research studies pertaining or relevant to Marbled Murrelets.

The EVOSTC also purchased lands within the spill area for habitat protection with the explicit purpose of promoting the restoration of injured species, including Marbled Murrelets. Most lands were purchased for their ability to promote the restoration of one or more injured species. Since 1993, the EVOSTC expended $375 million and purchased 643,835 acres in both a large parcel (>1,000 acres) and small parcel program. Most large parcels acquired by the EVOSTC were purchased from Alaska Native Corporations. Many of these were large blocks of land including substantial timber holdings. Large parcels purchased with high value as Marbled Murrelet nesting habitat included:

- 23,800 acres in Kachemak Bay State Park;
- 32,537 acres in Kenai Fjords National Park and adjacent islands within the Alaska Maritime National Wildlife Refuge;
- 26,665 acres on Shuyak Island, at the northern tip of the Kodiak archipelago;
- 41,549 acres of mature spruce forest in the Kodiak archipelago (now Afognak Island State Park); and
- 206,811 acres of land, and conservation and timber easements in Prince William Sound, including parcels on Bligh Island, Two Moon Bay, Eshamy Bay, Jackpot Bay, Port Gravina, Sheep Bay, and Windy Bay.

Although these acreages are small relative to the overall size of the region, because the lands included forest that could have been and perhaps were likely to have been logged, the transfer of the lands to public, protected status, is important to conservation of the Marbled Murrelets in the spill region.

Non-Governmental Entities

In 2001, partly in response to increased vessel traffic in Prince William Sound, the National Wildlife Federation sponsored a workshop on Biological Hot Spots in Prince William Sound. Collaborators included the USFWS, National Audubon Society, and the University of Alaska Marine Advisory Program. Specific areas of importance to Marbled Murrelets and their prey, as well as to other marine wildlife and habitats were identified in the workshop report (Adams and others, 2002).

British Columbia

As noted above, because the Marbled Murrelet is considered a threatened species in Canada and British Columbia, there is currently a concerted effort ongoing in British Columbia to plan for the species' recovery. Here, we provide a detailed review of these efforts.

Recovery Planning

The updated Canadian Marbled Murrelet Recovery Strategy has been drafted but is under review and should be released about June 2007. This document draws heavily on a Conservation Assessment undertaken by the CMMRT, the Federal government (Environment Canada), and the provincial government (British Columbia Ministries of Environment and Forestry), with the collaboration of universities, the forest industry, First Nations, and NGOs. The assessment produced three products: a biological review (Burger, 2002), management guidelines (Bertram and others, 2003), and risk modelling (Steventon and others, 2003). The final Recovery Strategy is expected to draw heavily from the management guidelines (Bertram and others, 2003). This document established two major goals for the recovery of Marbled Murrelets in Canada:

1. To down-list the species from Threatened to Special Concern. This would be possible by limiting the decline of the British Columbia population and its nesting habitat to less than 30 percent over three generations (30 years), during 2002 to 2032. The CMMRT recognized that the population in 2002 was likely reduced from historical levels, but believed that dealing with future declines was more realistic than trying to estimate and manage for past declines across the entire province; and
2. To ensure that the species would have a low risk of reduced viability after 2032. This might be achieved by maintaining sufficient suitable nesting habitat and reducing other threats at-sea and on land. This goal would allow the species to be considered for down-listing to Special Concern and eventually de-listed.

Marbled Murrelet recovery actions are aimed at ensuring that there will be less than a 30-percent loss in population and nesting habitat between 2002–32, and that human-induced population decline will cease after 2032. The guidelines (Bertram and others, 2003) further established seven principles for formulating the Canadian Recovery Strategy:

1. The initial goal of the Recovery Strategy will be to down-list the species from Threatened to Special Concern, using COSEWIC criteria for declining species. To down-list the species the immediate goal of the Recovery Strategy is to ensure that the population and suitable nesting habitat will not decline by more than 30 percent between 2002 and 2032;
2. The long-term goal of the Recovery Strategy will be to maintain the provincial population at a level which is sufficient to de-list the species using COSEWIC criteria. A key objective is to provide sufficient Marbled Murrelet nesting habitat at the end of this 30-year period, which

if maintained in the long term, will likely allow the provincial population to stabilize, within the accepted range of population fluctuations. If this habitat target is achieved, the habitat is maintained, and the population stabilized, the species may be de-listed;

3. The present range of Marbled Murrelets in British Columbia should be maintained. A basic principle in wildlife management for the responsible Canadian provincial and Federal agencies is to maintain the geographic range of a species. The historical breeding range of Marbled Murrelets appeared to cover most of the coast of British Columbia, although abundance varied widely across this range. Murrelets are still found through most of this range and management objectives should include efforts to maintain this distribution. The extirpation of a local population should be considered a serious loss. If possible, efforts should be made to restore the Marbled Murrelet to parts of its historical range from which most of the nesting habitat has disappeared (e.g., parts of eastern Vancouver Island and the southern mainland). Management should ensure sufficient habitat to maintain a viable population of Marbled Murrelets in each conservation region, distributed widely across the region in those areas capable of supporting the species. Maintaining a widespread range of the British Columbia population also is likely to reduce any negative effects that may result from global climate change;

4. Marbled Murrelets should remain a relatively abundant bird in British Columbia. The Marbled Murrelet was listed as Threatened by COSEWIC because of perceived declines in the population. Numerical abundance does not guarantee long-term survival of a species that is facing serious declines (Caughley, 1994; Pulliam and Dunning, 1994). The intention of the Recovery Strategy and management recommendations is to maintain the species as one of the widespread and numerically common seabird species in British Columbia;

5. Conservation goals should be aimed at acceptable, not minimal standards. The goal of the Recovery Strategy, management recommendations, and operational tactics is to prevent unacceptable population decline (>30 percent over the next 30 years), and to maintain the geographic range of the species in British Columbia. This will require maintenance of populations and habitat that are more than the minimum needed to prevent extirpation. This also is an application of the precautionary principle (Kriebel and others, 2001), which is particularly relevant to situations where the population size, population trends, habitat use, and population dynamics are poorly known, as in many areas of the murrelet's range in British Columbia;

6. Marbled Murrelets should be managed according to coast-wide and regional targets and habitat criteria. The Recovery Team identified six conservation regions (See fig. 7, section, "Population Status and Trends for British Columbia"), which approximately match both the variation in Marbled Murrelet habitat use and the British Columbia forest districts. Where possible, the team recommended province-wide standards and habitat criteria, but regionally specific habitat criteria should be applied where applicable; and

7. Uncertainties should be addressed by applying an adaptive management approach. The CMMRT lacked reliable knowledge of many aspects of Marbled Murrelet biology and responses to land use. This prevented them from confidently prescribing nesting habitat targets and characteristics that would sustain the species in British Columbia, and it made projections of future populations uncertain. Because logging and other human impacts on habitats would continue, however, the team could not wait until better information became available through research and inventories. Adaptive management will therefore be an important tool for improving habitat management as the recovery strategy and government conservation policies are implemented. To take full advantage of the adaptive management process, it must be implemented in a structured, systematic way with attention to scientific principles of project design and analysis (Holling, 1978; Walters, 1986; Walters and Holling, 1990; Nyberg, 1998). Adaptive management should be applied with caution, taking care not to preclude future opportunities for maintaining suitable habitat for murrelets.

The guidelines (Bertram and others, 2003) identify operational objectives to meet the strategic plan. The primary management goals are to identify and maintain sufficient nesting habitat to maintain the target populations in each region. Ideally the sequence of management steps include: identifying suitable nesting habitat in each region; mapping and estimating the areas of suitable habitat; tracking past and projected changes in the area and quality of nesting habitat; and monitoring selected populations using radar. General guidelines are provided for these steps, with the details to be spelled-out in more detail by Recovery Action Plans.

Under the Canadian SARA, the Recovery Strategy sets out the overall strategy for recovering a listed species, but one or more Recovery Action Plans lay out the details, responsibilities, and timetable for recovery actions. Three Action Plans are envisaged to support the Marbled Murrelet Recovery Strategy:

- Population Status and Trend Monitoring (by November 2006 an implementation group was being assembled but the plan is not drafted);

- Nesting Habitat Retention (an implementation group has met regularly since September 2004; the draft action plan was completed May 2006 and is currently in review by the Canadian and British Columbia governments); and
- Marine and Mortality Issues (by November 2006 an implementation group was being assembled but the plan is not drafted).

The Nesting Habitat Retention Action Plan was perceived as the most urgent. It will establish regional objectives for habitat retention in old forest, identify who will be responsible for selecting and maintaining habitat, and establish a timetable for these activities. This action plan also will identify and map the current distribution of likely suitable habitat using a range of algorithms applied to forest cover, satellite imagery and other Geographic Information Systems (GIS) data layers.

Under SARA, the recovery process also requires a socio-economic assessment of the costs and benefits of the recovery actions. A Federal-provincial working group is currently analyzing socio-economic data related to Marbled Murrelet recovery, but information on its deliberations is not available yet.

Provincial Recovery Actions

Although protection of the birds and their active nest sites is a federal responsibility, the great majority (about 80 percent) of the forest nesting habitat in British Columbia falls under provincial jurisdiction. The Marbled Murrelet is a Red-listed Species in British Columbia and also is an Identified Species under the British Columbia FRPA. Measures for protecting murrelets and other identified species are provided in the Identified Wildlife Management Strategy (2004). The province and Federal government are engaged in bilateral talks designed to ensure that IWMS and other provincial management approaches are consistent with SARA provisions. The IWMS measures are meant to be the fine-filter approach to maintaining areas of nesting habitat, with strategic decisions covering larger tracts of land being made by other means (see below). In practice, the IWMS measures usually apply to forest lands designated for timber extraction. Identified species are managed through the establishment of WHAs and other management practices specified in strategic or landscape level plans. The application of the IWMS is greatly hampered by the limit placed by the British Columbia government on timber impacts: only 1 percent of mature forest, by area, of each forest district is allocated from the timber harvesting land base to cover all species of Identified Wildlife combined (currently 85 species). Areas of suitable nesting habitats outside the timber harvesting land base (sometimes known as the noncontributing land base) can be used for murrelet WHAs, but these tend to be in high elevation or steep areas where forestry operations are difficult. They often do not offer suitable habitat for nesting murrelets, but fortunately, in some cases, they do.

The IWMS measures for Marbled Murrelets, based on the 2001–03 Conservation Assessment (see above), came into effect in 2004 (Identified Wildlife Management Strategy, 2004). Key goals are to identify appropriate nesting habitat and provide guidance on the size, location, and management of WHAs. Using parameters commonly used for landscape-level forestry mapping (e.g., stand age, tree height, canopy closure, distance from the sea) habitats can be classified as Most, Moderately, or Least likely to provide suitable nesting habitat to murrelets (details in Identified Wildlife Management Strategy, 2004). The measures recommend establishing WHAs in the “Most Likely” habitats. Habitat rated as “Moderately Likely” may be considered for WHAs, but require confirmation as suitable habitat using approved methods of ground or helicopter surveys. Areas rated as “Least Likely” should only be considered if there is evidence of nesting (nests, eggshells, or occupied detections), or strong evidence that the particular site provides the necessary attributes and is within commuting distance of foraging areas at sea. Other details are provided to help identify suitable habitat and the appropriate patch sizes (Identified Wildlife Management Strategy, 2004).

Marbled Murrelet nesting habitat also may be included in forests protected as old growth management areas, riparian habitat protected for stream and river integrity, and ungulate winter ranges. Small but strategically important areas of nesting habitat are currently maintained within the water catchment drainages of the cities of Vancouver and Victoria.

Much larger areas of habitat have been protected in provincial parks under the 1996 British Columbia Parks Act and the 2000 Protected Areas of British Columbia Act. These include extensive tracts in Carmanah-Walbran Provincial and Strathcona parks, and some watersheds around Clayoquot Sound. Other processes currently in progress which should protect some large areas of nesting habitat are the regional LRMPs and Land Use Plans (LUPs) directed by the Ministry of Agriculture and Lands. The LRMPs for the North Coast and Central Coast have been concluded, and proposals announced in February 2006 include large areas of protected areas and no-timber-harvesting zones that are anticipated to considerably increase the areas of suitable nesting habitat protected in those regions. The Haida Gwaii LUP is not complete and it is not possible to anticipate the level of protection of Marbled Murrelet nesting habitat. The Vancouver Island LUP includes provisions that extend old growth retention targets in the timber harvesting land base in specific areas to meet Marbled Murrelet needs.

Criticism has been directed at the British Columbia provincial government stating concern for the progress in implementing conservation measures for murrelet nesting habitat. Dechesne-Mansiere (2004) pointed out that since the Marbled Murrelet was listed as Threatened in 1990, about 400,000 ha of possible habitat had been logged (this represents habitat likely to be used by about 24,000 murrelets, taking the mean density from radar surveys in British Columbia;

0.06 bird per ha; Burger and others, 2004a). The pace of implementing the IWMS guidelines has been criticized by the British Columbia Forest Practices Board (FPB), an arms-length board that reviews the application of forest policies in British Columbia. As of November 2006, about 18,000 ha (about 2 percent of the nesting habitat available in 2002) had been protected as WHAs under the IWMS process. In 2003–05, the FPB released five reports on Marbled Murrelets[3], which criticized the lack of direction and action in protecting Marbled Murrelet nesting habitat (e.g., Forest Practices Board, 2004, 2005). In particular, in March 2005, the Board issued a strongly worded condemnation of the provincial government, stating that "there is a systemic failure in government policy to protect threatened species such as Marbled Murrelets on crown forest lands" (Forest Practices Board, 2005).

Other Efforts to Maintain Habitat in British Columbia

Several forest certification programs are applicable in coastal British Columbia that provide opportunities for forest companies to establish protected habitat for murrelets. These include:

- Canadian Standards Association (CSA) Z809;
- International Organization for Standardization (ISO) 14001;
- Forest Stewardship Council (FSC);
- Programme for Endorsement of Certification Schemes (PEFC); and
- Sustainable Forest Initiative (SFI).

Forest certification programs require forest companies to demonstrate their ability to meet environmental standards. Stewardship and certification plans can apply to both private and public (leased) forest lands. The most rigorous effort to date to meet certification standards and follow Burger's (2004) measures for Marbled Murrelets was by Canadian Forest Products, Ltd. (Canfor) for the Nimpkish Valley (Tree Farm Licence [TFL] 37) on Vancouver Island (Deal and Harper, 2004). Canfor used a combination of radar surveys, audio-visual surveys, low-level helicopter assessments, vegetation sampling, and GIS analysis to identify and map likely nesting habitat within their leased lands. They proposed the conservation of a total of 21,566 ha of potential nesting habitat, which included 50 percent of the area in the top four habitat quality ranks (Deal and Harper, 2004). No other forest company seems to have matched the efforts made by Canfor in identifying and meeting the needs of Marbled Murrelets in coastal British Columbia. Certainly no other company has made their intentions known so publicly and with so much scientific evidence. Canfor was recently purchased by Western Forest Products and it is not clear whether the Deal and Harper (2004) proposals for TFL 37 will be fully implemented by the new lessees.

Discussion

In this section, we first discuss factors relevant to the consideration of Distinct Population Segments (DPSs) (*sensu* ESA) of the Marbled Murrelet. The USFWS specifically asked us to include descriptions of populations that may qualify as DPSs. Although we do not make any recommendations in that regard, we did uncover information that might be relevant to the definition of DPSs for the Marbled Murrelet. The main purpose of this document is to assess the status of the Marbled Murrelet in Alaska and British Columbia. In the second half of this discussion, we return to the topic of population trends and explore some possible explanations for recent and widespread declines observed in Alaska and British Columbia.

Factors Relevant to Definition of Distinct Population Segments

This status review was prepared for the U.S. Fish and Wildlife Service to provide updated information on the Marbled Murrelet within the context of the species' listing under the Endangered Species Act. For vertebrate species, the USFWS must consider for listing any Distinct Population Segment, if information is sufficient to indicate such action may be warranted (FR 61, No. 26, February 7, 1996). The USFWS uses two elements to assess whether a population under consideration for listing may be recognized as a DPS: (1) the population segment's discreteness from the remainder of the species to which it belongs; and (2) the biological significance of the population segment to the species. A population segment may be considered discrete if: (1) it is markedly separated from other populations of the same taxon due to physical, physiological, ecological or behavioral factors (e.g., quantitative measures of genetic or morphological discontinuity may provide evidence of this separation); or, (2) it is delimited by International boundaries within which significant differences in control, exploitation, management of habitat, conservation status, or regulatory mechanisms exist. If the USFWS determines that a population is discrete,

---

[3] Available at http://www.fpb.gov.bc.ca/.

its biological and ecological significance must then be considered. Here, we briefly discuss the factors that may be relevant to definition of Discrete Population Segments for the Marbled Murrelet, based on our review of current knowledge for Alaska and British Columbia as compiled in this report.

Population Genetics

Several previous studies of Marbled Murrelet genetics (Congdon and others, 2000; Friesen and Piatt, 2003; Friesen and others, 1997, 2005; Pitocchelli and others, 1995), and the new findings presented in this report have found structure within Marbled Murrelet populations across their range. Using a variety of analytical techniques, Marbled Murrelets in the central and western Aleutian Islands and in central California have been found to be differentiated from each other and from Marbled Murrelets in the middle portion of their range, i.e., from northern California to the eastern Aleutian Islands. Marbled Murrelets between northern California and the eastern Aleutians, including those in Oregon, Washington, and British Columbia, do not appear to be genetically differentiated. Gene flow among these three regions occurs but is extremely low. These results are superficially incongruous with those of Peery and others (2006) who suggest that Marbled Murrelets in central California are a sink population that is augmented by individuals immigrating from populations to the north. However, the genetic identity of the central California population could be maintained if interbreeding is limited, if immigrants are selected against, or if migration into central California is a recent response to anthropogenic disturbance.

Distribution

The at-sea distribution of Marbled Murrelets during the breeding season approximates its onshore nesting distribution at the “landscape” scale. The nesting distribution of the Marbled Murrelet is considered to be relatively continuous from the western Aleutian Islands to northern California although many small to large habitat discontinuities exist throughout the species range as a result of island passes (e.g., in the Aleutian Islands), and other large water bodies, and breaks in nesting habitat in old-growth forests from logging and natural factors. From a DPS perspective, the one notable gap in its breeding distribution that we are aware of is the 450 km of coastline in California, between Humboldt County (northern California) and San Mateo County (central California) (Nelson 1997, McShane and others 2004). However, within this gap, small numbers of Marbled Murrelets have recently been found breeding in small patches of forested habitat in Mendocino County (McShane and others, 2004). This gap in nesting distribution separates the genetically differentiated murrelet population in central California from the middle population that is distributed from northern California to the eastern Aleutians. On the western end of the species range, sample collections from the Aleutians used in the genetic analysis were made at only three sites – Attu, Adak, and Unalaska (fig. 4), thus the geographic demarcation between Marbled Murrelets in the central and western Aleutian Islands with those from the middle population is imprecise.

Morphological, Behavioral, and Ecological Factors

Marbled Murrelets also are unique among the alcids in that breeding birds nest both on the ground and in trees. Where suitable trees and forests exist, Marbled Murrelets nest primarily in trees, but a small percentage also may breed on the ground. In western Alaska, where suitable trees and forests are lacking, Marbled Murrelets must nest on the ground. What controls nest site selection and preference is unknown. Nest site selection could simply reflect availability, it could be learned (i.e., birds nest in habitat similar to where they hatched) or it could be controlled by a functional gene.

Little morphological or genetic variation has been noted between presumed tree- and ground-nesting populations of Marbled Murrelets (Pitocchelli and others, 1995; Friesen and others, this report). Of 23 measurements of external and skeletal components, five differed significantly between presumed tree- and ground-nesting Marbled Murrelets. Adaptations for arboreal life in terrestrial birds often includes divergence in leg morphology, but of those characters measured, only the length of the tarsometatarsus differed significantly between ground- and tree-nesting murrelets (Pitocchelli and others,1995). Perhaps more morphological differences have not been observed between ground and tree-nesting murrelets because of over-riding adaptation to the marine environment where birds spend most of their time. If behavioral differences were important, the most important point of demarcation would likely be Kodiak Island and the Alaska Peninsula where the western boundary of the Gulf of Alaska is found and where Marbled Murrelets must therefore nest on the ground.

International Boundary

The USFWS is required to conduct a 5-year review of all species listed under the ESA to assess the best available information on how the species has fared since its original listing or previous review, and consider whether it is listed appropriately. The USFWS completed a 5-year review of the listed population of Marbled Murrelet in WOC in 2004 (U.S. Fish and Wildlife Service, 2004), and concluded that the WOC population does not satisfy the discreteness criteria for designation as a DPS under the USFWS’s 1996 DPS Policy. Specifically, the USFWS concluded that there was no marked separation of physical, physiological, ecological or behavioral differences of murrelets at the border with Canada, and that there were no differences in control of exploitation, management of habitat, conservation status, or regulatory mechanisms across the International border that are significant in light of the ESA.

In 2004, when the USFWS decided that the WOC population of Marble Murrelet did not satisfy the criteria for designation as a DPS, Canada's Species at Risk Act (SARA) had only recently passed. Like the ESA, SARA may effectively control the illegal exploitation of Marbled Murrelets from various forms of direct take. From the perspective of conservation of nesting habitat, it is difficult to make direct comparisons of the benefits to Marbled Murrelets between the two laws. The details of how SARA will be applied to Marbled Murrelets have not yet been finalized. The Canadian Marbled Murrelet Recovery Team drafted a Recovery Strategy, but this strategy is still under review by Federal and Provincial governments. At this time, only one of three Recovery Action Plans has been submitted for government review. The Recovery Strategy and its associated Recovery Action Plans will not likely be in place before 2008.

Unavailable at the time the USFWS completed its 5-year review of the Marbled Murrelet in WOC was a report by the Forest Practices Board (FPB) in British Columbia that was critical of the province's implementation of the existing forest practices regime for conservation of forest nesting habitat of this species (Forest Practices Board 2004). The Forest Practices Board is an independent, public watchdog that conducts audits and investigations on how well industry and the government are meeting the intent of British Columbia's forest practices legislation. The FPB concluded that conservation of Marbled Murrelet habitat under the Forest and Range Practices Act is limited and very slow. The FPB was particularly concerned that while the process of developing a conservation strategy for Marbled Murrelets is still ongoing, logging projects continue to be approved, thereby eliminating future options for murrelet habitat conservation, especially on the southern British Columbia coast where conservation is most needed. The FPB also was critical of British Columbia's implementation of the Identified Wildlife Management Strategy under the FRPA. Under this strategy, British Columbia arbitrarily restricted protection of forest habitat for all IWMS species to less than 1 percent of the mature timber land base (in which most murrelet nesting habitat occurs). In the FPB's view, this prevents conservation of the most important murrelet nesting habitat and deflects conservation to less suitable habitat.

In summary, information on population genetics and distribution may be the most important factors to consider if the USFWS decides to re-examine the issue of DPSs for the Marbled Murrelets. In contrast, existing information on morphology, behavior and ecology appears less instructive although the tree line on Kodiak Island and the Alaska Peninsula provides an approximate boundary between primarily tree-nesting murrelets and ground-nesting murrelets. The USFWS also may wish to examine new information on forest habitat management in British Columbia and in particular the efficacy of existing laws and regulations in promoting the conservation of Marbled Murrelet nesting habitat there.

Population Status and Trends in Alaska and British Columbia

As reported earlier, populations of Marbled Murrelets in Alaska may have declined by approximately 70 percent during the past few decades. Our analyses found that Marbled Murrelet populations had declined at 5 of 8 trend sites in Alaska at rates of -5.4 to -12.7 percent per year. We also found statistically significant declining population trends for Marbled Murrelets at all 8 trend sites in British Columbia with rates ranging from -5.8 to -31 percent per year.

The apparent change in population size and rates of decline reported here for murrelets are extraordinary and we therefore put them to the "straight-face test" by asking and answering four questions: (1) Are declines of this magnitude even possible?, (2) Is it possible that survey methods or statistics have led us to erroneous measures of trend?, (3) Are there precedents for changes of this magnitude in other wildlife populations?, and, (4) Is there a plausible explanation for these findings? The answer to the first three questions is "yes", and the last is "yes, but not a single explanation." We examine each of these questions below.

Are Declines of This Magnitude Even Possible?

Yes. Even under natural conditions where environmental conditions vary in "normal" fashion (i.e., without recurring extraordinary events such as El Niño), members of the seabird family Alcidae may exhibit a wide range of trends in population size, both increasing and decreasing (Hudson, 1985). Trends of more than about ±10 percent are uncommon, however, and may result from the addition of unnatural mortality factors. For a variety of seabirds in Alaska (petrels, gulls, auklets, murres, puffins, etc) where significant trends could be measured at colonies located around the State during the past 30 years (40 of 92 possible species-colony sites, Dragoo and others, 2006), 19 were increasing at an average rate of 7.3 percent per year (± 6.7 s.d., range 0.9–29 percent) while 21 were decreasing at an average rate of 6.8 percent per year (± 4.9 s.d., range 1.7–21 percent). The remainder of species-colony sites (52) had either stable populations or counts were insufficient to measure trend. Thus, the observed rates of decline for Marbled Murrelets are not out of line with the range observed in other seabirds in Alaska. The difference, of course, is that murrelets are declining throughout their range and not just at a few sites here and there.

When we used a reasonable suite of population parameter values to model population dynamics for Marbled Murrelets in Alaska (see section, "Demographics and Population Dynamics"), and introduced random variability in the parameters, we found that it was possible to observe trends of more than ±20–30 percent per year over 20- or 30-year periods of study. However, the chances of observing this magnitude of change "naturally" are low. Indeed, such rates are rarely observed in field studies of alcids unless anthropogenic factors strongly influence survival or productivity (e.g., sustained adult mortality from net bycatch, collapse of a prey stock from overfishing, or recovery of a population after removal of an introduced predator). All trends we observed were less than ±15 percent where we had reasonably long time series. Therefore, we conclude that the trends observed in Alaska and British Columbia are possible from random variability alone, but more likely influenced to some degree by unnatural (anthropogenic) factors.

Is It Possible That the Methods or Statistics Have Led Us to Erroneous Measures of Trend?

Yes. Data were obtained from a variety of surveys and investigators and it is important to recognize that few of these surveys were initiated to monitor populations of Marbled Murrelets specifically, and none were designed with both statistics and murrelet biology in mind. Indeed, the use of at-sea surveys to monitor populations has never been validated. Most population monitoring for seabirds takes place at colonies— where birds return each year to breed and may therefore be censused with relative ease. At Alaska-wide spatial scales, at-sea counts are correlated with colony counts for several seabird species (Piatt and Ford, 1993). At the scale of bays, fjords and sounds, however, we have little independent corroboration of at-sea census data. In Prince William Sound, marine bird surveys that we used here to assess murrelet trends also showed that populations of black-legged kittiwakes (*Rissa tridactyla*) were highly variable and declining through the 1990s (Irons and others, 2000) although numbers have recently returned to 1989 levels (McKnight, 2005). In contrast, counts of kittiwakes at breeding colonies within Prince William Sound reveal much smaller year-to-year variation, local upward and downward trends, but no long-term trend for the sound as a whole (Suryan and Irons, 2001). Irons and others (2000) attribute the lack of concordance between at-sea and colony trends to the volatility in movement of foraging kittiwakes as food supplies apparently diminished in the mid-1990s (Suryan and Irons, 2001). Variability also may arise from differences among years in the abundance of non-breeding birds and flux of birds from the Gulf of Alaska.

In any case, it is important to acknowledge that while we have a relatively good grasp on sources of variation in attendance by seabirds at their breeding colonies, our understanding of how and why seabird populations at sea fluctuate over time is minimal. In the case of Marbled Murrelets, we have evidence for persistent foraging of nesting birds in proximity to nesting areas, but also for long-range (100+ km) excursions of breeding birds to distant foraging areas. Additionally, we believe that there is a large and highly mobile pool of subadult birds, non-breeding birds, failed breeders and successful post-breeding birds that are not constrained geographically by having to return to nests, and therefore may move widely around any area that is being surveyed (Kuletz, 2005). Indeed, our demographic modeling suggests that about 25 percent of all birds in the population at any one time may be subadults. Seasonal changes in distribution and abundance could affect trend analyses, but with such limited numbers of surveys in Alaska, we have little way to evaluate the magnitude of this error at the appropriate spatial scales (but see Speckman and others, 2000). However, the trend analysis of data from British Columbia was based on averages of multiple counts made within each survey year, and temporal variability was therefore accounted for in that analysis.

As far as survey "design" is concerned, historical surveys included transects that were selected randomly, systematically, for their logistic convenience, because they were "representative," or simply in haphazard fashion. Only surveys currently employed in California, Oregon, and Washington were designed specifically for monitoring murrelet populations (Huff and others, 2006). Thousands of kilometers of transects using these methods were conducted by the U.S. Forest Service in Southeast Alaska during the early 1990s (see appendix M), but none were repeated and so we could not examine trends using those data.

Given these issues, how much credence should be placed in the population trend information presented in this assessment? We used appropriate statistical analyses, and we have indicated where we think methodological issues might cause error, but we cannot evaluate the underlying assumption that at-sea survey data provide an accurate estimate of populations and trends. More work is needed to validate at-sea survey methods, and we need to develop wholly new approaches to censusing murrelets in Alaska (e.g., using radar on watersheds) that might be used to corroborate (or replace) water-based surveys. In the meantime, we acknowledge that the estimates of population size and rates of decline could be exaggerated or simply incorrect. In the end, however, we are struck by the consistency of the data in showing a declining trend, and apparent rates of decline ranging from -5.4 to -31 percent per year in the cases showing statistically significant change. Although the absolute rates could be inaccurate, the weight of statistical evidence leads us to err on the side of caution and assume that a biologically meaningful decline in the core population of murrelets has occurred during the past 15–20 years, at least until new data can be collected to improve measures of trend.

In this regard, some of the uncertainty about the decline could be cleared up by repeating a region-wide survey of Southeast Alaska like the one conducted in 1994 by Agler and others (1998). This survey covered the entire region that has been and likely remains the center of the species' abundance. Obtaining a new estimate of population size in Southeast Alaska would answer the immediate questions about the status of the species overall. Continuing surveys of the other trend sites, especially Prince William Sound and lower Cook Inlet, also would be useful.

Are There Precedents for Changes of This Magnitude in Other Marine Wildlife Populations in the Northeastern Pacific Ocean?

Yes. In particular, it appears that populations of closely related Kittlitz's Murrelet also are declining rapidly throughout their range (Kuletz and others, 2003; Robards and others, 2003), which overlaps almost completely with Marbled Murrelet from about Glacier Bay westward. Several species of seabirds in Alaska are undergoing similar or larger rates of decline at specific colonies (Dragoo and others, 2006), although no other species is currently undergoing declines in most areas of its range at the same time. Tufted puffins have shown consistent increases of 2.5 to 17.9 percent per year at eight colonies stretching from Prince William Sound to the western Aleutians, and consistent decreasing trends of -1.0 to -16.9 percent at nine colonies stretching from Southeast Alaska to California (Piatt and Kitaysky, 2002). Pelagic and red-faced cormorants have undergone precipitous declines of 90–95 percent at rates of as much as 13 percent per year during the past 20 years at most colonies in the Gulf of Alaska, eastern Aleutians and western Aleutians, but not in the central Aleutians (Dragoo and others, 2006).

There are parallels with changes in marine mammal populations as well (reviewed by Springer and others, 2007). The western stock of Steller's sea lions declined during the past 30 years at all 36 rookeries scattered over a 2,000 km range from the northeast Gulf of Alaska to the western Aleutians. Decline rates of about 6 percent per year at some rookeries in the 1970s increased to a more rapid and widespread decline of 16 percent per year through the 1980s and early 1990s. Harbor seal populations at the largest rookery in Alaska (Tugidak Island) declined at a rate of 19 percent per year during the 1970s, leveling off to a persistent decline of 7 percent per year through the 1980s until recovering partially in the mid-1990s. The harbor seal declines were widespread, and populations declined rapidly by 63 percent in Prince William Sound during only a 10-year period in the 1980s. Similar rapid declines were noted at Kodiak (-66 percent) and the Pribilof islands (-80 percent). Finally, populations of sea otters rebounded after harvest ended in the early 1900s, and populations increased dramatically for decades in many areas of Alaska at rates of 9–13 percent per year. However, in the late 1980s populations of the southwest stock (including the Aleutians and Alaska Peninsula) plummeted at rates of 17–25 percent per year. In contrast, sea otter populations in Prince William Sound appear stable, while in Southeast Alaska populations increased at nearly 20 percent through the late 20th century and have subsequently stabilized (Esslinger and Bodkin, 2006).

Is There a Plausible Explanation for These Findings?

Yes, but not a single explanation. There is no one factor that can be invoked to explain changes of this magnitude, and it is likely that many factors acting in concert could result in the observed population declines. This is certainly the case for the major population fluctuations observed in Alaska for cormorants, tufted puffins, Steller's sea lions, harbor seals and sea otters. Factors influencing these populations are complicated, possibly additive and in some instances impossible to evaluate for relative importance. This has led to vigorous debate and widespread disagreement about how these wildlife populations are ecologically regulated in Alaska (Springer and others, 2007). In previous sections of this document, we have reviewed in detail all factors that may possibly impact murrelet populations in Alaska and British Columbia. In the following, we briefly review that list again, and try to identify the most important factors, if possible.

Anthropogenic Factors Influencing the Marbled Murrelet

We have identified several factors that arise from human activities and that have a negative influence on murrelet populations. In an approximate order of potential importance these include:

- Destruction of old-growth nesting habitat.
- By-catch of birds in fishing gear.
- Oil pollution.
- Competition from commercial fisheries.
- Vessel disturbance.
- Overuse for commercial or scientific purposes.

Evidence suggests that the past removal of large areas of old-growth nesting habitat in British Columbia (33–49 percent) and Alaska (probably <15 percent) has had a direct negative impact on populations. Thus, it may be reasonable to assume that future harvests would result in proportional reductions in nesting habitat and therefore eventually population size (Burger and others, 2004a). However, recent rates of harvest of suitable nesting habitat in Alaska appear to be less than 1 percent per year and this cannot by itself explain declines of 5–13 percent in Southeast Alaska and Prince William Sound (even if loss of habitat translated immediately into population declines, which seems unlikely for birds that may live to 15–25 years of age). The observed population trends may reflect some time-lag in population effects on these long-lived birds as a result of logging from previous decades, especially in British Columbia and southern Southeast Alaska. However, such an effect would not explain population declines in northern Southeast Alaska and Prince William Sound, where losses of nesting habitat to logging are much less pronounced. An additional by-product of large scale logging is habitat fragmentation, which brings an increased threat of disturbance and predation (see below).

The quantity of data available on the impact of fishing bycatch, oil pollution, and competition from commercial fisheries are simply inadequate to draw firm conclusions about the relative or absolute impact of these factors on murrelet population dynamics. It is usually difficult to measure the impact of these factors on seabirds, even in well-documented cases involving colonial species that are relatively easy to census. We have evidence that oil pollution and gill-nets kill hundreds to thousands of Marbled Murrelets each year in Alaska and British Columbia. Even if populations are in the low 100,000s this would amount to increasing adult mortality by only a few percent, perhaps to 6–7 percent in local populations (Carter and Kuletz, 1995). Therefore, it seems unlikely that these factors, by themselves, could account for the population declines we have observed. A critical question, however, is whether or not mortality from these anthropogenic factors are additive to natural mortality or compensated for in density-dependent mortality (Piatt and Nettleship, 1987). Recent analysis of a long-term dataset on survival of murres in the North Atlantic indicates that oil spills have a strong impact on over-winter survival of murres and that the effect is additive to effects of environmental variation (Votier and others, 2005). This could be important to populations under stress.

Finally, we found little or no evidence that vessel disturbance or use of murrelets for scientific purposes has any significant impact on populations at the present time. Increased levels of disturbance at sea, however, increase energy demands and could reduce fitness under adverse environmental conditions (Agness, 2005).

Natural Factors Influencing the Marbled Murrelet

We have identified several natural factors that can have a negative (or positive) influence on murrelet populations. In an approximate order of potential importance these include:

- Ocean climate change and marine ecosystem regime shifts.
- Disease or predation.
- Natural changes in terrestrial habitat.

Periodic (e.g., El Niño) or cyclical changes in marine climate are known to cause profound changes in marine systems at local and basin scales. In the Northeastern Pacific Ocean, environmental conditions cycle between warm and cold phases on a multi-decadal time scale (Francis and others, 1998). At least two cycles are apparent in this century, with strong phase reversals occurring around 1925, 1947, and 1977 (Mantua and others, 1997). In the most recent event, the Aleutian Low Pressure system shifted and intensified during the late 1970s leading to stronger westerly winds and warmer surface waters in the Gulf of Alaska. This apparently strengthened the flow of the Alaska Current, and resulted in increased primary and secondary production in the Gulf of Alaska. Warm water periods were associated with changes in the magnitude and timing of primary and secondary production, and marked increases in groundfish recruitment and salmon catches in Alaska (Francis and others, 1998). Conversely, some populations of marine birds and mammals exhibited signs of food stress (Piatt and Anderson, 1996; but see Springer, 2007 for a different interpretation).

The shift in climate regime in the late 1970s triggered a complete reorganization of trophic structure in the Gulf of Alaska ecosystem (Anderson and Piatt, 1999). Important forage taxa such as pandalid shrimp, capelin, and herring declined by 95 percent or more in less than 15 years and never recovered in much of their range, probably owing to recruitment failure and predator forcing. This trophic reorganization apparently occurred at the expense of some piscivorous marine birds and mammals in the Gulf of Alaska. During the initial transition in the early 1980s, as stocks of common forage species such as capelin and herring collapsed, these fatty fish disappeared from diets of seabirds—particularly Marbled Murrelets—and were replaced largely by lean juvenile pollock (Piatt and Anderson, 1996). Pollock have substantially lower energetic value than more typical forage species such as capelin (Van Pelt and others, 1997) and are not assimilated as efficiently by growing chicks (Romano and others, 2006). Even when consumed at a caloric rate equal to capelin, pollock induces nutritional stress (Kitaysky and others, 1999) and results in little fat deposition (Romano and others, 2006) in seabirds. Thus, the change in predator diets may have had a negative effect on productivity, recruitment and survival in murrelets.

There is evidence for another weak North Pacific climate regime shift in 1999 (Bond and others, 2003) and evidence that climate-related physical changes (e.g., winds, SST) have had pervasive biological effects on marine animals (Grebmeier and others, 2006; but see Litzow, 2006). If so, the period of decline in murrelet numbers that apparently began after the 1977 regime shift (Agler and others, 1999) could have been slowed or halted by a later regime shift in 1999. Trends in murrelet numbers counted in Barkley Sound, British Columbia and Icy Strait, Alaska, suggest the possibility that declining trends stopped after 1999 in these areas.

In any case, changes in marine climate and so-called "regime shifts" have clearly had pervasive impacts on marine communities in the Northeastern Pacific Ocean. Indeed, this is the only factor we have examined that has the potential to explain large declines in murrelet numbers over a broad area of the Northeastern Pacific Ocean. Not surprisingly, the 1977 regime shift is often implicated in the rapid and large declines observed in Steller's sea lion, sea otter, and harbor seal, although the mechanisms of change are unclear and other factors are almost certainly at work (Springer, 2007).

One of those other factors is predation, and Springer and others (2003) argues that predation of marine mammals by orca could have been a driving force in reducing these populations in Alaska. We know that Marbled Murrelets have adapted more than any other member of the Alcidae to minimize predation of adults and their young (Nelson, 1997). Predation occurs at the nest, in forest habitats and on the sea. Although we have little quantitative data with which to assess the numerical impact of predation on murrelets, it is prudent not to underestimate the importance of this powerful force in regulating animal populations (Sinclair and others, 1998, Parrish and others, 2001, Springer and others, 2003). It is noteworthy that populations of five of seven known murrelet predators observed on Christmas Bird Counts have increased substantially (by 2–8 fold) in British Columbia or Alaska during the past 30 years. Predation is one of only a few factors we have identified that has the potential to cause the rates of change that we observed in murrelet populations.

We found little evidence for significant effects of disease in murrelets, or for significant changes in terrestrial ecosystems (fire, pest infestations, precipitation, forest community composition) that could account for the changes observed in murrelet populations.

Conclusion

We observed declining trends in populations of murrelets at eight trend sites in British Columbia and at five of eight trend sites in Alaska. If methods for detecting these trends are sound, then populations in Alaska may have declined by more than 70 percent during the past 20 years. A model of population dynamics and observations of other seabirds in Alaska suggest that such trends could result from stochastic variability in population parameters, but additional factors likely are influencing populations. Declines are possibly the result of combined and cumulative effects of human activities (logging, gillnet bycatch, oil pollution) and natural factors such as ocean regime shifts or predation. Important questions remain to be addressed about methods for measuring population status and change, adult mortality (major sources, density dependence, seasonal concordance), and the movements of wintering populations.

Acknowledgments

This review was prepared for the U.S. Fish and Wildlife Service, Region 7, by the U.S. Geological Survey under Interagency Agreement # 70181-5-N242, and supported with funding from both the USFWS and USGS-Alaska Science Center.

Once underway, it became clear that this project was going to need full-time coordination to make sure all the pieces came together at the same time. The authors are grateful to Karen Oakley (USGS) for stepping in as project manager, establishing goals and deadlines, and coordinating biologists and support staff in a steadfast fashion. Her knowledge of murrelet biology was a real asset in pulling together the various sections, identifying gaps, and helping us to deal with all the reviews. She did a goodly share of editing as well. Karen deserves as much credit as anyone else for making this happen.

This compilation and analysis of the growing body of information about Marbled Murrelets in Alaska and British Columbia would not have been possible without contributions from the many people who have been involved in seabird research in this region. Our ability to produce a document that is both up-to-date and comprehensive is due in large measure to extra efforts of those who provided unpublished data and willingly reviewed our drafts. We thank especially John Lindell, Michelle Kissling, Jack Hodges, Debbie Groves, Dennis Zwiefelhofer, Shawn Stephenson and Joel Reynolds of the USFWS for access to unpublished data and assistance with analysis of boat survey data collected by the USFWS. We thank also Kathy Dale, Geoff LeBaron, and Stan Senner of the Audubon Society for assistance in obtaining Christmas Bird Count data sets. We also appreciate helpful insights from Colin Beier (UAF), Dave Albert (TNC), and Francis Biles (USDA Forest Service) on Tongass forest issues. Bill van Hees and Jane Reid (USDA Forest Service) provided information and data from the FIA program. Dede Bohn improved our understanding of *Exxon Valdez* Oil Spill Trustee Council actions relative to the Marbled Murrelet. Gus Van Vliet, Matt Kirchoff (ADF&G), G. Vernon Byrd (USFWS), Alan Springer (University of Alaska Fairbanks), Lyman Thorsteinson (USGS), Nancy Naslund, Harry Carter (Carter Consulting), and Alison Agness saw early drafts and provided critical comments on various sections of the document. Michael Fleming (SAIC) and Page Spencer (National Park Service) provided land-cover information for the Kodiak archipelago. We thank Rob DeVelice (USFS) for providing his unpublished nesting habitat model for the Prince William Sound region. We also thank Dave Albert and John Schoen for providing HSI and other forest data for Southeast Alaska. Karen Murphy (USFWS) provided vessel statistics for Prince William Sound.

Contributors of unpublished data to the British Columbia sections include Alan Burger (University of Victoria), Harry Carter (Carter Consulting, Victoria), John Deal (Canfor), Bill Harper (Osiris Consulting), Laskeek Bay Conservation Society (Greg Martin), David Lindsay (TimberWest), Parks Canada (Bob Hansen, Danielle Edwards, Danielle Bellefleur), and Anne Stewart (Bamfield Marine Sciences Centre). Others who helped with the British Columbia reviews include Doug Bertram (Canadian Wildlife Service), Trudy Chatwin (British Columbia Ministry of Environment), Alvin Cober (British Columbia Ministry of Environment), Anne Harfenist, Andrea Lawrence, Monica Mather (British Columbia Ministry of Environment), Ken Morgan (Canadian Wildlife Service), Jo Smith (University of Washington), and Steve Young (formerly Sierra Club of Canada).

Samples used for the genetic study were obtained through the assistance of S. Beissinger, T. Bloxton, E. Burkett, V. Byrd, H.Carter, F. Cooke, A. Derocher, R. Golightly, T. Hofstra, G. Kaiser, M. Kassera, S. Kitaysky, K. Kuletz, R. Lowe, K. Martin, K. Nelson, Z. Peery, J. Piatt, M. Raphael, T. van Pelt, J. Pitocchelli, A. Pritchard, L. Roberts, D. Roseneau, H. Sakai, S. Speckman, W. Sydeman, J. Williams, and the Captain and Crew of the *R/V Tiglax*. Help with data collection and interpretation was provided by C. Crossman, G. Gissing, D. Harrison, G. Ibarguchi, R. Kristensen, D. Michaud, V. Poland, and L.Veit. K. Warheit and P. Palsboll facilitated the development of microsatellite primers. Funding was provided by the British Columbia Ministry of Forests, California Department of Fish and Game, Canadian Wildlife Service, the *Exxon Valdez* Oil Spill Trustee Council, Government Works and Public Services Canada, the Natural Sciences and Engineering Research Council of Canada, a Premier's Research Excellence Award, Scotia Pacific Lumber, the U.S. National Park Service, the U.S. Fish and Wildlife Service, the U.S. Geological Survey, and Washington State Fish and Wildlife Service.

Lyman McDonald and Shay Howlin (WEST Inc.) worked with us from the beginning to ensure our analyses of the pertinent archived datasets were statistically sound. Matt Kirchhoff (ADF&G) also helped with statistical evaluation of the trend data.

We thank Michelle St. Peters (USGS), who played a significant role in compiling the recent literature which jumpstarted the process of completing this review. Liz Labunski (USFWS) compiled information for the marine habitat section, and Tom Hamer, Erin Colclazier, and Nathalie Denis, of Hamer Environmental, provided a summary of Marbled Murrelet conservation status and provided extensive review material on threats to nesting habitat. Paula Winningham (USGS) cheerfully expedited our contracts. Mary Whalen (USGS) provided graphical support. Katherine Burke (USGS) compiled the document, tracked down literature, copy edited, and performed numerous other supporting tasks. Linda S. Rogers (USGS) provided superb editing and technical assistance in publication of this report.

We are grateful to Kristine Paulus and Lucy Fowler Williams at the University of Pennsylvania Museum for help with obtaining photographs and documentation on the Murrelet Hat.

Finally, we are indebted to our peer reviewers. The report was much improved by the thoughtful and thorough comments of John R. Sauer (USGS-Patuxent Wildlife Research Center), Martin G. Raphael (U.S. Forest Service-Pacific Northwest), David (Dov) Lank (Simon Fraser University), Sandra L. Talbot (USGS-Alaska Science Center), Timothy L. King (USGS-Leetown Science Center), and Robert H. Day, Adrian E. Gall, Alex K. Pritchard and Brian Cooper (all of ABR, Inc.). We thank them for their contributions to this assessment.

References Cited

Abookire, A.A., Piatt, J.F., and Speckman, S.G., 2002, Nearsurface, daytime occurrence of two mesopelagic fish species (*Stenobrachius leucopsarus* and *Leuroglossus schmidti*) in a glacial fjord: Fisheries Bulletin, v. 100, p. 376-380.

Adams, J., Lavin, P., and Turrini, A., 2002, Prince William Sound biological hot pots workshop report: Anchorage, National Wildlife Federation Alaska Office.

Agler, B.A., Kendall, S.J., Irons, D.B., and Klosiewski, S.P., 1999, Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift: Waterbirds, v. 22, no. 1, p. 98-103.

Agler, B.A., Kendall, S.J., Seiser, P.E., and Irons, D.B., 1998, Abundance and distribution of Marbled and Kittlitz's murrelets in south central and southeast Alaska: Condor, v. 100, no. 2, p. 254-265.

Agness, A.M., 2006, Effects and impacts of vessel activity on Kittlitz's Murrelets (*Brachyramphus brevirostris*) in Glacier Bay, Alaska: Thesis, Seattle, University of Washington.

Ainley, D.G., Allen, S.G., and Spear, L.B., 1995a, Offshore occurrence patterns of Marbled Murrelets in central California, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Fish and Wildlife Service, Pacific Southwest Research Station, General Technical Report 152, p. 361-369.

Ainley, D.G., Sydeman, W.J., and Norton, J., 1995b, Upper-trophic level predators indicate interannual negative and positive anomalies in the California Current food web: Marine Ecology Progress Series, v. 118, p. 69-79.

Alaska Department of Fish and Game, 2006, Our wealth maintained: Strategy for conserving Alaska's diverse wildlife and fish resources: Juneau, Alaska, 824 p.

Alaska Department of Natural Resources, 1999, *Exxon Valdez* oil spill restoration habitat protection and acquisition atlas: Anchorage, Alaska, Unpublished Report, 53 p.

Albert, D., and Schoen, J., 2006, Conservation assessment tand resource synthesis for the coastal forests and mountain ecoregion in southeast Alaska and the Tongass National Forest, *in* Schoen, J. and Dovichin, E., eds., Southeastern Alaska and the Tongass National Forest: Conservation assessment and resource synthesis: Anchorage, Audubon Alaska and Nature Conservancy.

American Ornithologists' Union, 1957, Check-list of North American birds: Baltimore, Maryland, 5th ed.

American Ornithologists' Union, 1997, Forty-first supplement to the American Ornithologists' Union checklist of North American birds: Auk, v. 114, no. 3, p. 542-552.

Andersen, H.L., and Beissinger, S.R., 1995, Preliminary observations on juvenile:adult ratios of Marbled Murrelets in Auke Bay, southeast Alaska: Northwestern Naturalist, v. 76, no. 6, p. 79-81.

Anderson, P.J., and Piatt, J.F., 1999, Trophic reorganisation in the Gulf of Alaska following ocean climate regime shift: Marine Ecology Progress Series, v. 189, p. 117-123.

Andrén, H., 1995, Effects of landscape composition on predation rates at habitat edges, *in* Hansson, L., Fahrig, L., and Merriam, G., eds., Mosaic landscapes and ecological processes: London, United Kingdom, Chapman and Hall, p. 225-255.

Anthony, J.A., Roby, D.D., and Turco, K.R., 2000, Lipid content and energy density of forage fishes from the northern Gulf of Alaska: Journal of Experimental Marine Biology and Ecology, v. 248, p. 53-78.

Barbour, R.J., Zaborske, R.R., McClellan, M.H., Christian, L., and Golnick, D., 2005, Young-stand management options and the implications for wood quality and other values: Landscape and Urban Planning, v. 72, p. 79-94.

Bartonek, J.C., and Gibson, D.D., 1972, Summer distribution of pelagic birds in Bristol Bay, Alaska: Condor, v. 74, p. 416-422.

Batschelet, E., 1971, Introduction to mathematics for life scientists: New York, Springer-Verlag.

Beamish, R.J., Noakes, D.J., McFarlane, G.A., Klyashtorin, L., Ivanov, V.V., and Kurashov, V., 1999, Regime concept and natural trends in the production of Pacific salmon: Canadian Journal of Fisheries and Aquatic Sciences, v. 56, p. 516-526.

Beauchamp, W.D., Cooke, F., Lougheed, C., Lougheed, L.W., Ralph, C.J., and Courtney, S.P., 1999, Seasonal movements of Marbled Murrelets: Evidence from banded birds: Condor, v. 101, no. 3, p. 671-674.

Becker, B.H., and Beissinger, S.R., 2003, Scale-dependent habitat selection by a nearshore seabird, the Marbled Murrelet, in a highly dynamic upwelling system: Marine Ecology Progress Series, v. 256, p. 243-255.

Becker, B.H., and Beissinger, S.R., 2005a, Centennial decline in the trophic level of an endangered seabird after fisheries decline: Conservation Biology, v. 5, no. 2, p. 470-479.

Becker, B.H., and Beissinger, S.R., 2005b, Overfishing may drive endangered seabird to rely upon lower quality food: This appears to be a press release not a publication. http://www.eurekalert.org/pub_releases/2005-12/uoc--omd121705.php.

Bédard, J., 1966, New records of alcids from St. Lawrence Island, Alaska: Condor, v. 68, p. 503-506.

Beerli, P., and Felsenstein, J., 1999, Maximum-likelihood estimation of migration rates and effective population numbers in two populations using a coalescent approach: Genetics, v. 152, p. 763-773.

Beissinger, S.R., 1995a, Final report on the effects of net fisheries on Marbled Murrelet population trends: Olympia, Washington, U.S. Fish and Wildlife Service, Ecological Services.

Beissinger, S.R., 1995b, Population trends of the Marbled Murrelet projected from demographic analyses, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 385-393.

Beissinger, S.R., and Nur, N., 1997, Population trends of the Marbled Murrelet projected from demographic analyses, *Appendix B in* Recovery plan for the threatened Marbled Murrelet (*Brachyramphus marmoratus*) in Washington, Oregon and California: Portland, Oregon, U.S. Fish and Wildlife Service, B1-B35.

Bellefleur, D., Edwards, D., Hansen, B., and Burger, A.E., 2005, Marine distribution and abundance of Marbled Murrelets in Pacific Rim National Park Reserve of Canada, 1995-2004: Ucluelet, British Columbia, Parks Canada, Pacific Rim National Park Reserve.

Benson, A.J., and Trites, A.W., 2002, Ecological effects of regime shifts in the Bering Sea and eastern North Pacific Ocean: Fish and Fisheries, v. 3, p. 95-113.

Bent, A.C., 1963, Life histories of North American diving birds: New York, Dover Publications, U.S. National Museum Bulletin 107, 239 p.

Bentivoglio, N., Baldwin, J., Evans Mack, D., Max, T., Miller, S., Nelson, S.K., Ralph, C.J., Raphael, M., Strong, C., Thompson, C., Ostrom, K., and Wilk, R., 2002, Northwest Forest Plan Marbled Murrelet effectiveness monitoring: Portland, Oregon, U.S. Fish and Wildlife Service, 2000 Annual Report, 72 p.

Berg, C., 2003, Best practices for migratory bird care during oil spill response: Anchorage, Alaska, U.S. Fish and Wildlife Service, Ecological Services.

Bertram, D.F., Burger, A.E., Chatwin, T.A., Chutter, M.J., Guy, S., Cooke, F., Lank, D.B., Deal, J.A., Hay, D.E., Jones, T.L., Lindsay, D.J., Manley, I.A., Reader, B., Steventon, J.D., Waterhouse, F.L., and Williams, E., 2003, Canadian Marbled Murrelet Recovery Team advisory document on conservation and management, *Part B in* Marbled Murrelet conservation assessment 2003: Delta, British Columbia, CWS, Working Document 1, 31 p.

Bigger, D., Peery, M.Z., Baldwin, J., Chinnici, S., and Courtney, S.P., 2006, Power to detect trends in Marbled Murrelet populations using audio-visual and radar surveys: Journal of Wildlife Management, v. 70, p. 493-504.

Binford, L.C., Elliot, B.G., and Singer, S.W., 1975, Discovery of a nest and the downy young of the Marbled Murrelet: Wilson Bulletin, v. 87, p. 303-319.

BirdLife International, 2005, *Brachyramphus marmoratus*, *in* IUCN, Red list of threatened species, Gland, Switzerland.

Birky, C.W. Jr, Fuerst, P., and Maruyama, T., 1989, Organelle gene diversity under migration, mutation, and drift: Equilibrium expectations, approach to equilibrium, effects of heteroplasmic cells, and comparison to nuclear genes: Genetics, v. 121, p. 613-627.

Bleich, V.C., Bowyer, R.T., Pauli, A.M., Nicholson, M.C., and Anthenes, R.W., 1994, Mountain sheep (*Ovis canadensis*) and helicopter surveys: Ramifications for the conservation of large mammals: Biological Conservation, v. 70, p. 1-7.

Boldt, J., Batchelder, J., Crawford, W., Hollowed, A., King, J., McFarlane, G., Mueter, F., Perry, I., and Schweigert, J., 2005, Recent ecosystem changes in the Gulf of Alaska, *in* King, J.R., ed., Report of the study group on fisheris and ecosystem responses to recent regime shifts, PICES Scientific Report 28, p. 87-116.

Bond, N.A., Overland, J.E., Spillane, M., and Stabeno, P., 2003, Recent shifts in the state of the North Pacific: Geophysical Research Letters, v. 30, p. 2183-2187.

Booth, J.A., and Rueggeberg, H., 1989, Marine birds and aquaculture in British Columbia: Assessment and management interactions. Phase II Report: Assessment of geographical overlap: Delta, British Columbia, Canadian Wildlife Service, Pacific and Yukon Region, Technical Report 73, 53 p.

Boucher, T.V., and Mead, B.R., 2006, Vegetation change and forest regeneration on the Kenai Peninsula, Alaska following a spruce beetle outbreak: Forest Ecology and Management, v. 227, p. 233-246.

Boulanger, J.G., 2000, Quantitative tools for the monitoring of threatened species: Marbled Murrelet case study, *in* Darling, L.M., ed., Biology and Management of Species and Habitats at Risk Conference, Kamloops, British Columbia, 1999, v. 1, p. 490.

Boulanger, J.G., Martin, K., Kaiser, G.W., and Derocher, A.E., 1999, Evaluating uncertainty in estimating population trends for research and conservation of Marbled Murrelets, *in* Diamond, A.W., and Nettleship, A.W., eds., Biology and conservation of forest birds [Proceedings], Fredericton, New Brunswick, 1999, Special Publication 1, p. 53-63.

Boyce, M.S., 1992, Population viability analysis: Annual Reviews of Ecology and Systematics, v. 23, p. 481-506.

Brackley, A.M., Rojas, T.D., and Haynes, R.W., 2006, Timber products output and timber harvests in Alaska: Projections for 2005-25: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, General Technical Report.

Bradley, R.W., 2002, Breeding ecology of radio-marked Marbled Murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia, Thesis: Burnaby, British Columbia, Simon Fraser University, 86 p.

Bradley, R.W., and Cooke, F., 2001, Cliff and deciduous tree nests of Marbled Murrelets in southwestern British Columbia: Northwestern Naturalist, v. 82, no. 2, p. 52-57.

Bradley, R.W., Cooke, F., Lougheed, L.W., and Boyd, W.S., 2004, Inferring breeding success through radiotelemetry in the Marbled Murrelet: Journal of Wildlife Management, v. 68, no. 2, p. 318-331.

Bradley, R.W., McFarlane Tranquilla, L.A., Vanderkist, B.A., and Cooke, F., 2002, Sex differences in nest visitation by chick-rearing Marbled Murrelets: Condor, v. 104, no. 1, p. 178-183.

Bradley, J.E., and Marzluff, J.M., 2003, Rodents as nest predators: Influences on predatory behavior and consequences to nesting birds: Auk, v. 120, p. 1180-1187.

Brazil, M.A., 1991, Birds of Japan: Washington, D.C., Smithsonian Institution Press, 266 p.

Brooks, A., 1926, Scarcity of the Marbled Murrelet: Murrelet, v. 7, p. 39.

Brown, M., Doerr, J.G., Fowler, J., Russell, A., and Walsh, P.J., 1999, Marbled Murrelet activity patterns and survey efficiency at inland sites in southeastern Alaska: Northwestern Naturalist, v. 80, p. 44-50.

Burger, A.E., 1992, Effects of oil pollution on seabirds off the west coast of Vancouver Island, *in* Vermeer, K., Butler, R.W., and Morgan, K.H., eds., Ecology, status and conservation of marine and shoreline birds on the west coast of Vancouver Island: Ottawa, Ontario, Canadian Wildlife Service, Occasional Paper 75, p. 120-128.

Burger, A.E., 1993a, Effects of the *Nestucca* oil spill on seabirds along the southwest coast of Vancouver Island in 1989: Delta, British Columbia, Canadian Wildlife Service, Pacific and Yukon Region, Technical Report 179.

Burger, A.E., 1993b, Mortality of seabirds assessed from beached-bird surveys in British Columbia: Canadian Field-Naturalist, v. 107, no. 2, p. 164-176.

Burger, A.E., 1995a, Inland habitat associations of Marbled Murrelets in British Columbia, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 151-162.

Burger, A.E., 1995b, Marine distribution, abundance, and habitats of Marbled Murrelets in British Columbia, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 295-312.

Burger, A.E., 2000, Bird in hot water: Responses by Marbled Murrelets to variable ocean temperatures off southwestern Vancouver Island, *in* Darling, L.M., ed., Biology and Management of Species and Habitats at Risk Conference, Kamloops, British Columbia, 1999, v. 2, p. 723-732.

Burger, A.E., 2001a, Habitat associations of Marbled Murrelets in Clayoquot Sound, British Columbia, showing population declines in logged watersheds: Northwestern Naturalist, v. 82, no. 2, p. 67.

Burger, A.E., 2001b, Using radar to estimate populations and assess habitat associations of Marbled Murrelets: Journal of Wildlife Management, v. 65, no. 4, p. 696-715.

Burger, A.E., 2002, Conservation assessment of Marbled Murrelets in British Columbia. Part A: Review of the biology, populations, habitat associations, and conservation: Delta, British Columbia, CWS, Pacific and Yukon Region, Technical Report 387, 194 p.

Burger, A.E., 2004, Standard methods for identifying and ranking nesting habitat of Marbled Murrelets (*Brachyramphus marmoratus*) in British Columbia using air photo interpretation and low-level aerial surveys: Victoria, British Columbia, Ministry of Water, Land, and Air Protection and Ministry of Forests, 37 p.

Burger, A.E., Booth, J.A., and Morgan, K.H., 1997, Preliminary identification of the processes and problems affecting marine birds in coastal and offshore areas of British Columbia: Delta, British Columbia, Canadian Wildlife Service, Pacific and Yukon Region, Technical Report 277.

Burger, A.E., Chatwin, T.A., Cullen, S.A., Holmes, N.P., Manley, I.A., Mather, M.H., Schroeder, B.K., Steventon, J.D., Duncan, J.E., Arcese, P., and Selak, E., 2004a, Application of radar surveys in the management of nesting habitat of Marbled Murrelets *Brachyramphus marmoratus*: Marine Ornithology, v. 32, no. 1, p. 1-11.

Burger, A.E., and Fry, D.M., 1993, Effects of oil pollution on seabirds in the northeast Pacific, *in* Vermeer, K., Briggs, K.T., Morgan, K.H., and Siegel-Causey, D., eds., Status, ecology and conservation of marine birds of the North Pacific: Ottawa, Ontario, CWS, Special Publication, p. 254-263.

Burger, J., and Galli, J., 1987, Factors affecting distribution of gulls (*Larus* spp.) on two New Jersey coastal bays: Environmental Conservation, v. 14, no. 1, p. 59-65.

Burger, J., and Gochfeld, M., 1990, Risk discrimination of direct versus tangential approach by basking Black Iguanas (*Ctenosaura similis*): Variation as a function of human exposure: Journal of Comparative Physiology, v. 104, p. 388-394.

Burger, J., and Gochfeld, M., 1991, Human activity influence and diurnal and nocturnal foraging of Sanderlings (*Calidris alba*): Condor, v. 93, p. 259-265.

Burger, A.E., Hitchcock, C.L., and Davoren, G.K., 2004b, Spatial aggregations of seabirds and their prey on the continental shelf off southwest Vancouver Island: Marine Ecology Progress Series, v. 283, p. 279-292.

Burger, A.E., Hobbs, J., and Hetherington, A., 2005, Testing models of habitat suitability for nesting Marbled Murrelets, using low-level aerial surveys on the north coast British Columbia: Report to Ministry of Water, Land, and Air Protection; Smithers, British Columbia.

Burger, A.E., Masselink, M.N.M., Tillmanns, A.R. , Szabo, A.R., Farnholtz, M., and Krkosek, M.J., 2004c, Effects of habitat fragmentation and forest edges on predators of Marbled Murrelets and other forest birds on southwest Vancouver Island, *in* Hooper, T.D., ed., Species at Risk 2004: Victoria, British Columbia, Pathways to Recovery Conference, p. 1-19.

Burkett, E.B., 1995, Marbled Murrelet food habits and prey ecology, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 223-246.

Burns, R.A., Prestash, L.M., and Kuletz, K.J., 1994, Pilot study on the capture and radio tagging of murrelets in Prince William Sound, Alaska: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, Restoration Project 93051-3 Final Report, 78 p.

Cam, E., Lougheed, L.W., Bradley, R.W., and Cooke, F., 2003, Demographic assessment of a Marbled Murrelet population from capture-mark-recapture and radio telemetry data: Conservation Biology, v. 17, no. 4, p. 1118-1126.

Campbell, R.W., 1967, Fishing lures, hazard to sea birds: Blue Jay, v. 25, p. 71-72.

Campbell, R.W., Dawe, N.K., McTaggart-Cowan, I., Cooper, J.M., Kaiser, G.W., and McNall, M.C.E., 1997, Nonpasserines: Diurnal birds of prey through woodpeckers: Victoria, University of British Columbia Press, Birds of British Columbia, v. 2, 642 p.

Campbell, S., van Hees, W.S., and Mead, B., 2005, South-central Alaska forests: Inventory highlights: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, General Technical Report 652, 28 p.

Canadian Marbled Murrelet Recovery Team. 2003. Marbled Murrelet Conservaiton Assessment 2003, Part B: Marbled Murrelet Recovery Team Advisory Document on Conservation and Management. Canadian Marbled Murrelet Recovery Team Working Document No. 1, accessed December 2006, http://www.sfu.ca/biology/wildberg/bertram/mamurt/links.htm.

Caouette, J.P., and DeGayner, E.J., 2005, Predictive mapping for tree sizes and densities in southeast Alaska: Landscape and Urban Planning, v. 72, no. 1-3, p. 49-63.

Capp, J., Van Zee, B., and Alaback, P., 1992, Ecological definitions of old-growth forest types in southcentral Alaska: Juneau, U.S. Forest Service, Alaska Region, R10-TP-28, 30 p.

Carter, H.R., 1984, At-sea biology of the Marbled Murrelet (*Brachyramphus marmoratus*) in Barkley Sound, British Columbia, Thesis: Winnipeg, University of Manitoba.

Carter, H.R., and Erickson, R.A., 1992, Status and conservation of the Marbled Murrelet in California, 1892-1987: Western Foundation of Vertebrate Zoology Proceedings, v. 5, p. 92-108.

Carter, H.R., and Kuletz, K.J., 1995, Mortality of Marbled Murrelets due to oil pollution in North America, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 261-269.

Carter, H.R., McAllister, M.L.C., and Isleib, M.E.P., 1995, Mortality of Marbled Murrelets in gill nets in North America, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 271-283.

Carter, H.R., and Morrison, M.L., 1992, Status and conservation of the Marbled Murrelet in North America: Western Foundation of Vertebrate Zoology Proceedings, v. 5, no. 1, p. 1-134.

Carter, H.R., and Sealy, S.G., 1984, Marbled Murrelet (*Brachyramphus marmoratus*) mortality due to gill-net fishing in Barkley Sound, British Columbia, *in* Nettleship, D.N., Sanger, G.A., and Springer, P.F., eds., Marine birds: Their feeding ecology and commercial fisheries relationships, Pacific Seabird Group Symposium, Seattle, Washington, 1985, p. 212-220.

Carter, H.R., and Sealy, S.G., 1986, Year-round use of coastal lakes by Marbled Murrelets: Condor, v. 88, no. 4, p. 473-477.

Carter, H.R., and Sealy, S.G., 1987, Fish-holding behavior of Marbled Murrelets: Wilson Bulletin, v. 99, no. 2, p. 289-291.

Carter, H.R., and Sealy, S.G., 1990, Daily foraging behavior of Marbled Murrelets: Studies in Avian Biology, v. 14, p. 93-102.

Carter, H.R., and Stein, J.L., 1995, Molts and plumages in the annual cycle of the Marbled Murrelet, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 99-112.

Catton, T., 1995, Land reborn: History of administration and visitor use in Glacier Bay National Park and Preserve: Gustavus, Alaska, U.S. National Park Service, Glacier Bay National Park and Preserve.

Caughley, G., 1994, Directions in conservation biology: Journal of Animal Ecology, v. 63, p. 215-244.

Chavez, F.P., Ryan, J., Lluch-Cota, S.E., and Niquen, M., 2003, From anchovies to sardines and back: Multidecadal change in the Pacific Ocean: Science, v. 299, p. 217-221.

Chilton, G., and Sealy, S.G., 1987, Species roles in mixed-species feeding flocks of seabirds: Journal of Field Ornithology, v. 58, no. 4, p. 456-463.

Cohen, P., and Aylesworth, R., 1990, Oil spill risk for southern British Columbia / northern Washington coast marine area, Province of British Columbia and the states of Washington, Oregon, Alaska, and California, Final Report of the States / British Columbia Oil Spill Task Force, Appendix 7, 105 p.

Congdon, B.C., Piatt, J.F., Martin, K., and Friesen, V.L., 2000, Mechanisms of population differentiation in Marbled Murrelets: Historical versus contemporary processes: Evolution, v. 54, no. 3, p. 974-986.

Conroy, C.J., Bahn, V., Rodway, M.S., Ainsworth, L., and Newsom, D., 2002, *in* Burger, A.E. and Chatwin, T.A., eds., Estimating nest densities for Marbled Murrelets in three habitat suitability categories in the Ursus Valley, Clayoquot Sound: Victoria, British Columbia, Ministry of Water, Land, and Air Protection, Special Report Series, p. 123-140.

Cooke, F., 1999, Population studies of Marbled Murrelets (*Brachyramphus marmoratus*) in British Columbia, *in* Nettleship, A.W., and Diamond, D.N., eds., Biology and conservation of forest birds [Proceedings], Fredericton, New Brunswick, 1999, Special Publication 1, p. 43-51.

Cooper, B.A., 1993, Feasibility of using boat-based marine radar to study Marbled Murrelets in Kenai Fjords National Park, Alaska: Anchorage, Alaska Biological Research, Inc., Report to U.S. Fish and Wildlife Services, Migratory Bird Management.

Cooper, B.A., and Blaha, R.J., 2002, Comparisons of radar and audio-visual counts of Marbled Murrelets during inland forest surveys: Wildlife Society Bulletin, v. 30, no. 4, p. 1182-1194.

Cooper, B.A., Raphael, M.G., and Evans Mack, D., 2001, Radar-based monitoring of Marbled Murrelets: Condor, v. 103, no. 2, p. 219-229.

Cooper, B.A., Raphael, M.G., and Peery, M.Z., 2006, Trends in radar-based counts of Marbled Murrelets on the Olympic Peninsula, Washington, 1996-2004: Condor, v. 108, p. 936-947.

Cote, I.M., and Sutherland, W.J., 1997, Effectiveness of removing predators to protect bird populations: Conservation Biology, v. 11, no. 2, p. 395-405.

Day, R.H., Kuletz, K.J., and Nigro, D.A., 1999, Kittlitz's Murrelet (*Brachyramphus brevirostris*), *in* Poole, A., and Gill, F., eds., Birds of North America: Washington, D.C., Academy of Natural Science and American Ornithologists' Union, p. 28.

Day, R.H., and Nigro, D.A., 2000, Feeding ecology of Kittlitz's and Marbled murrelets in Prince William Sound, Alaska: Waterbirds, v. 23, no. 1, p. 1-14.

Day, R.H., Oakley, K.L., and Barnard, D.R., 1983, Nest sites and eggs of Kittlitz's and Marbled Murrelets: Condor, v. 85, no. 3, p. 265-273.

Day, R.H., Prichard, A.K., and Nigro, D.A., 2003, Ecological specialization and overlap of Brachyramphus murrelets in Prince William Sound, Alaska: Auk, v. 120, no. 3, p. 680-699.

Deal, J.A., and Harper, W.L., 2004, Marbled Murrelet nesting habitat conservation plan for the Nimpkish Valley, north central Vancouver Island, *in* Hooper, T.D., ed., Species at Risk 2004: Victoria, British Columbia, Pathways to Recovery Conference, p. 1-16.

Dechesne-Mansiere, S.B.C., 2004, Marbled Murrelet habitat management in British Columbia: Background analysis report for the chair of the Forest Practices Board: Victoria, British Columbia, Forest Practices Board, 23 p.

DeGange, A.R., 1996, Conservation assessment for the Marbled Murrelet in southeast Alaska: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, General Technical Report 388, 72 p.

DeGange, A.R., Day, R.H., Takekawa, J.E., and Mendenhall, V.M., 1993, Losses of seabirds in gill nets in the North Pacific, *in* Vermeer, K., Briggs, K.T., Morgan, K.H., and Siegel-Causey, D., eds., Status, ecology and conservation of marine birds of the North Pacific: Ottawa, Ontario, CWS, Environment Canada, Special Publication, p. 204-211.

DeLapp, J.A., DeVelice, R.L., and Hubbard, C.J., 2000, Kenai Peninsula forest condition assessment: Anchorage, Alaska, U.S. Forest Service, Chugach Naitonal Forest, 46 p.

Demarchi, D.A., 2001, Species account for Marbled Murrelet based on 1:250,000 broad ecosystem inventory habitat mapping: Victoria, British Columbia, Ministry of Environment, Lands and Parks, Resources Inventory Branch.

Demarchi, D.A., and Button, A.A., 2001a, Marbled Murrelet nesting habitat capability in British Columbia: Map 2 - Weighted average *capability*: Victoria, British Columbia, Ministry of Environment, Lands and Parks, Resources Inventory Branch, 1:300,000 Scale Map.

Demarchi, D.A., and Button, A.A., 2001b, Marbled Murrelet nesting habitat capability in British Columbia: Map 3 - Weighted average s*uitability*: Victoria, British Columbia, Ministry of Environment, Lands and Parks, Resources Inventory Branch, 1:300,000 Scale Map.

Department of Fisheries and Oceans Canada, 2004, Integrated fisheries management plan: Euphausiids, January 1, 2004 to December 31, 2006, Pacific Region, Vancouver, British Columbia.

Department of Fisheries and Oceans Canada, 2006a, Integrated fisheries management plan: Food and bait herring, November 7, 2006 to February 9, 2007, Pacific Region, Vancouver, British Columbia.

Department of Fisheries and Oceans Canada, 2006b, Integrated fisheries management plan: Roe herring, February 10, 2006 to April 30, 2006: Pacific Region, Vancouver, British Columbia.

DeSanto, T.L., and Nelson, S.K., 1995, Comparative reproductive ecology of the Auks (Family Alcidae) with emphasis on the Marbled Murrelet, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 33-47.

Dick, M., 1979, Notes on the winter seabirds of Chiniak Bay, Kodiak Island, Alaska: Boulder, Colorado, National Oceanic and Atmospheric Administration, Environmental assessment of the Alaska Continental Shelf, Annual Reports of Principal Investigators, v. 2, p. 492-516.

Divoky, G.J., and Horton, M., 1995, Breeding and natal dispersal, nest habitat loss and implications for Marbled Murrelet populations, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 83-87.

Doerr, J.G., and Walsh, P.J., 1994, Seasonal activity patterns of Marbled Murrelets at an inland site on Mitkof Island, southeastern Alaska: Alaska, U.S. Forest Service, Petersburg Ranger District, Report on File, 8 p.

Donald, D.S., 2005, Testing the Recovery Team Marbled Murrelet predictability model using low level aerial assessment in the Zeballos Landscape Unit, Vancouver Island: Black Creek, British Columbia, Ministry of Water, Land, and Air Protection,Vancouver, British Columbia.

Dragoo, D.E., Byrd, G.V., and Irons, D.B., 2006, Breeding status, population trends and diets of seabirds in Alaska, 2003: Homer, Alaska, U.S. Fish and Wildlife Service, AMNWR 06/13

Esslinger, G.G., and Bodkin, J.L., 2006, Trends in southeast Alaska sea otter populations, 1969-2003: U.S. Geological Survey Open File Report, 24 p.

Evanno, G., Regnaut, S., and Goudet, J., 2005, Detecting the number of clusters of individuals using the software structure: a simulation study: Molecular Ecology, v. 14, p. 2611-2620.

Evans Mack, D., Raphael, M.G., and Laake, J.L., 2002, Probability of detecting Marbled Murrelets at sea: Effects of single versus paired observers: Journal of Wildlife Management, v. 66, no. 3, p. 865-873.

Everest, F.H., 2005, Setting the stage for the development of a science-based Tongass Land Management Plan: Landscape and Urban Planning, v. 72, p. 13-24.

Exxon Valdex Oil Spill Trustee Council (EVOSTC), 2006, Update on injured resources and services November 2006: Anchorage, Alaska, 41 p.

Evanno, G., Regnaut, S., and Goudet, J., 2005, Detecting the number of clusters of individuals using the software STRUCTURE: Simulation study: Molecular Ecology v. 14, p. 2611-2620.

Fadely, J., Gerlach, T.P., and Cody, M.B., 1993, Distribution and population estimates of marine birds in the near-shore and pelagic waters of Afognak Island, Alaska: Anchorage, Alaska, U.S. Fish and Wildlife Service, Division of Realty, Biological Report, 18 p.

Falk, K., Benvenuti, S., Dall'Antonia, L., Gilchrist, G., and Kampp, K., 2002, Foraging behaviour of Thick-Billed Murres breeding in different sectors of the North Water polynia: Inter-colony comparison: Marine Ecology Progress Series, v. 231, p. 293-302.

Field, L.J., 1988, Pacific sand lance, Ammodytes hexapterus, with notes on related Ammodytes species, *in* Wilimovsky, N.J., Incze, L.C., and Westerheim, S.J., eds., Species synopses: Life histories of selected fish and shellfish of the Northeast Pacific and Bering Sea: Seattle, University of Washington, p. 15-33.

Fisher, J., 1966, Fulmar population of Britain and Ireland, 1959: Bird Study, v. 13, p. 5-76.

Food and Agriculture Organization, 1995, Code of conduct for responsible fisheries: Rome, Italy, United Nations.

Food and Agriculture Organization, 1999, International plan of action for reducing the incidental catch of seabirds in longline fisheries: Rome, Italy, United Nations.

Ford, C., and Brown, M., 1995, Unusual Marbled Murrelet nest: Wilson Bulletin, v. 107, no. 1, p. 178-179.

Ford, R.G., Bonnell, M.L., Varougean, D.H., Page, G.W., Sharp, B.E., Heinemann, D., and Casey, J.L., 1991, Assessment of direct seabird mortality in Prince William Sound and the western Gulf of Alaska resulting from the *Exxon Valdez* oil spill: Washington, D.C., Ecological Consulting, Inc., Final Report to U.S. Fish and Wildlife Service.

Ford, R.G., and Ward, J.C., 1999, Carcass scavenging rates study for the *M/V Kure* / Humboldt Bay oil spill: Portland, Oregon, R.G. Ford Consulting, Final report to the U.S. Department of Interior.

Ford, R.G., and Ward, J.C., 2000, Bird carcass detection rates following the *M/V Kure* / Humboldt Bay oil spill: Portland, Oregon, R.G. Ford Consulting, Final report to the U.S. Department of Interior.

Ford, R.G., Bonnell, M.L., Varoujean, D.H., Page, G.W., Carter, H.R., Sharp, B.E., Heinemann, D., and Casey, J.L., 1996, Total direct mortality of seabirds resulting from the *Exxon Valdez* oil spill, *in* Rice, S.D. , Spies, R.B., Wolfe, D.A., and Wright, B.A., eds., *Exxon Valdez* Oil Spill Symposium, Anchorage, Alaska, 1996, American Fisheries Society Symposium 18, p. 684-711.

Forest Practices Board, 2004, Lack of direction: Improving Marbled Murrelet habitat conservation under the Forest and Range Practices Act: Victoria, British Columbia, Special Report 21, 12 p.

Forest Practices Board, 2005, Provincial systems fail to protect threatened species: British Columbia, News Release.

Forney, K.A., Benson, S.R., and Cameron, G., 2001, Central California effort and bycatch of sensitive species, 1990-98, *in* Melvin, E.F., and Parrish, J.K., eds., Seabird bycatch: Trends, roadblocks, and solutions: Fairbanks, University of Alaska Sea Grant, p. 141-160.

Forsell, D.J., and Gould, P.J., 1981, Distribution and abundance of marine birds and mammals wintering in the Kodiak area of Alaska: Washington, D.C., U.S. Fish and Wildlife Service, Office of Biological Services, Report 81/13, 72 p.

Foy, R.J., and Paul, A.J., 1999, Winter feeding and changes in somatic energy content of age-0 Pacific herring in Prince William Sound, Alaska: American Fisheries Society Transactions, v. 128, p. 1193-1200.

Fadely, J., Gerlach, T., and Cody, M.B., 1993, Distribution and population estimates of marine birds and mammals in the near-shore and pelagic waters of Afognak Island, Alaska: U.S.Fish and Wildlife Service, Region 7, Anchorage, Alaska.

Francis, R.C., Hare, S.R., Hollowed, A.B., and Wooster, W.S., 1998, Effects of interdecadal climate variability on the oceanic ecosystems of the northeast Pacific: Fisheries Oceanography, v. 7, p. 1-21.

Freeland, H.J., 1992, Physical oceanography of the west coast of Vancouver Island, *in* Vermeer, K., Butler, R.W., and Morgan, K., eds., Ecology, status and conservation of marine and shoreline birds on the west coast of Vancouver Island: Ottawa, Ontario, CWS, Occasional Paper 75, p. 10-14.

Friesen, V.L., Baker, A.J., and Piatt, J.F., 1996a, Phylogenetic relationships within the Alcidae (Charadriiformes: Aves) inferred from total molecular evidence: Molecular Biology and Evolution, v. 13, no. 2, p. 359-367.

Friesen, V.L., Birt, T.P., Piatt, J.F., Golightly, R.T., Newman, S.H., Hébert, P.N., Congdon, B.C., and Gissing, G., 2005, Population genetic structure and conservation of Marbled Murrelets (*Brachyramphus marmoratus*): Conservation Genetics, v. 6, no. 4, p. 607-614.

Friesen, V.L., Congdon, B.C., Kidd, M.G., and Birt, T.P., 1999, PCR primers for the amplification of five nuclear introns in vertebrates: Molecular Ecology, v. 8, p. 2147-2149.

Friesen, V.L., Congdon, B.C., Walsh, H.E., and Birt, T.P., 1997, Intron variation in Marbled Murrelets detected using analyses of single-stranded conformational polymorphisms: Molecular Ecology, v. 6, no. 11, p. 1047-1058.

Friesen, V.L., and Piatt, J.F., 2003, Genetic study to aid in restoration of murres, guillemots and murrelets to the Gulf of Alaska: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, Restoration Project 00169 Final Report, 121 p.

Friesen, V.L., Piatt, J.F., and Baker, A.J., 1996b, Evidence from cytochrome b sequences and allozymes for a 'new' species of Alcid: The Long-Billed Murrelet (*Brachyramphus perdix*): Condor, v. 98, no. 4, p. 681-690.

Fry, D.M., 1995, Pollution and fishing threats to Marbled Murrelets, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 257-260.

Gaggiotti, O.E., Lange, O., Rassmann, K., and Gliddon, C., 1999, Comparison of two indirect methods for estimating average levels of gene flow using microsatellite data: Molecular Ecology, v. 8, p. 1513-1520.

Gardenfors, U., Rodriquez, J.P., Hilton-Taylor, C.P., Hyslop, C., Mace, G., Molur, S., and Poss, S., 1999, Draft guidelines for the application of Red List criteria at national and regional levels: Species, v. 31-32, p. 58-70.

Gaston, A.J., 1996, Seabird distributions in Laskeek Bay, *in* Gaston, A.J., ed., Laskeek Bay Conservation Society: Queen Charlotte City, British Columbia, Annual Scientific Report, 1995, p. 2-28.

Gaston, A.J., Collins, B.T., and Diamond, A.W., 1987, Estimating densities of birds at sea and the proportion in flight from counts made on transects of indefinite width: Ottawa, Ontario, CWS, Occasional Paper 59, 16 p.

Gaston, A.J., and Jones, I., 1998, Auks Alcidae: United Kingdom, Oxford University Press, Birds of the world, 388 p.

Gillespie, G.G., and Westrheim, S.J., 1997, Synopsis of information on marine fishes utilized as prey by marine and shoreline birds in the Queen Charlotte Islands, *in* Vermeer, K. and Morgan, K.H., eds., Ecology, status, and conservation of marine and shoreline birds of the Queen Charlotte Islands: Ottawa, Ontario, CWS, Occasional Paper 93, p. 36-55.

Golet, G.H., Kuletz, K.J., Roby, D.D., and Irons, D.B., 2000, Adult prey choices affects chick growth and reproductive success in Pigeon Guillemots: Auk, v. 117, no. 1, p. 82-91.

Goodman, L.A., 1969, Analysis of population growth when the birth and death rates depend on several factors: Biometrics, v. 25, p. 659-681.

Goudet, J., 1995, FSTAT (version 1.2): Computer program to calculate *F*-statistics: Journal of Heredity, v. 86, p. 485-486.

Gould, P.J., and Forsell, D.J., 1989, Techniques for shipboard surveys of marine birds: Washington, D.C., U.S. Fish and Wildlife Service Technical Report 25, 22 p.

Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLaughlin, F.A., and McNutt, S.L., 2006, Major ecosystem shift in the northern Bering Sea: Science, v. 311, p. 1461-1464.

Green, R.N., and Klinka, K., 1994, Field guide to site identification and interpretation for the Vancouver Forest Region: Victoria, British Columbia, Ministry of Forests, Resources Branch, Land Management Handbook 28, 285 p.

Grosse, D.J., and Hay, D.E., 1988, Pacific Herring, *Clupea harengus pallasi*, in the northeast Pacific and Bering Sea, *in* Wilimovsky, N.J., Incze, L.C., and Westrheim, S.J., eds., Species synopses: Life histories of selected fish and shellfish of the northeast Pacific and Bering Sea: Seattle, University of Washington, p. 34-54.

Haldorson, L., Shirley, T., Coyle, K.L., and Thorne, R., 1999, Forage species studies in Prince William Sound, *in* Duffy, D.C., ed., APEX project: Alaska predator ecosystem experiment in Prince William Sound and the Gulf of Alaska: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, Restoration Project 98163A Annual Report, Appendix A.

Hamer, T.E., and Nelson, S.K., 1995, Characteristics of Marbled Murrelet nest trees and nesting stands, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 69-82.

Hamer, T.E., and Thompson, C., 1997, Avoidance of boats by Marbled Murrelets during marine surveys: Olympia, Washington, U.S. Fish and Wildlife Service, 17 p.

Hanley, T.A., Smith, W.P., and Gende, S.M., 2005, Maintaining wildlife habitat in southeastern Alaska: Implications of new knowledge for forest management and research: Landscape and Urban Planning, v. 72, no. 1-3, p. 113-133.

Hanna, G.D., 1920, Additions to the avifauna of the Pribilof Islands, Alaska, including four species new to North America: Auk, v. 37, p. 248-254.

Hare, S.R., and Mantua, N.J., 2000, Empirical evidence for North Pacific regime shifts in 1977 and 1989: Progress in Oceanography, v. 47, p. 103-145.

Harlin-Cognato, A., Bickham, J.W., Roughlin, T.R., and Honeycutt, R.L., 2006, Glacial refugia and the phylogeography of Stellar's sea lion (*Eumatopias jubatus*) in the North Pacific: Journal of Evolutionary Biology, v. 19, p. 955-969.

Harris, A.S., 1989, Wind in the forests of southeast Alaska and guides for reducing damage: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, General Technical Report 244, 63 p.

Hatch, S.A., 2003, Statistical power for detecting trends with applications to seabird monitoring: Biological Conservation, v. 111, p. 317-329.

Hay, D.E., Healey, M.C., Richards, L.J., and Marliave, J.B., 1989, Distribution, abundance and habitat of prey fishes in the Strait of Georgia, *in* Vermeer, K. and Butler, R.W., eds., Ecology and status of marine and shoreline birds in the Strait of Georgia, British Columbia: Ottawa, Ontario, CWS, Special Publication, p. 37-49.

Hay, D.E., Healey, M.C., Ware, D.M., and Wilimovsky, N.J., 1992, Distribution, abundance and habitat of prey fish on the west coast of Vancouver Island, *in* Vermeer, K., Butler, R.W., and Morgan, K.H., eds., Ecology, status, and conservation of marine and shoreline birds on the west coast of Vancouver Island: Ottawa, Ontario, CWS, Occasional Paper 75, p. 22-29.

Hay, D.E., and McCarter, P.B., 1997, Continental shelf area and distribution, abundance, and habitat of herring in the North Pacific, *in* Role of Forage Fishes in Marine Ecosystems International Symposium, Anchorage, Alaska, 1996, p. 559-572.

Hayashi, K., 1991, PDR-SSCP: a simple and sensitive method for detection of mutations in the genomic DNA: PCR Methods Application, v. 1, no. 1, p. 34-8.

Haynes, T.B., 2006, Modeling habitat use of young-of-the-year Pacific sand lance (*Ammodytes hexapterus*) in the nearhore region of Barkley Sound, British Columbia: MSc Thesis, British Columbia, University of Victoria.

Haynes, T., Robinson, C., Shepperd, P., and Hansen, B., 2004, Determining critical marine foraging habitats of the threatened Marbled Murrelet (*Brachyramphus marmoratus*) in Pacific Rim National Park Reserve of Canada, *in* Hooper, T.D., ed., Species at Risk 2004: Victoria, British Columbia, Pathways to Recovery Conference, p. 1-8.

Hayward, G.D., and Iverson, C.G., 1998a, Challenge of evaluating population trends for conservation management: Marbled Murrelets in Alaska: Northwest Science, v. 72, no. 4, p. 315-319.

Hayward, G.D., and Iverson, C.G., 1998b, Long-term trend in Marbled Murrelets in southeast Alaska based on Christmas Bird Counts: Northwest Science, v. 72, no. 3, p. 170-179.

Hebert, P.N., Carter, H.R., Golightly, R.T., and Orthmeyer, D.L., 2003, Radio-telemetry evidence of re-nesting in the same season by the Marbled Murrelet: Waterbirds, v. 26, p. 261-265.

Hedrick, P., 1999, Perspective: Highly variable loci and their interpretation in evolution and conservation: Evolution, v. 53, p. 313-318.

Heifetz, J., 1997, Workshop on the potential effects of fishing gear on benthic habitats: National Marine Fisheries Service, AFSC Processed Report 97-04, 17 p.

Henkel, L.A., and Harvey, J.T., 2006, Potential prey resources for Marbled Murrelets in central California: California Fish and Game, v. 92, no. 4, p. 191-206.

Hennon, P.E., D'Amore, D.V., Zeglen, S., and Grainger, M., 2005, Yellow-cedar decline in the north coast forest district of British Columbia: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, Research Note 549, 20 p.

Hennon, P.E., and McClellan, M.H., 2003, Tree mortality and forest structure in the temperate rain forests of southeast Alaska: Canadian Journal of Forest Research, v. 33, p. 1621-1634.

Hennon, P.E., and Shaw, C.G., 1994, Did climatic warming trigger the onset and development of yellow-cedar decline in southeast Alaska?: European Journal of Forest Pathology, v. 24, p. 399-418.

Hentze, N.T., 2006, Effects of boat disturbance on seabirds off southwestern Vancouver Island, British Columbia: MSc Thesis: British Columbia, University of Victoria.

Heusser, C.J., 1990, Late Quarternary vegetation of the Aleutian Islands, southwestern Alaska: Canadian Journal of Botany, v. 68, p. 1320-1326.

Hirsch, K.V., Woodby, D.A., and Astheimer, L.B., 1981, Growth of a nestling Marbled Murrelet: Condor, v. 83, p. 264-265.

Hobbs, J., 2003, Marbled Murrelet nesting habitat in the Mid Coast Forest District: Assessment of the Mid Coast Model: Victoria, British Columbia, Ministry of Water, Land and Air Protection.

Hobson, K.A., 1990, Stable isotope analysis of Marbled Murrelets—Evidence for fresh-water feeding and determination of trophic level: Condor, v. 92, no. 4, p. 897-903.

Holling, C.S., 1978, Adaptive environmental assessment and management: Chichester, New York, John Wiley and Sons.

Hollowed, A.B., Hare, S.R., and Wooster, W.S., 2001, Pacific basin climate variability and patterns of northeast Pacific marine fish production: Progress in Oceanography, v. 49, p. 257-282.

Hollowed, A.B., and Wooster, W.S., 1995, Decadal-scale variations in the eastern subarctic Pacific: II. Response of northeast Pacific fish stocks, *in* Beamish, R.J., ed., Climate change and northern fish populations, p. 373-385.

Holsten, E.H., and Werner, R.A., 1990, Comparison of white, Sitka, and Lutz spruce as hosts of the spruce beetle in Alaska: Canadian Journal of Forest Research, v. 20, p. 292-297.

Holt, R.F., 2004, Environmental conditions report for the Haida Gwaii/Queen Charlotte Islands land use plan: Victoria, British Columbia, Ministry of Sustainable Resource Management.

Hudson, P.J., 1985, Population parameters for the Atlantic Alcidae, *in* Nettleship, D.N., and Birkhead, T.R., ed., Atlantic Alcidae: New York, Academic Press, p. 233-261.

Hull, C.L., 1999, Status report update on Marbled Murrelet, *Brachyramphus marmoratus* (Gmelin): Burnaby, British Columbia, Simon Frasier University, Department of Biological Sciences, Centre for Wildlife Ecology, Report to COSEWIC, Ottawa, Ontario, 66 p.

Hull, C.L., Kaiser, G.W., Lougheed, C., Lougheed, L.W., Boyd, W.S., and Cooke, F., 2001, Intraspecific variation in commuting distance of Marbled Murrelets (*Brachyramphus marmoratus*): Ecological and energetic consequences of nesting further inland: Auk, v. 118, no. 4, p. 1036-1046.

Hunt, G.L. Jr., 1995, Monospecific and mixed species foraging associations of Marbled Murrelets, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, 255-256.

Hunt, G.L. Jr., and Schneider, D.S., 1987, Scale-dependent processes in the physical and biological environment of marine birds, *in* Croxall, J.P., ed., Seabirds: Feeding ecology and role in marine ecosystems: United Kingdom, Cambridge University Press, p. 7-41.

Hunt, G.L. Jr, and Stabeno, P.J., 2002, Climate change and the control of energy flow in the southeastern Bering Sea: Progress in Oceanography, v. 55, no. 1-2, p. 5-22.

Ibarguchi, G., Birt, T.P., Warheit, K.I., Boag, P.T., and Friesen, V.L., 2000, Microsatellite loci from Common and Thick-Billed murres, *Uria aalge* and *U. lomvia*: Molecular Ecology, v. 9, p. 629-644.

Identified Wildlife Management Strategy, 2004, Marbled Murrelet (*Brachyramphus marmoratus*), *in* Accounts and measures for managing identified wildlife: Victoria, British Columbia, Ministry of Water, Air, and Land Protection, Biodiversity Branch, v. 5, 15 p.

Integral Consulting, Inc., 2006, Information synthesis and recovery recommendations for resources and services injured by the *Exxon Valdez* oil spill: Mercer Island, Washington, *Exxon Valdez* Oil Spill Restoration Project 060783 Final Report.

Irons, D.B., Kendall, S.J., Erickson, W.P., and McDonald, L.L., 2000, Nine years after the *Exxon Valdez* oil spill: Effects on marine bird populations in Prince William Sound, Alaska: Condor, v. 102, no. 4, p. 723-737.

Isleib, M.E.P., and Kessel, B., 1973, Birds on the north Gulf Coast - Prince William Sound Region, Alaska: Fairbanks, University of Alaska Press, Biological Paper 14, 149 p.

Iverson, G.C., Hayward, G.D., Titus, K., DeGayner, E., Lowell, R.E., Crocker-Bedford, D.C., Schempf, P.F., and Lindell, J., 1996, Conservation assessment for the Northern Goshawk in southeast Alaska: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, General Technical Report 387.

Jacobson, M.J., and Hodges, J.I., 1999, Population trend of adult bald eagles in southeast Alaska: Journal of Raptor Research, v. 33, p. 295-298.

Jodice, P.G.R., Garman, S.L., and Collopy, M.E., 2001, Using resampling to assess reliability of audio-visual survey strategies for Marbled Murrelets in inland forest sites: Waterbirds, v. 24, p. 331-344.

Jones, P.H., 2001, Marbled Murrelets of the Caren Range and Middlepoint Bight: Vancouver, British Columbia, Western Canada Wilderness Committee.

Julin, K.R., 1997, Assessments of wildlife viability, old-growth timber volume estimates, forested wetlands, and slope stability, *in* Shaw, C.G. III, tech. coord., Conservation and resource assessments for the Tongass land management plan revision: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, General Technical Report 392, 58 p.

Kaiser, G.W., Barclay, H.J., Burger, A.E., Kangasniemi, D., Lindsay, D.J., Munro, W.T., Pollard, W.R., Redhead, R., Rice, J., and Seip, D.R., 1994, National recovery plan for the Marbled Murrelet: Ottawa, Ontario, Recovery of Nationally Endangered Wildlife Committee, Report 8, 36 p.

Kaiser, G.W., Mahon, T.E., and Fawcett, M.D., 1991, Studies of Marbled Murrelets in marine habitats, during 1990: Delta, British Columbia, CWS, Pacific and Yukon Region, Technical Report 131, 52 p.

Keller, V., 1991, Effects of disturbance from roads on the distribution of feeding sites on geese wintering in northeast Scotland: Ardea, v. 79, p. 229-231.

Kelson, J.D., Manley, I.A., and Carter, H.R., 1995, Decline of the Marbled Murrelet in Clayoquot Sound, British Columbia: 1982-1993: Northwestern Naturalist, v. 76, no. 1, p. 90-98.

Kessel, B., and Gibson, D.D., 1978, Status and distribution of Alaska birds: Albuquerque, New Mexico, Cooper Ornithological Society, Studies of Avian Biology v. 1.

King, J.R., 2005, Report of the study group on fisheries and ecosystem responses to recent regime shifts, PICES Scientific Report 28, 162 p.

King, J.R., and Sanger, G.A., 1979, Oil vulnerability index for marine oriented birds, *in* Bartonek, J.C. and Nettleship, D.N., eds., Conservation of marine birds in northern North America: Washington, D.C., U.S. Fish and Wildlife Service Research Report 11, p. 227-239.

Kissling, M.M., Reid, M., Lukacs, P., Gende, S.M., and Lewis, S., 2005, Temporal and spatial variation of juvenile and adult Kittlitz's Murrelets in Icy Bay, Alaska: Juneau, Alaska, U.S. Fish and Wildlife Service, Final Field Plan and Draft Report.

Kitaysky, A.S., Piatt, J.F., Wingfield, J.C., and Romano, M., 1999, Adrenocortical stress-response of Black-legged Kittiwake chicks in relation to dietary restrictions: Journal of Comparative Physiology (B), v. 169, p. 303-310.

Klosiewski, S.P., and Laing, K.K., 1994, Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, State / Federal Natural Resource Damage Assessment Final Report, Bird Study 2, 88 p.

Knapp, G., 1992, Native timber harvests in southeast Alaska: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, General Technical Report 284, 48 p.

Knapton, R.W., Petrie, S.A., and Herring, G., 2000, Human disturbance of diving ducks on Long Point Bay, Lake Erie: Wildlife Society Bulletin, v. 28, no. 4, p. 923-930.

Knight, R.L., and Gutzwiller, K.J., 1995, Wildlife and recreationists: Coexistence through management and research: Washington, D.C., Island Press.

Korschgen, C.E., George, L.S., and Green, W.L., 1985, Disturbance of diving ducks by boaters on a migrational staging area: Wildlife Society Bulletin, v. 13, no. 3, p. 290-296.

Kozie, K., 1993, Coastal wildlife survey - Seabirds and marine mammals along the Malaspina Forelands 1992: Glenallen, Alaska, Wrangell-St. Elias National Park and Preserve, Research and Resource Management Report 92-07.

Kramer, M.G., Hansen, A.J., Taper, M.L., and Kissinger, E.J., 2001, Abiotic controls on long-term windthrow disturbance and temperate rain forest dynamics in southeast Alaska: Ecology, v. 82, no. 10, p. 2749-2768.

Krasnow, L.D., and Sanger, G.A., 1982, Feeding ecology of marine birds in the nearshore waters of Kodiak Island: Anchorage, Alaska, U.S. Fish and Wildlife Service, National Fishery Research Center, Migratory Bird Section, Final Report to OCSEAP, Research Unit 45, p. 505-630.

Krebs, C.J., 1978, Ecology: Experimental analysis of distribution and abundance: New York, Harper and Row, ed. 2.

Kriebel, D., Tickner, J., Epstein, P., Lemons, J., Levins, R., Loechler, E.L., Quinn, M., Rudel, R., Schettler, T., and Stoto, M., 2001, Precautionary principle in environmental science: Environmental Health Perspectives, v. 109, p. 871-876.

Krkosek, M., Lewis, M.A., Morton, A., Frazer, L.N., and Volpe, J.P., 2006, Epizootics of wild fish induced by farm fish: National Academy of Sciences (USA) Proceedings, v. 103, p. 15506-15510.

Kuletz, K.J., 1994, Marbled Murrelet abundance and breeding activity at Naked Island, Prince William Sound, and Kachemak Bay, Alaska, before and after the Exxon Valdez oil spill: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, State / Federal Natural Resource Damage Assessment Final Report, Bird Study 6, 62 p.

Kuletz, K.J., 1996, Marbled Murrelet abundance and breeding activity at Naked Island, Prince William Sound, and Kachemak Bay, Alaska, before and after the *Exxon Valdez* oil spill, In Rice, S.D., Spies, R.B., Wolfe, D.A., and Wright, B.A., eds., *Exxon Valdez* Oil Spill Symposium, Anchorage, Alaska, 1996, American Fisheries Society Symposium 18, p. 770-784.

Kuletz, K.J., 1997, Marbled Murrelet *Brachyramphus marmoratus*: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, Restoration Notebook Series.

Kuletz, K.J., 2001, Marine bird and mammal surveys pre- and post-spill for areas affected by the Windy Bay oil spill in Prince William Sound, Summer 2001: U.S. Fish and Wildlife Service, Anchorage, Alaska,.

Kuletz, K.J., 2005, Foraging behavior and productivity of a non-colonial seabird, the Marbled Murrelet (*Brachyramphus marmoratus*), relative to prey and habitat: Dissertation, British Columbia, University of Victoria.

Kuletz, K.J., Irons, D.B., Agler, B.A., Piatt, J.F., and Duffy, D.C., 1997, Long-term changes in diets and populations of piscivorous birds and mammals in Prince William Sound, Alaska., *in* Role of Forage Fishes in Marine Ecosystems International Symposium, Anchorage, Alaska, 1996, Lowell Wakefield Fisheries Symposium, Sea Grant College Program Report 97-01, p. 703-706.

Kuletz, K.J., and Kendall, S.J., 1998, Productivity index for Marbled Murrelets in Alaska based on surveys at sea: Journal of Wildlife Management, v. 62, no. 2, p. 446-460.

Kuletz, K.J., and Kendall, S.J., 1999, Marbled Murrelet productivity relative to forage fish abundance and chick diet, *in* Wright, B.A. and Duffy, D.C., APEX Project: Alaska Predator Ecosystem Experiment in Prince William Sound and the Gulf of Alaska: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, Restoration Project 98163R Annual Report, p. 349-363.

Kuletz, K.J., Labunski, E.A., and Brenneman, K.M., 2003a, Distribution and abundance of Kittlitz's Murrelets in Prince William Sound, Alaska, in Summer 2001: Anchorage, Alaska, U.S. Fish and Wildlife Service.

Kuletz, K.J., and Marks, D.K., 1997, Post-fledging behavior of a radio-tagged juvenile Marbled Murrelet: Journal of Field Ornithology, v. 68, no. 3, p. 421-425.

Kuletz, K.J., Marks, D.K., Flint, D., Burns, R.A., and Prestash, L.M., 1995a, Marbled Murrelet foraging patterns and a pilot productivity index for murrelets in Prince William Sound, Alaska: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, Restoration Project 94102 Final Report, 175 p.

Kuletz, K.J., Marks, D.K., Naslund, N.L., and Cody, M.B., 1995b, Marbled Murrelet activity relative to forest characteristics in the Naked Island area, Prince William Sound, Alaska: Northwestern Naturalist, v. 76, no. 1, p. 4-11.

Kuletz, K.J., Marks, D.K., Naslund, N.L., Goodson, N.J., and Cody, M.B., 1994a, Information needs for habitat protection: Marbled Murrelet habitat identification: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, Restoration Project 93051B Final Report, 70 p.

Kuletz, K.J., Marks, D.K., Naslund, N.L., Goodson, N.J., and Cody, M.B., 1995c, Inland habitat suitability for the Marbled Murrelet in south central Alaska, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 141-149.

Kuletz, K.J., Naslund, N.L., and Marks, D.K., 1994b, Identification of Marbled Murrelet nesting habitat in the *Exxon Valdez* oil spill zone: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, Restoration Project R15 Final Report, 67 p.

Kuletz, K.J., and Piatt, J.F., 1999, Juvenile Marbled Murrelet nurseries and the productivity index: Wilson Bulletin, v. 111, no. 2, p. 257-261.

Kuletz, K.J., Stephensen, S.W., Irons, D.B., Labunski, E.A., and Brenneman, K.M., 2003b, Changes in distribution and abundance of Kittlitz's Murrelets *Brachyramphus brevirostris* relative to glacial recession in Prince William Sound, Alaska: Marine Ornithology, v. 31, no. 2, p. 133-140.

Lack, D., 1966, Population studies of birds: London, Oxford University Press.

Lance, B.K., Irons, D.B., Kendall, S.J., and McDonald, L.L., 2001, Evaluation of marine bird population trends following the *Exxon Valdez* oil spill, Prince William Sound, Alaska: Marine Pollution Bulletin, v. 42, no. 4, p. 298-309.

Lank, D.B., Parker, N.R., Krebs, E.A., and McFarlane Tranquilla, L.A., 2003, Geographic distribution, habitat selection, and population dynamics with respect to nesting habitat characteristics of Marbled Murrelets (*Brachyramphus marmoratus*): Vancouver, British Columbia, Simon Fraser University, Centre for Wildlife Ecology, 62 p.

Leigh-Spencer, S., Anderson, J., and Hobbs, J., 2002, Aerial survey of Marbled Murrelet nesting habitat suitability ratings within the Mid Coast Forest District: Williams Lake, British Columbia, Ministry of Water, Land and Air Protection.

Leslie, P.H., 1945, On the use of matrices in certain population mathematics: Biometrika, v. 33, p. 183-212.

Lessica, P., and Allendorf, F.W., 1995, When are peripheral populations valuable for conservation?: Conservation Biology, v. 9, p. 753-760.

Lewis, S.B., Titus, K., and Fuller, M.R., 2006, Northern goshawk diet during the nesting season in southeast Alaska: Journal of Wildlife Management, v. 70, p. 1151-1160.

Lindell, J.R., 2005, Results of at-sea *Brachyramphus* murrelet surveys in Icy Strait and other selected areas of southeast Alaska, 1993-1999: Juneau, Alaska, U.S. Fish and Wildlife Service, Final report.

Litzow, M.A., 2006, Climate regime shifts and community reorganization in the Gulf of Alaska: How do recent shifts compare with 1976/1977?: Journal of Marine Sciences, v. 63, p. 1386-1396.

Lougheed, C., 1999, Breeding chronology, breeding success, distribution and movements of Marbled Murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia: Thesis, Burnaby, British Columbia, Simon Fraser University, 89 p. CWS Technical Report 352.

Lougheed, C., Lougheed, L.W., Cooke, F., and Boyd, W.S., 2002a, Local survival of adult and juvenile Marbled Murrelets and their importance for estimating reproductive success: Condor, v. 104, no. 2, p. 309-318.

Lougheed, C., Vanderkist, B.A., Lougheed, L.W., and Cooke, F., 2002b, Techniques for investigating breeding chronology in Marbled Murrelets, Desolation Sound, British Columbia: Condor, v. 104, no. 2, p. 319-330.

Luginbuhl, J.M., Marzluff, J.M., Bradley, J.E., Raphael, M.G., and Varland, D.E., 2001, Corvid survey techniques and the relationship between corvid relative abundance and nest predation: Journal of Field Ornithology, v. 72, p. 556-572.

Mack, D.E., Raphael, M.G., and Laake, J, 2002, Probablility of detecting marbled murrelets at sea: effects of single versus paired observers: Journal of Wildlife Management, v. 66, p. 865-873.

Mackas, D.L., Goldblatt, R., and Lewis, A.G., 1998, Interdecadal variation in developmental timing of Neocalanus plumchrus populations at Ocean Station P in the subarctic north Pacific: Canadian Journal of Fisheries and Aquatic Sciences, v. 55, p. 1878-1893.

Mackas, D.L., Thomson, R.E., and Galbraith, M., 2001, Changes in the zooplankton community of British Columbia continental margin, 1985-1999, and their covariation with oceanographic conditions: Canadian Journal of Fisheries and Aquatic Sciences, v. 58, p. 685-702.

Mahon, T.E., Kaiser, G.W., and Burger, A.E., 1992, Role of Marbled Murrelets in mixed-species feeding flocks in British-Columbia: Wilson Bulletin, v. 104, no. 4, p. 738-743.

Maniscalco, J.M., and Ostrand, W.D., 1997, Seabird behaviors at forage fish schools in Prince William Sound, Alaska, *in* Role of Forage Fishes in Marine Ecosystems International Symposium, Anchorage, Alaska, 1996, Lowell Wakefield Fisheries Symposium, Sea Grant College Program Report 97-01, p. 175-189.

Manley, I.A., 1999, Behaviour and habitat selection of Marbled Murrelets nesting on the Sunshine Coast: Thesis, Burnaby, British Columbia, Simon Fraser University, 163 p.

Manley, I.A., and Nelson, S.K., 1999, Habitat characteristics associated with nest success and predation at Marbled Murrelet tree nests: Pacific Seabirds, v. 26, no. 1, p. 40.

Manly, B.F.J., 1997, Randomization, bootstrap and Monte Carlo methods in biology: London, Chapman and Hall.

Manly, B.F.J., 2006a, Incidental catch and interactions of marine mammals and birds in the Cook Inlet salmon driftnet and setnet fisheries, 1999-2000: Cheyenne, Wyoming, Western EcoSystems Technology, Inc., Draft Final Report to National Marine Fisheries Service.

Manly, B.F.J., 2006b, Incidental take and interactions of marine mammals and birds in the Kodiak Island salmon set gillnet fishery, 2002 and 2005: Cheyenne, Wyoming, Western EcoSystems Technology, Inc., Final Report to National Marine Fisheries Service.

Manly, B.F.J., Van Atten, A.S., Kuletz, K.J., and Nations, C., 2003, Incidental catch of marine mammals and birds in the Kodiak Island set gillnet fishery in 2002: Cheyenne, Wyoming, WEST, Inc., Final Report to NOAA NMFS, 91 p.

Maravelias, C.D., and Reid, D.G., 1997, Identifying the effects of oceanographic features and zooplankton on prespawning herring abundance using generalized additive models: Marine Ecology Progress Series, v. 147, p. 1-9.

Marcström. V, Keith, L.B., Engren, E., and Cary, J.R., 1989, Demographic responses of Arctic hares (*Lepus timidus*) to experimental reductions of red foxes (*Vulpes vulpes*) and martens (*Martes martes*): Canadian Journal of Zoology, v. 67, p. 658-668.

Marks, D.K., and Kuletz, K.J., 2001, Use of treeless and forested habitat by Marbled Murrelets in south-central Alaska: Waterbirds, v. 24, no. 2, p. 161-168.

Marks, D.K., Kuletz, K.J., and Naslund, N.L., 1995, Use of boat-based surveys to determine coastal inland habitat associations of Marbled Murrelets in Prince William Sound, Alaska: Northwestern Naturalist, v. 76, no. 1, p. 63-72.

Marks, D.K., and Naslund, N.L., 1994, Sharp-Shinned Hawk preys on a Marbled Murrelet nesting in old-growth forest: Wilson Bulletin, v. 106, no. 3, p. 565-567.

Marty, G.D., Freiberg, E.F., Meyers, T.R., Wilcock, J.F.T.B., and Hinton, D.E., 1998, Viral hemorrhagic septicemia, *Ichthyophonus hoferi*, and other causes of mortality of Pacific herring, *Clupea pallasi*, spawning in Prince William Sound, Alaska, USA: Diseases of Aquatic Organisms, v. 32, p. 15-40.

Mason, A., Burger, A.E., and Hansen, B., 2002, At-sea surveys of Marbled Murrelets in Clayoquot Sound, 1996-2000, *in* Burger, A.E. and Chatwin, T.A., eds., Multi-scale studies of populations, distribution and habitat associations of Marbled Murrelets in Clayoquot Sound, British Columbia: Victoria, British Columbia, Ministry of Water, Land and Air Protection, p. 15-33.

Mathews, N.J.C., and Burger, A.E., 1998, Diving depth of a Marbled Murrelet: Northwestern Naturalist, v. 79, no. 2, p. 70-71.

McArthur, R.H., and Pianka, E.R., 1966, Optimal use of a patchy environment: American Naturalist, v. 100, p. 603-609.

McCune, B., Amsberry, K.A., Camacho, F.J., CLery, S., Cole, C., Emerson, C., Felder, G., French, P., Greene, D., Harris, R., Hutten, M., Larson, B., Lesko, M., Majors, S., Markwell, T., Parker, G.G., Pendergrass, K., Peterson, E.B., Peterson, E.T., Platt, J., Proctor, J., Rambo, T., Rosso, A., Shaw, D., Turner, R., and Widmer, M., 1997, Vertical profile of epiphytes in a Pacific Northwest old-growth forest: Northwest Science, v. 71, no. 2, p. 145-152.

McCune, B., Rosentreter, R., Ponzetti, J.M., and Shaw, D.C., 2000, Epiphyte habitats in an old conifer forest in western Washington: Bryologist, v. 103, no. 3, p. 417-427.

McFarlane Tranquilla, L.A., Bradley, R.W., Lank, D.B., Williams, T.D., Lougheed, L.W., and Cooke, F., 2003a, Reliability of brood patches in assessing reproductive status in the Marbled Murrelet: Words of caution: Waterbirds, v. 26, no. 1, p. 108-118.

McFarlane Tranquilla, L.A., Bradley, R.W., Parker, N.R., Lank, D.B., and Cooke, F., 2003b, Replacement laying in Marbled Murrelets: Marine Ornithology, v. 31, no. 1, p. 75-81.

McFarlane Tranquilla, L.A., Parker, N.R., Bradley, R.W., Lank, D.B., Krebs, E.A., Lougheed, L.W., and Lougheed, C., 2005, Breeding chronology of Marbled Murrelets varies between coastal and inshore sites in southern British Columbia: Journal of Field Ornithology, v. 76, no. 4, p. 357-367.

McFarlane Tranquilla, L.A., Williams, T.D., and Cooke, F., 2003c, Using vitellogenin to identify interannual variation in breeding chronology of Marbled Murrelets (*Brachyramphus marmoratus*): Auk, v. 120, no. 2, p. 512-521.

McGowan, J.A., Cayan, D.R., and Dorman, L.M., 1998, Climate-ocean variability and ecosystem response in the northeast Pacific: Science, v. 281, no. 5374, p. 210-217.

McKnight, A., Sullivan, K.M., Irons, D.B., Stephensen, S.W., and Howlin, S., 2006, Marine bird and sea otter population abundance of Prince William Sound, Alaska: Trends following the T/V *Exxon Valdez* oil spill, 1989-2005: Anchorage, Alaska, USFWS, *Exxon Valdez* Oil Spill Restoration Project 050751 Annual Report.

McLennan, D., Veenstra, V., and Manley, I.A., 2000, Preliminary landscape-level habitat suitability algorithms for Marbled Murrelet and Queen Charlotte Goshawk on the Queen Charlotte Islands/Haida Gwaii: Smithers, British Columbia, Oikos Ecological Services, Report to Ministry of Environment, Lands and Parks.

McShane, C., Hamer, T.E., Carter, H.R., Swartzman, G., Friesen, V.L., Ainley, D.G., Tressler, R., Nelson, S.K., Burger, A.E., Spear, L.B., Mohagen, T., Martin, R., Henkel, L.A., Prindle, K., Strong, C., and Keany, J., 2004, Evaluation report for the 5-year status review of the Marbled Murrelet in Washington, Oregon,and California: Seattle, Washington, EDAW, Inc., Final report for U.S. Fish and Wildlife Service, Portland, Oregon, 356 p.

Meehan, J.P., 1996, Status of Marbled and Kittlitz's murrelets at the Adak Naval Reservation, Alaska: Adak, Alaska, U.S. Fish and Wildlife Service, AMNWRR 08, Department of Defense Legacy Projects 400 and 1658, 48 p.

Melvin, E.F., and Parrish, J.K., 2001, Seabird bycatch: Trends, roadblocks and solutions: Fairbanks, University of Alaska, Sea Grant 01-01.

Melvin, E.F., Parrish, J.K., and Conquest, L.L., 1999, Novel tools to reduce seabird bycatch in coastal gillnet fisheries: Conservation Biology, v. 13, no. 6, p. 1386-1397.

Melvin, E.F., Parrish, J.K., and Conquest, L.L., 2001, Novel tools to reduce seabird bycatch in coastal gillnet fisheries, *in* Melvin, E.F., and Parrish, J.K., eds., Seabird bycatch: Trends, roadblocks, and solutions: Fairbanks, University of Alaska Sea Grant, p. 161-184.

Mendenhall, V.M., 1992, Distribution, breeding records, and conservation problems of the Marbled Murrelet in Alaska: Western Foundation of Vertebrate Zoology Proceedings, v. 5, no. 1, p. 5-16.

Meyer, C.B., Miller, S.L., and Ralph, C.J., 2002, Multi-scale landscape and seascape patterns associated with Marbled Murrelet areas on the U.S. west coast: Landscape Ecology, v. 17, p. 95-115.

Mikola, J., Miettinen, M., Lehikoinen, E., and Lehtila, K., 1994, Effects of disturbance caused by boating on survival and behavior of Velvet Scoter Melanitta fusca ducklings: Biological Conservation, v. 67, p. 119-124.

Miller, S.L., Meyer, C.B., and Ralph, C.J., 2002, Land and seascape patterns associated with Marbled Murrelet abundance offshore: Waterbirds, v. 25, no. 1, p. 100-108.

Minerals Management Service, 2003, Alaska Outer Continental Shelf: Cook Inlet Planning Area, Oil and gas lease sales 191 and 199 final environmental impact statement: Anchorage, OCS EIS/EA MMS 2003-055.

Morgan, K.H., Vermeer, K., and McKelvey, R.W., 1991, Atlas of pelagic birds of western Canada: Ottawa, Ontario, CWS, Occasional Paper 72, 72 p.

Moum, T., Johansen, S., Erikstad, K.E., and Piatt, J.F., 1994, Phylogeny and evolution of the Auks (Subfamily Alcinae) based on mitochondrial-DNA sequences: National Academy of Sciences (USA) Proceedings, v. 91, no. 17, p. 7912-7916.

Mundy, P.R., and Olsson, P., 2005, Climate and weather, *in* Mundy, P.R., ed., Gulf of Alaska: Biology and Oceanography: Fairbanks, Alaska Sea Grant, p. 25-34.

Munro, J.A., and Clemens, W.A., 1931, Waterfowl in relation to the spawning of herring in British Columbia, Canadian Fishery Research Board Bulletin 17.

Murphy, K.A., Suring, L.H., and Iliff, A., 2004, Western Prince William Sound human use and wildlife disturbance model: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, Restoration Project 99339 Final Report, 271 p.

Naslund, N.L., 1993, Why do Marbled Murrelets attend old-growth forest nesting areas year-round?: Auk, v. 110, no. 3, p. 594-602.

Naslund, N.L., Kuletz, K.J., Cody, M.B., and Marks, D.K., 1995, Tree and habitat characteristics and reproductive success at Marbled Murrelet tree nests in Alaska: Northwestern Naturalist, v. 76, no. 1, p. 12-25.

Naslund, N.L., and O'Donnell, B.P., 1995, Daily patterns of Marbled Murrelet activity at inland sites, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 129-134.

National Adubon Society, 2002, WatchList. Available at http://www.audubon.org/bird/watchlist/index.html.

National Oceanic and Atmospheric Administration, 2004, Final programmatic supplemental environmental impact statement on the Alaska groundfish fisheries, NMFS, Alaska Region.

National Oceanic and Atmospheric Administration, 2006, Ecosystem considerations for 2007. Appendix C of NPFMC stock assessment and evaluation report. Available at: http://www.afsc.noaa.gov/refm/stocks/assessments.htm.

NatureServe, 2006, Explorer: Online encyclopedia of life: Arlington, Virginia, version 6.0.

Nelson, J.B., 1966, Population dynamics of the gannet (*Sula bassana*) at the Bass Rock, with comparative information from other Sulidae: Journal of Animal Ecology, v. 35, p. 443-470.

Nelson, S.K., 1997, Marbled Murrelet (Brachyramphus marmoratus), *in* Poole, A., and Gill, F., eds., Birds of North America: Philadelphia, Pennsylvania, Academy of Natural Sciences and American Ornithologists' Union, p. 276.

Nelson, S.K., Fukuda, Y., and Oka, N., 2002, Status and conservation of the Long-Billed Murrelet in Japan: Yamashima Institute for Ornithology Journal, v. 33, no. 2, p. 88-106.

Nelson, S.K., and Hamer, T.E., 1995, Nest success and the effects of predation on Marbled Murrelets, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 89-97.

Nero and Associates, Inc., 1987, Seabird oil toxicity study: Washington, D.C., Minerals Management Services, Outer Continental Shelf Study 87-0005 Final Report.

Newman, S.H., Nelson, S.K., Whitworth, D.L., and Carter, H.R., 2006, Marbled Murrelet (*Brachyramphus marmoratus*) activity patterns and health in Port Snettisham, southeast Alaska, 2005: New York, Wildlife Trust, Report to the Alaska Department of Fish and Game, Juneau, Alaska,, 70 p.

Newman, S.H., Piatt, J.F., and White, J., 1997, Hematological and plasma biochemical reference ranges of Alaskan seabirds: Their ecological significance and clinical importance: Colonial Waterbirds, v. 20, no. 3, p. 492-504.

Nie, M., 2006, Governing the Tongass: National Forest conflict and political decision-making: Environmental Law, v. 36, p. 385-480.

Norcross, B.L., Brown, E.D., Foy, R.J., Frandsen, M., Gay, S.M., Kline, T.C. Jr., Mason, D.M., Patrick, E.V., Paul, A.J., and Stokesbury, K.D.E., 2001, Synthesis of life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska: Fisheries Oceanography, v. 10, no. Suppl. 1, p. 42-57.

North Pacific Pelagic Seabird Database, 2006, Anchorage, USGS, Alaska Science Center, and USFWS, ver. 1.0.

Nowacki, G.J., Spencer, P., Brock, T., Fleming, M., and Jorgenson, T., 2001, Narrative descriptions for the ecoregions of Alaska and neighboring territories: U.S. Geological Survey Open File Report 02-297.

Nowacki, G.J., and Kramer, M.G., 1998, Effects of wind disturbance on temperate rain forest structure and dynamics of southeast Alaska, *in* Julian, K.R., ed., Conservation and resource assessments for the Tongass Land Management Plan revision: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, General Technical Report 421, 25 p.

Nur, N., 1993, Establishing the demographic parameters of the Marbled Murrelet: Portland, Oregon, U.S. Fish and Wildlife Services.

Nyberg, J.B., 1998, Statistics and the practice of adaptive management, *in* Sit, V., and Taylor, B.S., eds., Statistical methods for adaptive management: Victoria, British Columbia, Ministry of Forests Research Branch, p. 1-7.

Oakley, K.L., and Kuletz, K.J., 1979, Summer distribution and abundance of marine birds and mammals in the vicinity of Naked Island, Prince William Sound, Alaska, in 1978, and aspects of the reproductive ecology of the Pigeon Guillemot: Anchorage, Alaska, U.S. Fish and Wildlife Service, 95 p.

Oja, W., Freeman, R., Black, M., and Shuster, B., 1999, Kenai Peninsula spruce bark beetle management strategies and five year action schedule: Anchorage, Alaska, U.S. Forest Service, Chugach National Forest.

Orians, G.H., and Pearson, N.E., 1979, On the theory of central place foraging, *in* Horn, D.J., Mitchell, R.D., and Stairs, G.R., eds., Analysis of ecological systems: Columbus, Ohio State University Press, p. 154-177.

Ostrand, W.D., 1999, Marbled Murrelets as initiators of feeding flocks in Prince William Sound, Alaska: Waterbirds, v. 22, no. 2, p. 314-318.

Ostrand, W.D., Coyle, K.O., Drew, G.S., Maniscalco, J.M., and Irons, D.B., 1997, Selection of forage-fish schools by murrelets and Tufted Puffins in Prince William Sound, Alaska, *in* Role of Forage Fishes in Marine Ecosystems International Symposium, Anchorage, Alaska, 1996, Lowell Wakefield Fisheries Symposium, Sea Grant College Program Report 97-01, p. 171-173.

Ostrand, W.D., Coyle, K.O., Drew, G.S., Maniscalco, J.M., and Irons, D.B., 1998, Selection of forage-fish schools by murrelets and Tufted Puffins in Prince William Sound, Alaska: Condor, v. 100, no. 2, p. 286-297.

Ostrand, W.D., Howlin, S., and Gotthardt, T.A., 2004, Fish school selection by Marbled Murrelets Brachyramphus marmoratus in Prince William Sound, Alaska: Reponses to changes in availability: Marine Ornithology, v. 32, no. 1, p. 69-76.

Paine, R.T., Ruesink, J.L., Sun, A., Soulanille, E.L., Wonham, M.J., Harley, C.D.G., Brumbaugh, D.R., and Secord, D.L., 1996, Trouble on oiled waters: Lessons from the *Exxon Valdez* oil spill: Annual Review of Ecology and Systematics, v. 27, no. 1, p. 197-235.

Panjabi, A.O., Dunn, E.H., Blancher, P.J., Hunter, W.C., Altman, B., Bart, J., Beardmore, C.J., Berlanga, H., Butcher, G.S., Davis, S.K., Demarest, D.W., Dettmers, R., Easton, W., Gomez de Silva Garza, H., Ińigo-Elias, E.E., Pashley, D.N., Ralph, C.J., Rich, T.D., Rosenberg, K.V., Rustay, C.M., Ruth, J.M., Wendt, J.S., and Will, T.C., 2005, Partners in Flight handbook on species assessment, Rocky Mountain Bird Observatory Technical Series.

Parker, N.R., Cam, E., Lank, D.B., and Cooke, F., 2003, Post-fledging survival of Marbled Murrelets *Brachyramphus marmoratus* estimated with radio-marked juveniles in Desolation Sound, British Columbia: Marine Ornithology, v. 31, no. 2, p. 207-212.

Parrish, J.K., Marvier, M., and Paine, R.T., 2001, Direct and indirect effects: Interactions between bald eagles and common murres: Ecological Applications, v. 11, p. 1858-1869.

Pearse, T., 1946, Notes on changes in bird populations in the vicinity of Comox, Vancouver Island - 1917 to 1944: Murrelet, v. 27, p. 4-9.

Pearson, W.H., Elston, R.A., Bienert, R.W., Drum, A.S., and Antrim, L.D., 1999, Why did the Prince William Sound, Alaska, Pacific herring (*Clupea pallasi*) fisheries collapse in 1993 and 1994? Review of hypotheses: Canadian Journal of Fisheries and Aquatic Sciences, v. 56, p. 711-737.

Peck, J.E., Hong, W.S., and McCune, B., 1995, Diversity of epiphytic bryophytes on three host tree species, Thermal Meadow, Hotsprings Island, Queen Charlotte Islands, Canada: Bryologist, v. 98, no. 1, p. 123-128.

Peery, M.Z., Becker, B.H., and Beissinger, S.R., 2006a, Combining demographic and count-based approaches to identify source-sink dynamics of a threatened seabird: Ecological Applications, v. 16, p. 1516-1528.

Peery, M.Z., Beissinger, S.R., Becker, B.H., and Newman, S.H., 2002, Marbled Murrelet (*Brachyramphus marmoratus*) demography in central California: 2001 Progress Report, California Department of Fish and Game, U.S. Fish and Wildlife Services, and California State Parks.

Peery, M.Z., Beissinger, S.R., Burkett, E., and Newman, S.H., 2006b, Local survival of Marbled Murrelets in central California: Roles of oceanographic processes, sex, and radiotagging: Journal of Wildlife Management, v. 70, no. 1, p. 78-88.

Peery, M.Z., Beissinger, S.R., Newman, S.H., Becker, B.H., Burkett, E., and Williams, T.D., 2004a, Individual and temporal variations in inland flight behavior of Marbled Murrelets: Implications for population monitoring: Condor, v. 106, p. 344-353.

Peery, M.Z., Beissinger, S.R., Newman, S.H., Burkett, E.B., and Williams, T.D., 2004b, Applying the declining population paradigm: Diagnosing causes of poor reproduction in the Marbled Murrelet: Conservation Biology, v. 18, no. 4, p. 1088-1098.

Piatt, J.F., 1994, Monitoring seabird populations in areas of oil and gas development on the Alaskan continental shelf: Oceanic, shelf and coastal seabird assemblages at the mouth of a tidally-mixed estuary (Cook Inlet): Anchorage, National Biological Service, Alaska Science Center, Final Report to Minerals Management Service, Environmental Studies Program 93-0072, 69 p.

Piatt, J.F., 1998, Marbled Murrelets have declined in Alaska: Northwest Science, v. 72, no. 4, p. 310-314.

Piatt, J.F., (ed.), 2002, Response of seabirds to fluctuations in forage fish density: Final Report to Exxon Valdez Oil Spill Trustee Council (Restoration Project 00163M) and Minerals Management Service (Alaska Region OCS Study MMS 2002-068). Alaska Science Center, U.S. Geological Survey, Anchorage, Alaska. 406 p.

Piatt, J.F., 2005, Bibliography of literature on the Marbled Murrelet (*Brachyramphus marmoratus*) in Alaska and British Columbia: Anchorage, U.S. Geological Survey, Alaska Science Center, Final Report to U.S. Fish and Wildlife Service, 52 p.

Piatt, J.F., and Anderson, P., 1996, Response of Common Murres to the *Exxon Valdez* oil spill and long-term changes in the Gulf of Alaska marine ecosystem, *in* Rice, S.D., Spies, R.B., Wolfe, D.A., and Wright, B.A., eds., *Exxon Valdez* Oil Spill Symposium, Anchorage, Alaska, 1993, American Fisheries Society Symposium 18, p. 720-737.

Piatt, J.F., Conant, B., and Iverson, C.G., 1991, Comparison of aerial and boat-based surveys for Marbled Murrelets in southeast Alaska, July 23-28, 1991: Anchorage, Alaska, U.S. Fish and Wildlife Service, 14 p.

Piatt, J.F., and Ford, R.G., 1993, Distribution and abundance of Marbled Murrelets in Alaska: Condor, v. 95, no. 3, p. 662-669.

Piatt, J.F., and Kitaysky, A.S., 2002, Poole, A. , and Gill, F., eds., Birds of North America: Philadelphia, Pennsylvania, p. 1-32.

Piatt, J.F., Lensink, C.J., Butler, R.W., Kendziorek, M., and Nysewander, D.R., 1990, Immediate impact of the *Exxon Valdez* oil spill on marine birds: Auk, v. 107, no. 22, p. 387-397.

Piatt, J.F., and Naslund, N.L., 1995, Abundance, distribution, and population status of Marbled Murrelets in Alaska, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 285-294.

Piatt, J.F., and Nettleship, D.N., 1987, Incidental catch of marine birds and mammals in fishing nets off Newfoundland, Canada: Marine Pollution Bulletin, v. 18, p. 344-349.

Piatt, J.F., Romano, M.D., Gill, V., and DeGange, A.R., 2005, Density and abundance of Kittlitz's Murrelets (*Brachyramphus brevirostris*) in the Near Islands, Aleutian Islands, Alaska, July 2003: Anchorage, USGS Alaska Science Center, Final Report to USFWS, 24 p.

Pielou, E., 1969, Introduction to mathematical ecology: New York, Wiley-Interscience.

Pierce, D., Ritchie, W., and Kruezigar, R., 1994, Preliminary findings of seabird interactions with non-treaty salmon gillnet fishery: Puget Sound and Hood Canal, Washington: Olympia, Washington Department of Fish and Wildlife.

Pitocchelli, J., Piatt, J.F., and Cronin, M.A., 1995, Morphological and genetic divergence among Alaska populations of *Brachyramphus* murrelets: Wilson Bulletin, v. 107, no. 2, p. 235-250.

Pollard, J.H., 1966, On the use of the direct matrix product in analysing certain stochastic population models: Biometrika, v. 53, p. 397-415.

Porter, J.M., and Sealy, S.G., 1981, Dynamics of seabird multispecies feeding flocks: Chronology of flocking in Barkley Sound, British Columbia, in 1979: Colonial Waterbirds, v. 4, p. 104-113.

Porter, J.M., and Sealy, S.G., 1982, Dynamics of seabird multispecies feeding flocks: Age-related feeding behaviour: Behaviour, v. 81, p. 91-109.

Potts, G.R., Coulson, J.C., and Deans, I.R., 1980, Population dynamics and breeding success of the shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland: Journal of Animal Ecology, v. 49, p. 465-484.

Pritchard, J.K., Stephens, M., and Donnelly, P., 2000, Inference of population structure using multilocus genotype data: Genetics, v. 155, p. 945-959.

Pritchard, J.K., and Wen, W., 2003, Documentation for Structure Software: Ver. 2.

Pulliam, H.R., and Dunning, J.B., 1994, Demographic processes: Population dynamics on heterogeneous landscapes, *in* Meffe, G.K., and Carroll, C.R., ed., Principles of conservation biology: Sunderland, Massachusetts, Sinauer Associates, p. 179-205.

Purcell, J.E., and Sturdevant, M.V., 2001, Prey selection and dietary overlap among zooplanktivorous jellyfish and juvenile fishes in Prince William Sound, Alaska: Marine Ecology Progress Series, v. 210, p. 67-83.

Quinlan, S.E., and Hughes, J.H., 1990, Location and description of a Marbled Murrelet tree nest site in Alaska: Condor, v. 92, no. 4, p. 1068-1073.

Quinlan, S.E., and Hughes, J.H., 1992, Techniques for capture and radio tagging of Marbled Murrelets: Western Foundation of Vertebrate Zoology Proceedings, v. 5, no. 1, p. 117-121.

Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., 1995a, Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, 420 p.

Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., 1995b, Overview of the ecology and conservation of the Marbled Murrelet in North America, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 3-22.

Ralph, C.J., and Long, L.L., 1995, Productivity of Marbled Murrelets in California from observations of young at sea, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 371-377.

Ralph, C.J., and Miller, S.L., 1995, Offshore population estimates of Marbled Murrelets in California, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 353-360.

Raphael, M.G., Galleher, B.M., Huff, M.H., Miller, S.L., Nelson, S.K., and Young, R.D., 2006, Spatially explicit estimates of potential nesting habitat for the Marbled Murrelet, *in* Huff, M.H., Raphael, M.G., Miller, S.L., Nelson, S.K., and Baldwin, J., Northwest Forest Plan - The first 10 years (1994-2003): Status and trends of populations and nesting habitat for the Marbled Murrelet: Pacific Northwest Research Station, Portland, Oregon, General Technical Report 650, p. 97-146.

Raphael, M.G., Evans Mack, D., and Cooper, B.A., 2002a, Landscape-scale relationships between abundance of Marbled Murrelets and distribution of nesting habitat: Condor, v. 104, no. 2, p. 331-342.

Raphael, M.G., Evans Mack, D., Marzluff, J.M., and Luginbuhl, J.M., 2002b, Effects of forest fragmentation on populations of the Marbled Murrelet: Studies in Avian Biology, v. 25, no. 1, p. 221-235.

Resource Inventory Committee, 1999, British Columbia wildlife habitat rating standards, ver. 2.0: Victoria, British Columbia.

Rew, M.B., Peery, M.Z., Beissinger, S.R., Bérubé, M., Lozier, J.D., Rubidge, E.M., and Palsboll, P.J., 2006 , Cloning and characterization of thirty tetranucleotide and two dinuleotide polymorphic microsatellite loci from the endangered Marbled Murrelet (*Brachyramphis marmoratus*): Molecular Ecology Notes, v. 6, p. 241-244.

Ricketts, T.H., Dinerstein, E., Olson, D.M., and Loucks, C.J., 1999, Terrestrial ecoregions of North America: Conservation assessment: Washington, D.C., Island Press, 470 p.

Robards, M.D., Anthony, J.A., Rose, G.A., and Piatt, J.F., 1999a, Changes in proximate composition and somatic energy content for Pacific sand lance (*Ammodytes hexapterus*) from Kachemak Bay, Alaska relative to maturity and season: Journal of Experimental Marine Biology and Ecology, v. 242, p. 245-258.

Robards, M.D., Piatt, J.F., and Rose, G.A., 1999b, Maturation, fecundity, and intertidal spawning of Pacific sand lance in the northern Gulf of Alaska: Journal of Fish Biology, v. 54, p. 1050-1068.

Robards, M.D., Willson, M.F., Armstrong, R.H., and Piatt, J.F., 1999c, Sand lance: Review of biology and predator relations and annotated bibliography: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, Research Paper 521, 327 p.

Robards, M., Drew, G.S., Piatt, J.F., Anson, J.M., Abookire, A., Bodkin, J.L., Hooge, P., and Speckman, S.G., 2003, Ecology of selected marine communities in Glacier Bay: Zooplankton, forage fish, seabirds and marine mammals: Anchorage, USGS Alaska Science Center, Final Report to USNPS, GBNPP, 156 p.

Rodway, M.S., 1990, Status report on the Marbled Murrelet, Brachyramphus marmoratus, in Canada: Ottawa, Ontario, COSEWIC, 64 p.

Rodway, M.S., Carter, H.R., Sealy, S.G., and Campbell, R.W., 1992, Status of the Marbled Murrelet in British Columbia: Western Foundation of Vertebrate Zoology Proceedings, v. 5, no. 1, p. 17-41.

Rodway, M.S., and Regehr, H.M., 2002, Inland activity and forest structural characteristics as indicators of Marbled Murrelet nesting habitat in Clayoquot Sound, *in* Burger, A.E. and Chatwin, T.A., eds., Multi-scale studies of populations, distribution and habitat associations of Marbled Murrelets in Clayoquot Sound, British Columbia: Victoria, British Columbia, Ministry of Water, Land and Air Protection, Special Report, p. 39-90.

Rodway, M.S., Regehr, H.M., and Savard, J.-P.L., 1993, Activity levels of Marbled Murrelets in different inland habitats in the Queen Charlotte Islands, British Columbia: Canadian Journal of Zoology, v. 71, no. 5, p. 977-984.

Rodway, M.S., Savard, J.-P.L., Garnier, D.C., and Lemon, M.J.F., 1995, At-sea activity patterns of Marbled Murrelets adjacent to probable inland nesting areas in the Queen Charlotte Islands, British Columbia: Northwestern Naturalist, v. 76, no. 1, p. 82-89.

Rodway, M.S., Savard, J.-P.L., and Regehr, H.M., 1991, Habitat use and activity patterns of Marbled Murrelets at inland and at-sea sites in the Queen Charlotte Islands, British Columbia: Delta, British Columbia, Environment Canada, Pacific and Yukon Region, Canadian Wildlife Service Technical Report 122, 152 p.

Romano, M.D., Piatt, J.F., and Roby, D.D., 2006, Testing the junk-food hypothesis on marine birds: Effects of prey type on growth and development: Waterbirds, v. 29, p. 407-516.

Romano, M.D., Piatt, J.F., and DeGange, A.R., 2005a, At-sea density and abundance of Kittlitz's and Marbled murrelets around Unalaska Island, Alaska, June 2005: Anchorage, USGS Alaska Science Center, Final Report to the U.S. Fish and Wildlife Service, 29 p.

Romano, M.D., Piatt, J.F., Williams, J., and DeGange, A.R., 2005b, At-sea density and abundance of Kittlitz's Murrelets (*Brachyramphus brevirostris*) and Marbled Murrelets (*Brachyramphus marmoratus*) at Atka Island, Alaska, June 2004: Anchorage, USGS Alaska Science Center, Final Report to the U.S. Fish and Wildlife Service, 26 p.

Ronconi, R.A., and Cassady St. Clair, C., 2002, Management options to reduce boat disturbance on foraging black guillemots (*Cepphus grylle*) in the Bay of Fundy: Biological Conservation, v. 108, p. 265-271.

Rueggeberg, H., and Booth, J., 1989, Marine birds and aquaculture in British Columbia: Assessment and management of interactions. Final Report: Summaries and conculsions: Vancouver, British Columbia, Report to Environment Canada, Canadian Wildlife Service.

Sambrook, J., Fritsch, E.F., and Maniatis, T., 1989, Molecular Cloning: Laboratory Manual: Ress, New York, Cold Spring Harbor Lab, ed. 2.

Sanger, G.A., 1983, Diets and food web relationships of seabirds in the Gulf of Alaska and adjacent marine regions, NOAA, OCSEAP Final Report 45, p. 631-771.

Sanger, G.A., 1987, Winter diets of Common Murres and Marbled Murrelets in Kachemak Bay, Alaska: Condor, v. 89, no. 2, p. 426-430.

Sangster, M.E., Kurhajec, D.J., and Benz, C.T., 1978, Reproductive ecology of seabirds at Hinchinbrook Island and a census of seabirds at selected sites in Prince William Sound, 1977: Anchorage, Alaska, U.S. Fish and Wildlife Service, Ecological Services, Office of Special Studies, 98 p.

Sauer, J.R., Schwartz, S., and Hoover, B., 1996, Christmas Bird Count Home Page: Laurel, Maryland, Patuxent Wildlife Research Center, version 95.1.

Savard, J.-P.L., and Lemon, M.J.F., 1992, Summer distribution and abundance of Marbled Murrelets on the west and east coasts of Vancouver Island, *in* Vermeer, K., Butler, R.W., and Morgan, K.H., eds., Ecology, status and conservation of marine and shoreline birds on the west coast of Vancouver Island [Proceedings], Sidney, British Columbia, 1991, Occasional Paper 75, p. 114-119.

Scheel, D., and Hough, K.R., 1997, Salmon fry predation by seabirds near an Alaskan hatchery: Marine Ecology Progress Series, v. 150, no. 1/3, p. 35-48.

Schneider, S., Roessli, D., and Excoffier, L., 2000, Arlequin, ver. 2.0: Software for population genetic data analysis: Switzerland, Genetics and Biometry Laboratory, University of Geneva.

Schummer, M.L., and Eddleman, W.R., 2003, Effects of disturbance on activity and energy budgets of migrating waterbirds in south-central Oklahoma: Journal of Wildlife Management, v. 67, no. 4, p. 789-795.

Sealy, S.G., 1974, Breeding phenology and clutch size in the Marbled Murrelet: Auk, v. 91, no. 1, p. 10-23.

Sealy, S.G., 1975, Feeding ecology of the Ancient and Marbled murrelets near Langara Island, British Columbia: Canadian Journal of Zoology, v. 53, p. 418-433.

Sealy, S.G., and Carter, H.R., 1984, At-sea distribution and nesting habitat of the Marbled Murrelet in British Columbia: Problems in the conservation of a solitarily nesting seabird, *In* Croxall, J.P., Evans, P.G.H., and Schreiber, R.W., eds., Status and conservation of the world's seabirds: Cambridge, United Kingdom, International Council for Bird Preservation, Technical Publication 2, p. 737-756.

Sealy, S.G., Carter, H.R., and Alison, D., 1982, Occurrences of the Asiatic Marbled Murrelet [*Brachyramphus marmoratus perdix* (Pallas)] in North America: Auk, v. 99, no. 4, p. 778-781.

Searle, S.R., 1966, Matrix algebra for the biological sciences: London, Wiley and Sons.

Sillett, S.C., 1995, Branch epiphyte assemblages in the forest interior and on the clearcut edge of a 700-year-old Douglas fir canopy in western Oregon: Bryologist, v. 98, no. 3, p. 301-312.

Sillett, S.C., and Rambo, T.R., 2000, Vertical distribution of dominant epiphytes in Douglas-fir forests of the central Oregon Cascades: Northwest Science, v. 74, no. 1, p. 44-49.

Simons, T.R., 1980, Discovery of a ground-nesting Marbled Murrelet: Condor, v. 82, no. 1, p. 1-9.

Sinclair, A.R.E., Peck, R.P., Dickman, C., Hik, D., Mahon, P., and Newsome, A.E., 1998, Predicting effects of predation on conservation of endangered prey: Conservation Biology, v. 12, p. 564-575.

Slatkin, M., 1995, A measure of population subdivision based on microsatellite allele frequencies: Genetics, v. 139, p. 457-462.

Smith, J.L., and Morgan, K.H., 2005, Assessment of seabird bycatch in longline and net fisheries in British Columbia: Delta, British Columbia, Canadian Wildlife Service, Pacific and Yukon Region, Technical Report 401.

Smith, W.P., and Harke, V.L., 2001, Marbled Murrelet surveys: Site and annual variation, sampling effort, and statistical power: Wildlife Society Bulletin, v. 29, no. 2, p. 568-577.

Snyder, C., 2006, Forest health conditions in Alaska - 2005, U.S. Forest Service, General Technical Report R10-PR-5, 92 p.

Sokal, R.R., and Rohlf, F.J., 1981, Biometry: New York, W.H. Freeman.

Spear, L., Nur, N., and Ainley, D.G., 1992, Comment: Estimating absolute densities of flying seabirds using analysis of relative movement: Auk, v. 109, no. 4, p. 937-938.

Speckman, S.G., 1996, Marbled Murrelet distribution and abundance in relation to the marine environment: Thesis, Fairbanks, University of Alaska, 89 p.

Speckman, S.G., Piatt, J.F., and Kuletz, K.J., 2005, Population status and trends of Brachyramphus murrelets in Lower Cook Inlet, Alaska: Anchorage, USGS Alaska Science Center, Final Report to USFWS, Science Support Program / Species at Risk.

Speckman, S.G., Piatt, J.F., Minte-Vera, C.V., and Parrish, J.K., 2005, Parallel structure among environmental gradients and three trophic levels in a subarctic estuary: Progress in Oceanography, v. 66, p. 25-65.

Speckman, S.G., Piatt, J.F., and Springer, A.M., 2004, Small boats disturb fish-holding Marbled Murrelets: Northwestern Naturalist, v. 85, no. 1, p. 32-34.

Speckman, S.G., Springer, A.M., Piatt, J.F., and Thomas, D.L., 2000, Temporal variability in abundance of Marbled Murrelets at sea in southeast Alaska: Waterbirds, v. 23, no. 3, p. 364-377.

Speich, S.M., and Wahl, T.R., 1995, Marbled Murrelet populations of Washington - Marine habitat preferences and variability of occurrence, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 313-326.

Spies, R.B., Rice, S.D., Wolfe, D.A., and Wright, B.A., 1996, Effects of the *Exxon Valdez* oil spill on the Alaskan coastal environment, *in* Rice, S.D., Spies, R.B., Wolfe, D.A., and Wright, B.A., eds., *Exxon Valdez* Oil Spill Symposium, Anchorage, Alaska, 1996, American Fisheries Society Symposium 18, p. 1-16.

Springer, A.M., 2007, Seabirds in the Gulf of Alaska. Pp. 311-334 *in* Robert Spies (ed.), Long-term Ecological Change in the Northern Gulf of Alaska. Elsevier, Amsterdam.

Springer, A.M., Estes, J.A., van Vliet, G.B., Williams, T.M., Doak, D.F., Danner, E.M., Forney, K.A., and Pfister, B., 2003, Sequential megafaunal collapse in the North Pacific Ocean: Ongoing legacy of industrial whaling?: National Academy of Sciences (USA) Proceedings, v. 100, p. 12223-12228.

Springer, A.M., S.J. Iverson, J.L. Bodkin, 2007, Marine Mammal Populations, Pp. 352-377 in: Robert Spies (ed.), Long-term Ecological Change in the Northern Gulf of Alaska. Elsevier, Amsterdam.

Stephensen, S.W., and Andres, B.A., 2001, Marine bird and mammal survey of Yakutat Bay, Disenchantment Bay, Russell Fiord, and Nunatak Fiord, Alaska: Anchorage, Alaska, U.S. Fish and Wildlife Service, 24 p.

Steventon, J.D., Sutherland, G.D., and Arcese, P., 2003, Linking landscapes, population models, and decision analysis: Risk assessment framework for the Marbled Murrelet (*Brachyramphus marmoratus*) in British Columbia, *in* Beyond borders-linking landscapes, International Association for Landscape Ecology, Symposium 18, Banff, Alberta, 2003.

Stolen, E.D., 2003, Effects of vehicle passage on foraging behavior of wading birds: Waterbirds, v. 26, no. 4, p. 429-436.

Strachan, G., McAllister, M.L.C., and Ralph, C.J., 1995, Marbled Murrelet at-sea foraging behavior, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 247-254.

Strauch, J.G., 1985, Phylogeny of the Alcidae: Auk, v. 102, p. 520-539.

Strong, C.S., Keitt, B.S., McIver, W.R., Palmer, C.J., and Gaffney, I., 1995, Distribution and population estimates of Marbled Murrelets at sea in Oregon during the summers of 1992 and 1993, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 339-352.

Suryan, R.M., Irons, D.B., Kaufman, M., Benson, J., Jodice, P.G., Roby, D.D., and Brown, E.D., 2002, Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the Black-legged Kittiwake *Rissa tridactyla*: Marine Ecology Progress Series, v. 236, p. 273-287.

Szaro, R.C., Boyce, D.A., and Puchlerz, T., 2005, Challenges associated with developing science-based Tongass land management plan: Landscape and Urban Planning, v. 72, p. 3-12.

Templeton, A.R., 1998, Nested clade analyses of phylogeographic data: testing hypothese about gene flow and population history: Molecular Ecology, v.7, p. 381-397

Tetreau, M., 1998, Harbor seal decline studied in Kenai Fjords National Park: Park Science, v. 18, no. 1, p. 4.

Thomas, G.L., and Thorne, R.E., 2003, Acoustical-optical assessment of Pacific herring and their predator assemblage in Prince William Sound, Alaska: Aquatic Living Resources, v. 16, p. 247-253.

Thoresen, A.C., 1989, Diving times and behaviour of Pigeon Guillemots and Marbled Murrelets off Rosario Head, Washington: Western Birds, v. 20, p. 33-37.

Tomlins, M., and Gray, M., 2006, Marbled Murrelet nesting habitat trends for the Sunshine Coast Forest District: Victoria, British Columbia Ministry of Agriculture and Lands, Integrated Lands Management Bureau.

Tripp, T., 2001, Synopsis of Marbled Murrelet habitat suitability models in British Columbia: Victoria, British Columbia, Ministry of Water, Land and Air Protection, Habitat Branch.

U.S. Department of Transportation, Maritime Division, 2006, Vessel calls at U.S. and world ports 2005, 30 p.

U.S. Fish and Wildlife Service, 1996, Final designation of critical habitat for the Marbled Murrelet: Washington, D.C., Endangered and Threatened Wildlife and Plants, Final Rule, FR 61(102): 26256-26320.

U.S. Fish and Wildlife Service, 1997, Recovery plan for the threatened Marbled Murrelet (*Brachyramphus marmoratus*) in Washington, Oregon, and California: Portland, Oregon, 261 p.

U.S. Fish and Wildlife Service, 2002, Birds of conservation concern 2002: Arlington, Virginia, Migratory Bird Management, 99 p.

U.S. Fish and Wildlife Service, 2004, Marbled Murrelet (B*rachyramphus marmoratus*) 5-year review: Portland, Oregon, 28 p.

U.S. Fish and Wildlife Service, 2006, Endangered and threatened wildlife and plants: Designation of critical habitat for the marbled murrelet; proposed rule, Washington, D.C., Federal Register 71(176): 53838-53951, 50 CFR Part 17.

U.S. Forest Service, 2002a, Biodiversity, Chapter 3 in Final environmental impact statement: Chugach National Forest, Alaska Region, R10-MB-480d.

U.S. Forest Service, 2002b, Final environmental impacts statement and the revised lands and resource management plan for the Chugach National Forest: Anchorage, U.S. Forest Service, Alaska Region, R10-MB-480d.

U.S. Forest Service, 2004, Forest insect and disease conditions in Alaska in 2003: Anchorage, Alaska, Pest Management Technical Report R10-TP-123.

U.S. National Park Service, 2004, Live Feed video monitoring of Harbor Seals, *in* Scientific Studies in Kenai Fjords National Park 3, p. 25-29.

U.S. National Park Service, 2004, Scientific studies in Kenai Fjords National Park: Anchorage, Alaska Support Office.

van Hees, W.S., 2005, Timber resource statistics of south-central Alaska, 2003: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, Resource Bulletin 248, 24 p.

van Hees, W.S., and Mead, B.R., 2005, Extensive strategic assessment of southeast Alaska’s vegetative resources: Landscape and Urban Planning, v. 72, p. 25-48.

Van Pelt, T.I., and Piatt, J.F., 2003, Population status of Kittlitz’s and Marbled murrelets and surveys for other marine bird and mammal species in the Kenai Fjords area, Alaska: Anchorage, USGS Alaska Science Center, Science Support Program Annual Report to USFWS.

Van Pelt, T.I., and Piatt, J.F., 2005, Population status of Kittlitz’s Murrelet along the southern coast of the Alaska Peninsula: Anchorage, USGS Alaska Science Center, Final Report to the USFWS, Science Support Program, 65 p.

Van Pelt, T.I., Piatt, J.F., Lance, B.K., and Roby, D.D., 1997, Proximate composition and energy density of some North Pacific forage fishes: Comparative Biochemistry and Physiology, v. 118A, no. 4, p. 1393-1398.

Vermeer, K., 1992, Diet of birds as a tool for monitoring the biological environment, *in* Vermeer, K., Butler, R.W., and Morgan, K.H., eds., Ecology, status, and conservation of marine and shoreline birds on the west coast of Vancouver Island: Ottawa, Ontario, CWS, Occasional Paper 75, p. 41-50.

Vermeer, K., and Morgan, K.H., 1989. Mariculture and bird interactions in the Strait of Georgia. p. 174-176 *in* Vermeer, K., and Butler, R.W., eds., The ecology and status of marine and shoreline birds of the Strait of Georgia: Special Publication, Canadian Wildlife Service, Ottawa, ON.

Vermeer, K., Sealy, S.G., and Sanger, G.A., 1987, Feeding ecology of Alcidae in the eastern North Pacific Ocean, In Croxall, J.P., ed., Seabirds: Feeding ecology and role in marine ecosystems: United Kingdom, Cambridge University Press, p. 189-227.

Viereck, L.A., Dyrness, C.T., Batten, A.R., and Wenzlick, K.J., 1992, Alaska vegetation classification: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, General Technical Report 286, 278 p.

Viereck, L.A., and Little, E.L., 1972, Alaska trees and shrubs: Washington, D.C., U.S. Department of Agriculture, Forest Service Agricultural Handbook 410, 265 p.

Vucetich, J.A., and Waite, T.A., 2003, Spatial patterns of demography and genetic processes across the species range: Null hypotheses for landscape conservation genetics: Conservation Genetics, v. 4, p. 639-645.

Walters, C., 1986, Adaptive management of renewable resources: New York, Macmillan.

Walters, C.J., and Holling, C.S., 1990, Large-scale management experiments and learning by doing: Ecology, v. 71, p. 2060-2068.

Wanless, S., Harris, M.P., Redman, P., and Speakman, J.R., 2005, Low energy values of fish as a probable cause of a major seabird breeding failure in the North Sea: Marine Ecology Progress Series, v. 294, p. 1-8.

Waterhouse, F.L., Bradley, R.W., Markila, J., Cooke, F., and Lougheed, L.W., 2002, Use of airphotos to identify, describe, and manage forest structure of Marbled Murrelet nesting habitat at a coastal British Columbia site: Nanaimo, British Columbia, Ministry of Forests, Vancouver Forest Region, Research Section, Technical Report 016, 20 p.

Waterhouse, F.L., Donaldson, A.B., and Lank, D.B., 2004, Using airphotos to interpret Marbled Murrelet nesting habitat in British Columbia: Application of a preliminary classification scheme: Nanaimo, British Columbia, Ministry of Forests, Coast Forest Region Research Section, Technical Report 029, 37 p.

Waterhouse, F.L., Mather, M.H., and Seip, D.R., 2002, Distribution and abundance of birds relative to elevation and biogeoclimatic zones in coastal old-growth forests in southern British Columbia: Journal of Ecosystems and Management, v. 2, no. 2, p. 1-13.

Weingartner, T., 2005, Physical and geological oceanography: Coastal boundaries and coastal and ocean circulation, In Mundy, P.R., ed., Gulf of Alaska: Biology and oceanography: Fairbanks, Alaska Sea Grant, p. 35-48.

Werner, R.A., Holsten, E.H., Matsuoka, S.M., and Burnside, R.E., 2006, Spruce beetles and forest ecosystems in south-central Alaska: Review of 30 years of research: Forest Ecology and Management, v. 227, p. 195-206.

Whitworth, D.L., Nelson, S.K., Newman, S.H., van Vliet, G.B., and Smith, W.P., 2000, Foraging distances of radio-marked Marbled Murrelets from inland areas in southeast Alaska: Condor, v. 102, no. 2, p. 452-456.

Wild, P.W., 1990, Central California experience: Case history of California halibut set net laws and regulations, *in* Haugen, C.W., ed., California halibut, *Paralichthys californicus*, resource and fisheries, p. 321-339.

Willette, T.M., Cooney, R.T., Patrick, E.V., Thomas, G.L., and Kline, T.C. Jr., 2001, Ecological processes influencing mortality of juvenile pink salmon (*Oncorhynchus gorbuscha*) in Prince William Sound, Alaska: Fisheries Oceanography, v. 10, no. Suppl. 1, p. 14-41.

Williams, E.H., and Quinn, T.J. II, 2000, Pacific herring, *Clupea pallasi*, recruitment in the Bering Sea and north-east Pacific Ocean, II: Relationships to environmental variables and implications for forecasting: Fisheries Oceanography, v. 9, p. 300-315.

Wilson, G.A., and Rannala, B., 2005, Bayesian inference of recent migration rates using multilocus genotypes: Genetics, v. 163, p. 1177-1191.

Wilson, L.J., Daunt, F., and Wanless, S., 2005, Self-feeding and chick-provisioning diet differ in the Common Guillemot *Uria aalge*: Ardea, v. 92, no. 2, p. 197-208.

Witherell, D., and Pautzke, C., 1997, Brief history of bycatch management measures for eastern Bering Sea groundfish fisheries: Marine Fisheries Review, v. 59, p. 15-22.

Witherell, D., Pautzke, C., and Fluharty, D., 2000, Ecosystem-based approach for Alaska groundfish fisheries: Journal of Marine Sciences, v. 57, p. 771-777.

Woodby, D., Carlile, D., Siddeek, S., Funk, F., Clark, J.H., and Hulbert, L., 2005, Commerical Fisheries of Alaska: Anchorage, ADFG, Special Publication 05-09.

Woodby, D., Meyer, S., Mabry, K., O'Connell, V., Trowbridge, C., Schempf, J.H., Krygier, E., and Lloyd, D., 2002, Marine Protected Areas in Alaska: Recommendations for a public process: Juneau, Alaska Department of Fish and Game, Marine Protected Areas Task Force, Report to Alaska Board of Fisheries, Regional Information Report 5J02-08.

World Conservation Union, 2001, Categories and criteria for critically endangered, endangered, and vulnerable species: Gland, Switzerland.

World Conservation Union, 2004, Red list of threatened species: Gland, Switzerland.

Wright, S., 1931, Evolution in Mendelian populations: Genetics, v. 16, p. 97-159.

Wynne, K.M., Hicks, D.L., and Munro, N.R., 1991, 1990 Salmon gillnet fisheries observer programs in Prince William Sound and south Unimak Alaska: Anchorage, Alaska, Saltwater, Inc, Final Report to NOAA NMFS, 65 p.

Wynne, K.M., Hicks, D.L., and Munro, N.R., 1992, 1991 Marine mammal observer program for the salmon driftnet fishery of Prince William Sound: Anchorage, Alaska, Saltwater, Inc, Final Report to NOAA NMFS, 33 p.

Yen, P.P.W., Huettmann, F., and Cooke, F., 2004a, Large-scale model for the at-sea distribution and abundance of Marbled Murrelets (*Brachyramphus marmoratus*) during the breeding season in coastal British Columbia, Canada: Ecological Modelling, v. 171, no. 4, p. 395-413.

Yen, O.P.W., Sydeman, W.J., and Hyrenbach, K.D., 2004b, Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: Implications for trophic transfer and conservation: Journal of Marine Systems, v. 50, p. 79-99.

Zamon, J.E., 2003, Mixed species aggregations feeding upon herring and sand lance schools in a nearshore archipelago depend on flooding tidal currents: Marine Ecology Progress Series, v. 261, p. 243-255.

Zebdi, A., and Collie, J.S., 1995, Effect of climate on herring (*Clupea pallasi*) population dynamics in the northeast Pacific Ocean, *in* Beamish, R.J., ed., Climate change and northern fish populations, Canadian Special Publication in Fisheries and Aquatic Sciences, p. 277-290.

Zharikov, Y., Lank, D.B., Huettmann, F., Bradley, R.W., Parker, N.R., Yen, P.P.-W., McFarlane Tranquilla, L.A., and Cooke, F., 2006, Habitat selection and breeding success in a forest-nesting Alcid, the Marbled Murrelet, in two landscapes with different degrees of forest fragmentation: Landscape Ecology, v. 21, no. 1, p. 107-120.

Zwiefelhofer, D.C., and Forsell, D.J., 1989, Marine birds and mammals wintering in selected bays of Kodiak Island, Alaska: Five-year study plan: Anchorage, Alaska, U.S. Fish and Wildlife Service, 77 p.

Appendix A. Annotated Bibliography of Historical Information on Diet of the Marbled Murrelet in Alaska.

Sangster, M.E., Kurhajec, D.J., and Benz, C.T., 1978, Reproductive ecology of seabirds at Hinchinbrook Island and a census of seabirds at selected sites in Prince William Sound, 1977: Anchorage, Alaska, U.S. Fish and Wildlife Service, Ecological Services, Office of Special Studies, 98 p.

Sangster and others (1978) examined the feeding and breeding ecology of seabirds around Constantine Harbour, Hinchinbrook Island, at the entrance to Prince William Sound during the summer of 1977. Nine Marbled Murrelets were collected over the season, and prey items in the stomachs of eight birds keyed out to lowest possible taxon. Sand lance was found in 50 percent of the birds, capelin in 25 percent, unidentified fish in 12.5 percent, and the Decapod *T. inermis* in 25 percent of the birds.

Oakley, K.L., and Kuletz, K.J., 1979, Summer distribution and abundance of marine birds and mammals in the vicinity of Naked Island, Prince William Sound, Alaska, in 1978, and aspects of the reproductive ecology of the Pigeon Guillemot: Anchorage, Alaska, U.S. Fish and Wildlife Service, 95 p.

During the summer of 1978, Oakley and Kuletz (1979) collected 12 Marbled Murrelets from the western half of Naked Island and 2 from McPherson Bay in Prince William Sound. Seventy-three percent of all food items were fish. More than one-half of the fish fragments were unidentified. Pollock and sand lance were of similar importance and one bird contained capelin (see table A1).

Table A1. Frequency of occurrence of prey types in stomachs of murrelets collected near Naked Island, Prince William Sound, summer 1978.

[From Oakley and Kuletz (1979). *N* = 14 murrelets]

Prey	Percentage of occurrence
Fish	
Gadidae	
Theragra chalcogramma	21.4
Ammodytidae	
Ammodytes hexapterus	35.7
Osmeridae	
Mallotus villosus	7.1
Unidentified fish fragments	92.9
Crustacea	
Copepoda	
Calonord sp.	35.7
Caligorda sp.	7.1
Decapoda	
Shrimp larvae	14.3
Nemerea	
Nematoda sp.	42.9

Krasnow, L.D., and Sanger, G.A., 1982, Feeding ecology of marine birds in the nearshore waters of Kodiak Island: Anchorage, Alaska, U.S. Fish and Wildlife Service, National Fishery Research Center, Migratory Bird Section, Final Report to the Outer Continental Shelf Environmental Assessment Program (OCSEAP), Research Unit 45, p. 505-630.

Krasnow and Sanger (1982) collected 18 birds at sea in Chiniank Bay near Kodiak Island during the winter of 1976–77, and 19 murrelets (16 with food) during February 1978. Two additional Kodiak sites were sampled in 1978; 34 birds (25 with food) from Izhut Bay between April and August, and 26 birds (17 with food) from Northern Sitkalidak Strait between May and August.

Diet composition at Chiniak Bay differed between 1976–77 and 1978 (tables A2, A3). Whereas the Chiniak diet of 1976–77 was dominated (by volume) by capelin, with euphausiids and Osmeridae also important, the Chiniak diet of 1978 was dominated by mysids. Diversity was fairly high in both years. There also were clear monthly and regional differences in diet of birds collected in Izhut Bay and Northern Sitkalidak Strait in 1978 (Krasnow and Sanger, 1982; Burkett, 1995; table A4). For example, birds collected in Izhut Bay in May were feeding primarily on capelin, whereas birds in northern Sitkalidak Strait in May fed mostly on euphausiids. Izhut Bay birds fed largely on sand lance in April, but had no sand lance in their diet in May. In general, birds seemed to prey more on invertebrates during the winter of 1978 and more on fish during the summer months. The Krasnow and Sanger (1982) study highlights (a) the ability of murrelets to switch prey, and, (b) the importance influence of local and seasonal differences in food availability on the diet choice of murrelets.

Table A2. Indices of relative importance of prey eaten by Marbled Murrelets, Chiniak Bay, December 1976–April 1977.

[From Krasnow and Sanger, 1982. N = 18 stomachs, 612 items, 76 mL volume]

Species	%No	%Vol	%FO	IRI
Nereidae	0.3	0.1	5.6	3
Chaetognatha	0.2		5.6	1
Mysidacea	1.8	0.3	11.11	23
Acanthomysis spp.	0.5	0.3	5.6	4
Neomysis rayii	0.2	0.3	5.6	2
Thysanoessa inermis	36.4	16.2	22.2	1,169
T. spinifera	0.3	0.5	5.6	5
T. spp	2.9	3.7	11.1	74
Osteichthyes	0.3	0.3	5.6	3
Osmeridae	21.4	19.3	38.9	1,584
Mallotus villosus	35.6	59.1	5.6	526

Table A3. Indices of relative importance of prey eaten by Marbled Murrelets, Chiniak Bay, February 1978.

[From Krasnow and Sanger, 1982. N = 16 murrelets, 3 empty stomachs; 837 items, 80 mL items, 76 mL volume]

Species	%No	%Vol	%FO	IRI
Mysidea	11.6	12.2	18.8	447
Acanthomysis spp.	74.8	55.1	81.2	1,548
Neomysis spp.	8.1	15.1	37.5	870
Neomysis rayii	1.4	3	6.2	27
Thysanoessa raschii	0.6	0.1	6.2	4
Gammaridea	0.6	2.5	18.8	58
Decapoda	0.1	1.2	6.2	8
Pandalidae	0.1	0.8	6.2	6
Pandalus goniurus	0.1	0.6	6.2	4
Osteichthyes	0.6	1.9	25	62
Osmeridae	0.8	4.5	6.2	33
Mallotus villosus	0.7	2.6	12.5	41
Theragra chalcogramma	0.4	0.2	6.2	4

Table A4. Prey eaten by Marbled Murrelets in Izhut Bay and norther Sitkalidak Strait in 1978.

[From Krasnow and Sanger, 1982. N = 42 stomachs]

Izhut Bay						Northern Sitkalidak Strait					
Month/ Sample details	Species	% No.	% Vol.	% FO	IRI	Month	Species	% No.	% Vol.	% FO	IRI
April	*Thysaneossa raschii*	37.5	9.4	33.3	1,562						
n = 3	Osteichthyes	4.2	3.1	33.3	243						
24 items	*Ammodytes hexapterus*	58.3	87.5	66.7	9,725						
24 mL vol											
May	Crustacea	1.4	0.4	33.3	60	May	*Thysanoessa inermis*	96.6	92.5	100	18,910
N = 3	Osteichthyes	2.7	6.8	33.3	316	n = 4	Osteichthyes	0.8	2.5	25	82
74 items	Osmeridae	2.7	731	33.3	326	177 items	*Mallotus villosus*	2.6	5	25	190
14 mL vol	*Mallotus villosus*	93.2	85.7	33.3	5,957	12 mL vol					
June	Osteichthyes	80	50	57.1	7,423	June	Osteichthyes	37.5	32.7	57.1	4,008
n = 7	*Mallotus villosus*	20	50	42.9	3,003	n = 7	*Mallotus villosus*	43.8	27.3	28.6	2,003
15 items						16 items	*Trichodon trichodon*	6.2	3	14.3	132
14 mL vol						11mL vol	*Ammodytes hexapterus*	12.5	37	28.6	1,416
July	*Ammodytes hexapterus*	100	100	100	200,000	July	*Osteichthyes*	50	33.3	50	4,165
n = 3						n = 4	*Ammodytes hexapterus*	50	66.7	50	5,835
12 items						6 items					
22 mL vol						21 mL vol					
August	Osteichthyes	15.8	12.8	22.2	635	August	Osteichthyes	100	100	100	200,000
n = 9	*Mallotus villosus*	5.3	7.7	11.1	144	n = 2					
19 items	Gadidae	5.3	5.1	11.1	115	2 items					
39 mL vol	*Theragra chalcogramma*	5.3	10.3	11.1	173	2 mL vol					
	Ammodytes hexapterus	68.4	64.1	44.4	5,883						

Sanger, G.A., 1983, Diets and food web relationships of seabirds in the Gulf of Alaska and adjacent marine regions, National Oceanic and Atmospheric Administration, Outer Continental Shelf Environmental Assessment Program Final Report 45, p. 631-771.

Sanger's (1983) study presents a review and summary of murrelet diet data collected throughout the Gulf of Alaska in the 1970s (table A5). Birds collected at sea came from four primary sources: (1) Kodiak Island, 1977–78 (Krasnow and Sanger, 1982); (2) Kachemak Bay (Sanger and Jones, 1982); (3) Ocean Continental Shelf Environmental Assessment Program cruises from 1975 to 1978 in the Gulf of Alaska and southeastern Bering Sea; and (4) seabirds that had drowned in gillnets deployed from research vessels of National Marine Fisheries Service south of the Aleutian Islands and the Alaska Peninsula from 1969 to 1971, and from collections made by National Marine Fisheries Service in the southeastern Bering Sea in 1973–74. In total, fish constituted 50 percent of the prey numbers and 76 percent of the volume of Marbled Murrelet diet whereas crustaceans accounted for 49 percent of prey numbers and 23 percent of the volumes. Sanger's synthesis highlights the seasonal and spatial diversity of Marbled Murrelet diet. This flexibility enables a broad and constant supply of food and this may play an important role in the over-wintering survival of Marbled Murrelets (Sanger, 1987; Burkett, 1995).

Table A5. Comparison of the importance of the main prey species of Marbled Murrelets in Alaskan waters in the 1970s, by major geographic region and season.

[Prey importance levels based on their IRI values, as follows: 0–9 = trace (tr); 10–99 = 1; 100–999 = 2; 1,000–9,999 = 3, 10,000 and up = 4; x = present. Seasons: W = Winter; Sp = Spring; Su = Summer; F = Fall. From Sanger, 1983]

	E Gulf of Alaska	Kodiak			Lower Cook Inlet			NE Gulf of Alaska	
	Su	W	Sp	Su	W	Sp	F	Su	F
Sample size =	**5**	**31**	**11**	**45**	**13**	**6**	**2**	**15**	**1**
Prey name									
Nereid Polychaete	_	tr	_	_	_	_	_	_	_
L. sitkana (Periwinkle)	_	_	_	1	_	_	_	_	_
Unid. Gastropod	_	_	_	tr	_	_	_	_	_
Blue Mussel	_	_	_	tr	_	_	_	_	_
Cephalopoda	_	_	_	tr	_	_	_	_	_
Acanthomysis sp	_	3	_		_	_	_	_	_
Neomysis rayii	_	1	_	_	_	_	x	_	_
N. spp/unid Mysid	_	2	_	_	2	_	_	_	_
Gammarid Amphipod	_	tr	_	_	1	_	_	_	_
Euphausiids									
Thysanoessa inermis	_	2	2	1	1	_	_	3	_
T. raschii	_	tr	1	_	2	3	_	_	_
T. spinifera	_	tr	_	_	1	_	_	1	_
T. sp/Un. Euphausiid	2	1	_	tr	2	2	_	1	_
Pandalus borealis	_	tr	_	_	_	_	_	_	_
Unident.Decapod	_	_	_	tr	_	_	_	_	_
Arrow Worm (Chaetog.)	_	tr	_	_	_	_	_	_	_
Fish									
Capelin	_	2	3	3	3	3	_	1	x
Unid Osmeridae	2	2	1	_	tr	2	_	_	_
Walleye Pollock	_	tr	_	_	tr	_	_	_	_
Unid Gadid	_	_	_	tr	tr	_	_	_	_
Pacific Sandfish	2	_	_	1	_	_	_	2	_
Pacific Sandlance	2	_	2	3	2	_	x	3	x
Unid fish	3	1	1	3	2	_	_	2	_

Sanger, G.A., 1987, Winter diets of Common Murres and Marbled Murrelets in Kachemak Bay, Alaska: Condor, v. 89, no. 2, p. 426-430.

Sanger (1987) collected 21 adult murrelets (18 had stomach's examined) from January to April 1978 in Kachemak Bay. Capelin was the most dominant prey species (by volume), with sand lance, mysids and euphausiids also important (table A6). The consistent importance of euphausiids in the diet of murrelets from January to April suggests there are high concentrations in the deepwater portion of the inner bay (Sanger and Jones, 1982).

Piatt, J.F., and Anderson, P., 1996, Response of Common Murres to the *Exxon Valdez* oil spill and long-term changes in the Gulf of Alaska marine ecosystem, *in* Rice, S.D., Spies, R.B., Wolfe, D.A., and Wright, B.A., eds., *Exxon Valdez* Oil Spill Symposium, Anchorage, Alaska, 1993, American Fisheries Society Symposium 18, p. 720-737; and Piatt, J.F., unpub. data from 1989 to 1996, Alaska, adult murrelet stomach contents.

J.F. Piatt collected a total of 230 Marbled Murrelets from six geographic regions of Alaska between 1989–96 (table A7). All birds were collected during the summer months of June–September, most in July and August. This represents the widest geographic sampling of murrelets in Alaska. Diets were similar across the range, except Southeast Alaska. Diets were dominated by sand lance and juvenile pollock. In Southeast Alaska, most birds collected in Icy Strait were eating Myctophids. This represents an unusual diet situation for murrelets on the continental shelf, but reveals something about winter diet possibilities when murrelets are distributed in oceanic waters offshore. Most conspicuous in this sample is a near absence of capelin compared to samples collected along the Alaska Peninsula and around Kodiak in the 1970s–1980s (see above) when capelin were a very common component of diets during summer (Piatt and Anderson, 1996).

Speckman, S.G., Piatt, J.F., and Springer, A.M., 2003, Deciphering the social structure of Marbled Murrelets from behavioral observations at sea: Waterbirds, v. 26, no. 3, p. 266-274.

Speckman (1996) studied murrelets at sea in Auke Bay for 2 years for her MSc Thesis. She identified prey being carried by adults on the water. All fish-holding murrelets observed were in complete summer plumage, and all birds held a single fish crosswise in their bills. Only 12 fish-holders were seen during morning boat surveys in 1992, compared to 38 in 1993. A total of 203 fish-holders were observed, including opportunistic sightings as well as sightings during surveys. Of these, 81 (40 percent) were holding Pacific sand lance, four (2 percent) Pacific herring, seven (3 percent) capelin, seven (3 percent) were holding unidentified fish, but not sand lance, and 104 (51 percent) were holding an unidentified fish. No demersal or benthic fishes or invertebrates were identified.

Table A6. Winter diet of Marbled Murrelets in Katchemak Bay, Alaska, between January and April 1978.

[From Sanger (1987). N = 18 stomachs with food]

Prey	Totals:	% Nos. (n = 654)	%Vol. (82 mL)	%FO	IRI	% Total IRI	Length data (mm)				
							n	mean	SD	Min	Max
Crustaceans											
Unidentified		0.8	1.2	5.6	11	0.2					
Unidentified mysid		34.2	6.7	11.1	456	8.8	20	18	7.4	11	38
Unidentified gammarid amphipod		1.2	1.4	11.1	30	0.6	6	15	2.3	12	18
Euphausiids											
Thysanoessa inermis		0.5	1.2	5.6	9	0.2	2			15	21
Thysanoessa rachii		19.4	5.7	16.7	418	8	38	14	2.3	11	21
Thysanoessa spinifera		0.2	0.9	5.6	6	0.1	1	24			
Thysanoessa spp.		22.1	4	16.7	435	8.4	24	13	1.6	11	18
Fish											
Unidentified		3.6	8.3	22.2	264	5.1					
Mallotus villosus		11.1	51.8	50	3,146	60.6	18	63	18.1	28	105
Unidentified osmerid		0.2	0.1	5.6	1	0.1					
Theragra chalcogramma		0.2	0.2	5.6	2	0.1					
Ammodytes hexapterus		6.4	18.5	16.7	415	8.9	13	45	33.7	29	135

Table A7. Diet of Marbled Murrelets in Alaska, 1988–2006.

[From Piatt and Anderson, 1996, and J.F. Piatt, U.S. Geological Survey, unpub. data, 2006). N = 175 stomachs with food. Percent number examined and number empty are calculated using the total number of birds examined. Percent frequency of occurrence, number of individuals, and estimated wet weight are calculated using the number of birds containing prey items. **Abbreviations:** g, gram; n, number; <, less than]

	Central-West Aleutians		East Aleutians		Alaska Peninsula		Cook/ Kodiak		Prince William Sound		Southeast Alaska		Total	
	n	%	n	%	n	%	n	%	n	%	n	%	n	%
Number examined	19	8	23	10	52	23	58	25	43	19	35	15	230	100
Number empty	0	0	11	5	22	10	2	1	15	7	5	2	55	24
Frequency of Occurrence														
Invertebrates[1]	0	0	2	17	0	0	2	4	0	0	1	3	5	3
Capelin (*Mallotus villosus*)	0	0	0	0	0	0	10	18	0	0	2	7	12	7
Lanternfishes (Myctophidae)	0	0	0	0	0	0	0	0	0	0	17	57	17	10
Pollock and cod (Gadidae)	7	37	8	67	13	43	6	11	24	86	2	7	60	34
Sand lance (*Ammodytes hexapterus*)	11	58	2	17	9	30	31	55	2	7	7	23	62	35
Other[2]	1	5	0	0	8	27	7	13	2	7	1	3	19	11
Numbers of Individuals														
Invertebrates[1]	0	0	30	44	0	0	2	1	0	0	1	1	33	4
Capelin (*Mallotus villosus*)	0	0	0	0	0	0	22	14	0	0	2	1	24	3
Lanternfishes (Myctophidae)	0	0	0	0	0	0	0	0	0	0	174	88	174	23
Pollock and cod (Gadidae)	25	31	35	51	90	70	20	13	122	96	5	3	297	39
Sand lance (*Ammodytes hexapterus*)	54	68	3	4	14	11	92	60	3	2	15	8	181	24
Other[2]	1	1	0	0	25	19	17	11	2	2	1	1	46	6
Estimated Wet Weight (g)														
Invertebrates[1]	0	0	<1	3	0	0	4	1	0	0	2	<1	7	<1
Capelin (*Mallotus villosus*)	0	0	0	0	0	0	43	10	0	0	4	<1	47	3
Lanternfishes (Myctophidae)	0	0	0	0	0	0	0	0	0	0	406	87	406	28
Pollock and cod (Gadidae)	31	28	18	64	175	83	15	4	194	87	3	<1	435	30
Sand lance (*Ammodytes americanus*)	80	72	9	33	25	12	354	83	30	13	50	11	548	37
Other[2]	<1	<1	0	0	11	5	9	2	<1	<1	<1	<1	20	1

[1] Includes copepods and squid.

[2] Includes sculpin (Cottidae), flatfish (Pleuronectidae) and unidentified fish.

Day, R.H., and Nigro, D.A., 2000, Feeding ecology of Kittlitz's and Marbled Murrelets in Prince William Sound, Alaska: Waterbirds, v. 23, no. 1, p. 1-14.

Day and Nigro (2000) examined the feeding ecology of Kittlitz and Marbled Murrelets in Prince William Sound during the summers of 1996–98 by determining the distribution, abundance and foraging activity of murrelets on research cruises in four bays (Blackstone Bay; Harriman fjord; College Fjord; Unakwik Inlet). The number of Marbled Murrelets carrying fish varied across the season, with most birds (79 percent) observed during the late summer cruise (July 15–August 15). In total, 77 Marbled Murrelets were observed holding or eating fish: 17 (22.1 percent) were Pacific sand lance; six (7.8 percent) were Pacific herring, and 54 (70.1 percent) were unidentified. Overall mean prey length was 8.7 cm (± 3 SD, n = 40 fish).

K. Kuletz and E. Labunski, U.S. Fish and Wildlife Service (USFWS), unpub. data, 2004–06.

K. Kuletz and co-workers at the USFWS, Anchorage, Alaska, conducted at-sea surveys in Kachemak Bay, to examine the distribution and abundance of Kittlitz's and Marbled Murrelets. All surveys were conducted from a 25-ft Boston Whaler between 0700–1800 hrs. Surveys were conducted on a pre-determined transect route, and the presence and behavior of murrelets observed were recorded (fig. A1). Over all 3 years, a total of 10,139 Marbled Murrelets were observed, with 697 birds foraging (either actively diving or holding or eating a fish; table A8). A total of 57 birds were observed holding a fish, 88 percent were unidentified fish species, but 5 were Pacific sand lance and 1 was a herring (table A8).

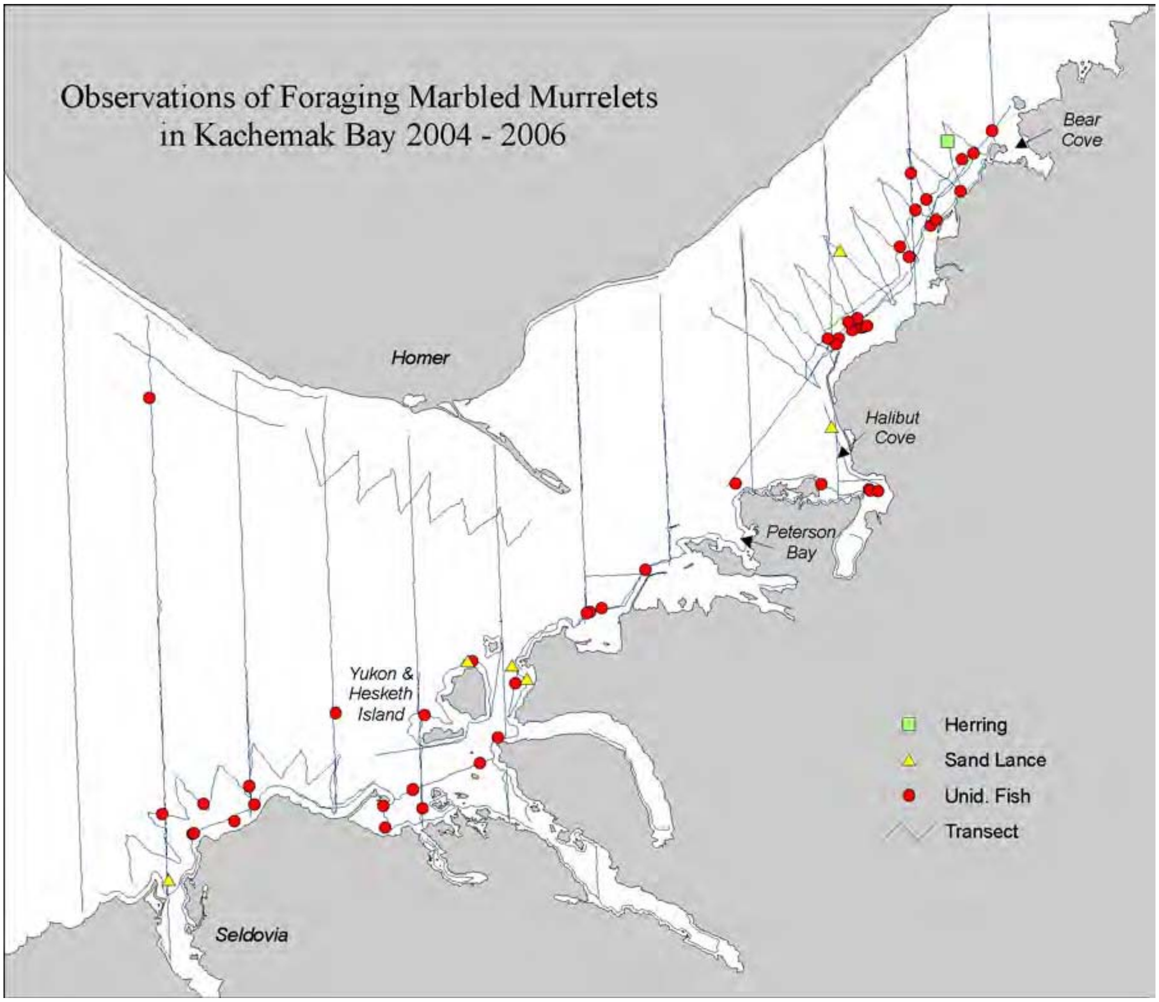


Figure A1. Transects and location of adults observed carrying fish for presumed self-consumption (Kuletz and Labunski, U.S. Fish and Wildlife Service, unpub. data, 2005).

Table A8. At-sea observations of Marbled Murrelets holding fish in Kachemak Bay, Alaska, 2004–06.

[Surveys were conducted during the day and food items are presumed to be for self feeding (K. Kuletz, U.S. Fish and Wildlife Service, unpub. data, 2004–06)]

Year	Month	Transect length (km)	No. total MAMU	No. MAMU foraging	No. unid. fish	No. sand lance	No. herring
2004	August	747	3,777	345	19	3	1
2005	April	35	6	0			
2005	June	175	78	2	2		
2005	July	228	558	13	3		
2005	August	629	2,011	129	12	1	
2006	June	166	146	5			
2006	July	197	552	16	1		
2006	August	ca 641	3,011	187	13	2	

K. Kuletz and E. Labunski, U.S. Fish and Wildlife Service, unpub. data., 2005.

K. Kuletz and co-workers at the USFWS, Anchorage, Alaska, conducted evening surveys in Kachemak Bay in August 2005 to specifically examine the prey species that murrelets were catching for their offspring. Murrelets holding fish in nearshore areas during the evening hours were presumed to be waiting for darkness for meal delivery. The survey was conducted between 1920–2100 hrs from a 25-ft Boston Whaler. Total transect distance was 21.1 km (fig. A2). The survey was an opportunistic survey of foraging murrelets and did not follow any predefined transect route. Observers scanned the water and investigated birds with fish to identify the prey down to species. A total of 51 birds were observed with 16 holding fish. Eight of the birds had a sand lance and 8 had an unidentified fish.

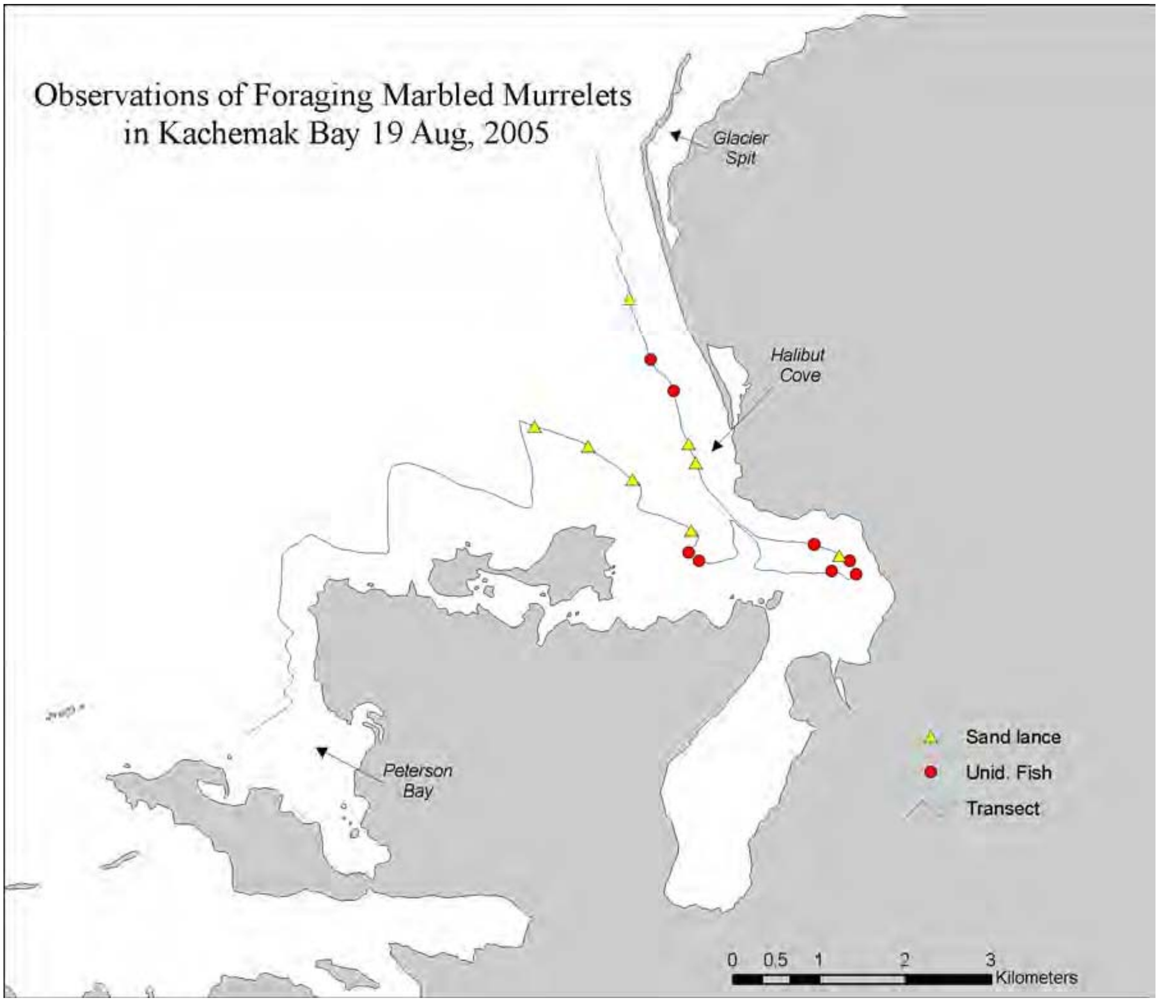


Figure A2. Transects and location of adults observed holding fish for chicks during a chick-diet survey in Kachemak Bay. (Kuletz and Labunski,U.S. Fish and Wildlife Service, unpub. data, 2005).

Kuletz, K.J., 2005, Foraging behavior and productivity of a non-colonial seabird, the Marbled Murrelet (*Brachyramphus marmoratus*), relative to prey and habitat, Dissertation: British Columbia, University of Victoria.

Kuletz (2005) examined the prey selection of Marbled Murrelets at two study sites (Naked Island and Jackpot Bay) in Prince William Sound during the summers (June to August) of 1997–99. Prey species and abundance was measured by sampling fish schools and aerial surveys. Adult prey were identified by (a) boat based and land based forage observations, (b) observations of fish held in the bill by other species foraging in the same feeding flock, and (c) capturing fish below foraging murrelets using a dip-net. Chick diet was identified by observing fish-holding adults during diet cruises in the morning (0330–0800 hrs) or evening (1900–2330 hrs).

Visually identified adult prey associated or eaten by adult murrelets in both areas (n= 61) were comprised of 41 percent herring, 52 percent sand lance, 5 percent capelin, and 2 percent gadids. Eighty-four percent of the herring were observed at Jackpot and most of the sand lance (94 percent) was at Naked. Fish caught in dip nets near foraging birds consisted mostly of 0+ and 1+ sand lance and 0+ herring.

Four hundred and eighty-two fish-holding birds at Jackpot, and 129 birds at Naked were observed during 94 diet cruises (n = 611 fish). 64 percent of the fish were identified down to species (table A9). Jackpot chicks primarily were fed 1+ juvenile herring (77–88 percent in a given year), whereas birds at Naked were feeding their chicks 67–100 percent sand lance.

Table A9. Species composition of identified prey used by Marbled Murrelets in Prince William Sound, Alaska, in summer, 1997–99.

[Samples caught below feeding adults (by dip-net) during mid-day were considered self-feeding samples. Observations of fish held by adults during diet surveys (< 0800 hr or > 1800 hr) were considered destined for delivery to chicks. Unidentified prey are not included here. (From Kuletz, 2005)]

Year	Site	Identified fish samples	Percent of total (by year and site)							
			Herring	Sandlance	Capelin	Gadid	Smelt	Salmon	Sandfish	Stickleback
		Fish caught below feeding adults Schools (number of fish)								
1998	Naked	15 (745)	66.7	33.3	0.0	0.0	0.0	0.0	0.0	0.0
	Jackpot	1	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1999	Naked	17 (208)	17.7	47.1	29.4	0.0	0.0	0.0	0.0	5.8
	Jackpot	0	nd							
s		Fish held for chick Adults with fish								
1997	Naked	34	0.0	94.1	0.0	2.9	0.0	0.0	2.9	0.0
	Jackpot	43	88.4	9.3	0.0	2.3	0.0	0.0	0.0	0.0
1998	Naked	16	0.0	100.0	0.0	0.0	0.0	0.0	0.0	0.0
	Jackpot	197	94.9	3.1	0.0	0.0	2.0	0.0	0.0	0.0
1999	Naked	12	16.7	66.7	16.7	0.0	0.0	0.0	0.0	0.0
	Jackpot	70	74.3	11.4	0.0	1.4	8.6	4.3	0.0	0.0

Newman, S.H., Nelson, A.K., Whitworth, D.L., and Carter, H.R., 2006, Marbled Murrelet (*Brachyraphus marmoratus*) activity patterns and health in Port Snettisham, aoutheast Alaska, 2005: New York, Wildlife Trust, Unpublished Report, 70 p.

Newman and colleagues conducted radio-telemetry and health assessment studies of Marbled Murrelets in Port Snettisham, Southeast Alaska, from June to August 2005. Four birds holding fish for their chick were captured whilst dip-netting adult murrelets for radio attachment. Three of the captured fish were large juvenile or first-year subadult capelin, and one was a first-year subadult Pacific sand lance.

References Cited

Day, R.H., Oakley, K.L., and Barnard, D.R., 1983, Nest sites and eggs of Kittlitz’s and Marbled Murrelets: Condor, v. 85, no. 3, p. 265-273.

Burkett, E.B., 1995, Marbled Murrelet food habits and prey ecology, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 223-246.

Krasnow, L.D., and Sanger, G.A., 1982, Feeding ecology of marine birds in the nearshore waters of Kodiak Island: Anchorage, Alaska, U.S. Fish and Wildlife Service, National Fishery Research Center, Migratory Bird Section, Final Report to OCSEAP, Research Unit 45, p. 505-630.

Piatt, J.F., and Anderson, P., 1996, Response of Common Murres to the *Exxon Valdez* oil spill and long-term changes in the Gulf of Alaska marine ecosystem, *in* Rice, S.D., Spies, R.B., Wolfe, D.A., and Wright, B.A., eds., *Exxon Valdez* Oil Spill Symposium, Anchorage, Alaska, 1993, American Fisheries Society Symposium 18, p. 720-737.

Sanger, G.A., 1987, Winter diets of Common Murres and Marbled Murrelets in Kachemak Bay, Alaska: Condor, v. 89, no. 2, p. 426-430.

Sanger, G.A., and Jones, R.D. Jr., 1982, Winter feeding ecology and trophic relationships of marine birds in Kachemak Bay, Alaska: Anchorage, Alaska, U.S. Fish and Wildlife Service, National Fishery Research Center, Migratory Bird Section, Final Report to the Outer Continental Shelf Environmental Assessment Program (OCSEAP), v. 16, Biological Studies, p. 161-294.

Speckman, S.G., 1996, Marbled Murrelet distribution and abundance in relation to the marine environment: Thesis, Fairbanks, University of Alaska, 89 p.

Appendix B. Source Code Listing (Javascript) for the Demographic Model LIFE

(Note: Line numbers are for reference only and should not be included in the runtime Javascript).

```
<script type=”text/javascript”>

   function calcLambda() {
          var form = document.form1;
          var alpha = form.alpha.value;
          var gamma = form.gamma.value;
          var delta = form.delta.value;
          var b1 = form.b1.value;
          var b2 = form.b2.value;
          var lambda;

          if (!isNumber(alpha) || !isNumber(gamma) || !isNumber(delta) || !isNumber(b1)
                || !isNumber(b2)) {
                alert(“One or more input values is non-numeric. Fix and try again.”);
                return;
          }

          if (alpha < 0 || gamma < 0 || b1 < 0 || b2 < 0 || !isPosInteger(delta)) {
                alert(“One or more input values invalid. Edit and try again.”);
                return;
          }

          if (delta < 2) {
                alert(“Age at first breeding must be >= 2.”);
                return;
          }

          alpha = parseFloat(alpha);
          gamma = parseFloat(gamma);
          delta = parseFloat(delta);
          b1 = parseFloat(b1);
          b2 = parseFloat(b2);

          var year1 = b1 * gamma;
          var year2 = b2 * gamma;
          var constant = alpha * year1 * year2 * (Math.pow(gamma,delta-2));

          var upperBound = 1.2
          var lowerBound = 0.8
          var midValue = 1.0
          var criterion = 0.0001
          var diff = 1 - gamma - constant;

          if (Math.abs(diff) < criterion) {
                form.lambda.value = “1.0000”;
                return;
          }
```

```
    if (diff < 0) {
        upperBound = 1.2;
        lowerBound = 1.0;
        if (Math.pow(upperBound,delta)-gamma*(Math.pow(upperBound,delta-1)) -
            constant < 0) {
            alert(“Population growth exceeds 20% per year. Run terminated.”)
            return;
        }
    } else {
        upperBound = 1.0;
        lowerBound = 0.8;
        if (Math.pow(lowerBound,delta)-gamma*(Math.pow(lowerBound,delta-1)) -
            constant > 0) {
            alert(“Population decline exceeds -20% per year. Run
             terminated.”)
            return;
        }
    }

    while (Math.abs(diff) >= criterion) {
        midValue = (upperBound + lowerBound)/2
        diff = Math.pow(midValue,delta) - gamma * Math.pow(midValue,delta-1) -
            constant;
        if (diff == 0) {
            form.lambda.value = formatLambda(midValue);
            return;
        }
        if (diff < 0) {
            lowerBound = midValue;
        } else {
            upperBound = midValue;
        }
    }
    form.lambda.value = formatLambda(midValue);
}

function isNumber(inputVal) {
    var oneDecimal = false;
    var oneChar;
    var inputStr = inputVal.toString();
    for (var i = 0; i < inputStr.length; i++) {
        oneChar = inputStr.charAt(i);
        if (i == 0 && oneChar == “-”) {
            continue;
        }
        if (oneChar == “.” && !oneDecimal) {
        oneDecimal = true;
        continue;
        }
        if (oneChar < “0” || oneChar > “9”) {
            return false;
        }
    }
```

```
        return true;
 }

 function isPosInteger(inputVal) {
        var inputStr = inputVal.toString();
        for (var i=0; i<inputStr.length; i++) {
              var oneChar = inputStr.charAt(i);
              if (oneChar < “0” || oneChar > “9”) {
                    return false;
        }
        }
        return true;
 }

 function formatLambda(midValue) {
        var roundup;
        if (midValue == 1.0) return “1.0000”;
        lambda = midValue.toString();
        roundup = (parseInt(lambda.substr(6,1)) >= 5)? true:false;
        if (roundup) lambda = (midValue + 0.0001).toString();
        return lambda.substr(0,6);
 }

</script>
```

This page left intentionally blank.

Appendix C. Source Code Listing (Fortran) for the Population Model MATRIX

(Note: Line numbers are for reference only and should not be compiled with source code).

```
  program matrix

  real(8), allocatable :: Nt(:)
  real(8), allocatable :: Nzero(:)
  real(8), allocatable :: M(:,:)
  real(8), allocatable :: detM(:,:)
  real(8), allocatable :: stableAD(:)
  real(8), allocatable :: oldAD(:)
  real(8), allocatable :: newAD(:)
  real(8), allocatable :: oldNt(:)
  real(8), allocatable :: newNt(:)
  real(8), allocatable :: detNt(:)
  real(8), allocatable :: stoNt(:)
  real span(0:29)
  integer E(1:1000,1:4),sumE,cutoff
  real(8) year1,year2,b1,b2,gamma,SDb1,SDb2,SDgamma,SDalpha
  integer delta,ubound,years,a,meanE
  real(8) y,rvcov,rvsummer,rvwinter,oldNtsum,newNtsum,sum
  real(8) oldSum,newSum,lambda
  real(8) upperbound,lowerbound,midvalue,diff
  real(8) criterion1,criterion2
  real(8) ntotal,Ntsum,sumN,Nstart,newN,classize
  real(8) detNtsum,stoNtsum
  real trends(1:3),alpha,adjAlpha,alpha_z
  character*1 cov,fixed,allowGTone,done,detDone,lambdaOne

  open (21,file=’c:\matrix_out\stableAD.txt’,status=’replace’)
  open (22,file=’c:\matrix_out\stats.txt’,status=’replace’)
  open (23,file=’c:\matrix_out\freqtrends_ind.txt’,status=’replace’)
  open (24,file=’c:\matrix_out\freqtrends_cov.txt’,status=’replace’)
  open (25,file=’c:\matrix_out\ext_times.txt’,status=’replace’)
  open (26,file=’c:\matrix_out\growth_det.txt’,status=’replace’)
  open (27,file=’c:\matrix_out\growth_sto_L1.txt’,
+       status=’replace’)
  open (28,file=’c:\matrix_out\growth_sto_Lcalc.txt’,
+       status=’replace’)

  data span/30*0/
  write(23,’(3a10)’) ‘trends10’,’trends20’,’trends30’
  write(24,’(3a10)’) ‘trends10’,’trends20’,’trends30’
  write(25,’(4a20)’) ‘ext_ind_L1’,’ext_cov_L1’,’ext_ind_Lcalc’,
+       ‘ext_cov_Lcalc’
  write(21,’(a5,2a20)’) ‘class’,’SAD(lambda=1)’,’SAD(lambda=calc)’

* Note: The following lines can be used for interactive user
* input of parameter values

```

```
* print *, ‘ ‘
* print *, ‘Enter first-year survival (as proportion of adult survival):’
* print *, ‘ ‘
* read (*,*) year1

* print *, ‘ ‘
* print *, ‘Enter SD of first-year survival (decimal value):’
* print *, ‘ ‘
* read (*,*) SDb1

* print *, ‘ ‘
* print *, ‘Enter second-year survival (as proportion of adult survival):’
* print *, ‘ ‘
* read (*,*) year2

* print *, ‘ ‘
* print *, ‘Enter SD of second-year survival (decimal value):’
* print *, ‘ ‘
* read (*,*) SDb2

* print *, ‘ ‘
* print *, ‘Enter adult survival (as proportion, not %):’
* print *, ‘ ‘
* read (*,*) gamma

* print *, ‘ ‘
* print *, ‘Enter SD of adult survival (decimal value):’
* print *, ‘ ‘
* read (*,*) SDgamma

* print *, ‘ ‘
* print *, ‘Enter age at first breeding (integer):’
* print *, ‘ ‘
* read (*,*) delta

* print *, ‘ ‘
* print *, ‘Enter fecundity (female offspring per adult female):’
* print *, ‘ ‘
* read (*,*) alpha

* print *, ‘ ‘
* print *, ‘Enter SD fecundity (decimal value):’
* print *, ‘ ‘
* read (*,*) SDalpha

* print *, ‘ ‘
* print *, ‘Enter starting population size (integer):’
* print *, ‘ ‘
* read (*,*) ntotal

* print *, ‘ ‘
* print *, ‘Could fecundity ever exceed 1.0 in this species? Enter “y” or “n”:’
* print *, ‘ ‘
* read (*,*) allowGTone

```

```
year1 = 0.701
year2 = 0.888
gamma = 0.880
SDb1 = 0.06
SDb2 = 0.06
SDgamma = 0.06
delta = 3
alpha = 0.294953
SDalpha = 0.10
ntotal = 3000
allowGTone = ‘n’

b1 = year1*gamma
b2 = year2*gamma

cutoff = 5   ! Sets maximum lifespan (% adults still living)

i=0
do while ((100*gamma**i).ge.cutoff)
      i=i+1
end do

ubound = i + delta

allocate (Nt(0:ubound))
allocate (M(0:ubound,0:ubound))
allocate (detM(0:ubound,0:ubound))
allocate (stableAD(0:ubound))
allocate (Nzero(0:ubound))
allocate (oldAD(0:ubound))
allocate (newAD(0:ubound))
allocate (oldNt(0:ubound))
allocate (newNt(0:ubound))
allocate (detNt(0:ubound))
allocate (stoNt(0:ubound))

do i=0,ubound             ! Initialize projection matrix
      do j=0,ubound
            M(i,j) = 0
      end do
end do

*Construct stable age distribution for lambda=1

Nzero(delta) = 100
i = delta-1
do while (i.gt.1)
      Nzero(i) = Nzero(i+1)/gamma
      i=i-1
end do

Nzero(1) = Nzero(2)/b2
Nzero(0) = Nzero(1)/b1

```

```
 do i = delta+1,ubound
       Nzero(i) = Nzero(i-1)*gamma
 end do

 Ntsum = 0
 do i = 0,ubound
       Ntsum = Ntsum + Nzero(i)
 end do

 do i = 0,ubound
       classize = Nzero(i)/Ntsum
       stableAD(i) = classize ! Save stableAD for lambda=1
       Nzero(i) = classize * ntotal
 end do

 Nt = Nzero
 Ntsum = sumNt()
 Nstart = Ntsum
 Nextinct = 0.05*Nstart ! Population “extinct” when <5% remains

*Find adjAlpha - fecundity that results in stationary population
*with given survival values (uses iterative interpolation)
*Also, create a fixed projection matrix and save
*a copy (detM) for later use

 oldNtsum = Ntsum
 adjAlpha = alpha
 criterion1 = .001

 M(1,0) = b1
 M(2,1) = b2
 do j = 2,ubound-1
       M(j+1,j) = gamma
 end do
 do j = delta,ubound
       M(0,j) = alpha
 end do

 detM = M

 Nt = matmul(M,Nt)
 newNtsum = sumNt()
 diff = newNtsum - oldNtsum

 if (diff.gt.0) then
       upperbound = alpha
       lowerbound = 0
 else if (diff.lt.0) then
       if (allowGTone.eq.’y’) then
             upperbound = 5
       else
             upperbound = 1
       end if
       lowerbound = alpha
 end if

```

```
 do while (abs(diff).ge.criterion1)
       Nt = Nzero
       adjAlpha = (upperbound + lowerbound)/2
       do j = delta,ubound
             M(0,j) = adjAlpha
       end do
       Nt = matmul(M,Nt)
       newNtsum = sumNt()
       diff = newNtsum - oldNtsum
       if (diff.lt.0) then
             lowerBound = adjAlpha;
       else
             upperBound = adjAlpha;
       end if
 end do

 Nt = Nzero

 call random_seed()

*Compute trend frequencies for intervals of 10,20,30 years
*Cov = ‘y’ means covarience of winter/summer random variates
*Cov = ‘n’ means winter/summer rates vary independently
*Lambda = 1

 do ifreq = 1,2
       if (ifreq.eq.1) then
             cov = ‘n’
       else
             cov = ‘y’
       end if
       do i=1,50
             years = 0
             Nt = Nzero
             Ntsum = Nstart
             do while (Ntsum.ge.Nextinct)
                   call fillMatrix(adjAlpha)
                   Nt = matmul(M,Nt)
                   Ntsum = sumNt()
                   if (years.le.29) then
                         span(years) = Ntsum
                   else
                         call calcTrends()
                   end if
                   years = years + 1
             end do
       end do
 end do

*Compute a large number of extinction times and
*calculate mean time to extinction when lambda=1

 do iext = 1,2
       if (iext.eq.1) then
             cov = ‘n’
       else
```

```
                   cov = ‘y’
             end if
             do i=1,1000
                   years = 0
                   Nt = Nzero
                   Ntsum = Nstart
                   do while (Ntsum.ge.Nextinct)
                         call fillMatrix(adjAlpha)
                         Nt = matmul(M,Nt)
                         Ntsum = sumNt()
                         years = years + 1
                   end do
                   E(i,iext) = years
             end do
       end do

      *Save 4 examples of population trajectories
      *for cov=’y’ and cov=’n’ when lambda=1

       cov = ‘n’
       do i=1,4
             years = 0
             write (27,’(a4,i1,i7,i10)’) ‘ind’,i,0,nint(Nstart)
             Nt = Nzero
             Ntsum = Nstart
             do while (Ntsum.ge.Nextinct)
                   call fillMatrix(adjAlpha)
                   Nt = matmul(M,Nt)
                   Ntsum = sumNt()
                   years = years + 1
                   write (27,’(a4,i1,i7,i10)’) ‘ind’,i,years,nint(Ntsum)
             end do
       end do

       cov = ‘y’
       do i=1,4
             years = 0
             write (27,’(a4,i1,i7,i10)’) ‘cov’,i,0,nint(Nstart)
             Nt = Nzero
             Ntsum = Nstart
             do while (Ntsum.ge.Nextinct)
                   call fillMatrix(adjAlpha)
                   Nt = matmul(M,Nt)
                   Ntsum = sumNt()
                   years = years + 1
                   write (27,’(a4,i1,i7,i10)’) ‘cov’,i,years,nint(Ntsum)
             end do
       end do

      *Find stable age distribution and lambda for the input
      *parameters as given (no stochasticity)

       oldAD = stableAD
       oldNt = Nzero
```

```
  do i=1,1000
        newNt = matmul(detM,oldNt)
        sum = 0
        do k=0,ubound
              sum = sum + newNt(k)
        end do
        do k=0,ubound
              newAD(k) = newNt(k)/sum
              newNt(k) = newAD(k) * ntotal
        end do
        oldNt = newNt
  end do
  do i=0,ubound
        write (21,’(i5,2(12x,F8.6))’) i,stableAD(i),newAD(i)
  end do

  sum = 0
  do i=0,ubound
        sum = sum + newNt(i)
  end do
  oldSum = sum
  newNt = matmul(detM,oldNt)
  newSum = 0
  do k=0,ubound
        newSum = newSum + newNt(k)
  end do
  lambda = 1 + (newSum-oldSum)/oldSum

* Calculate growth for parameters as given

  criterion2 = 0.000001
  lambdaIsOne = ‘n’
  if (abs(lambda-1).le.criterion2) lambdaIsOne = ‘y’
  Nt = Nzero
  Ntsum = Nstart
  years = 0
  write (26,’(a4,i7,i10)’) ‘det0’,0,nint(Nstart)
  if (lambdaIsOne.eq.’y’) then
        do i=1,100
              write (26,’(a4,i7,i10)’) ‘det0’,i,nint(Ntsum)
        end do
  else if (lambda.lt.1) then
        years = 0
        do while (Ntsum.ge.Nextinct)
              Nt = matmul(detM,Nt)
              Ntsum = sumNt()
              years = years + 1
              write (26,’(a4,i7,i10)’) ‘det0’,years,nint(Ntsum)
        end do
  else if (lambda.gt.1) then
        years = 0
        do while (Ntsum.le.50000000.and.years.lt.1000)
              Nt = matmul(detM,Nt)
```

```
                   Ntsum = sumNt()
                   years = years+1
                   write (26,’(a4,i7,i10)’) ‘det0’,years,nint(Ntsum)
             end do
 end if

*Compute a large number of extinction times and calculate
*mean extinction time when lambda = lambda(calc)

 do iext = 3,4
       if (iext.eq.3) then
             cov = ‘n’
       else if (iext.eq.4) then
             cov = ‘y’
       end if
       do i=1,1000
             years = 0
             Nt = Nzero
             Ntsum = Nstart
             do while (Ntsum.ge.Nextinct.and.years.lt.5000)
                   call fillMatrix(alpha)
                   Nt = matmul(M,Nt)
                   Ntsum = sumNt()
                   years = years + 1
             end do
             E(i,iext) = years
       end do
 end do

 do kk=1,1000
       write (25,’(4i20)’) (E(kk,kn),kn=1,4)
 end do

 do iext = 1,4
       sumE = 0
       do kk = 1,1000
             sumE = sumE + E(kk,iext)
       end do
       meanE = sumE/1000
       if (iext.eq.1) then
             meanEind_L1 = meanE
       else if (iext.eq.2) then
             meanEcov_L1 = meanE
       else if (iext.eq.3) then
             meanEind_Lcalc = meanE
       else
             meanEcov_Lcalc = meanE
       end if
 end do

 write (22,’(a19,12x,f8.6)’) ‘Lambda (calculated)’,lambda
 write (22,’(a23,8x,i8)’) ‘Mean ext lambda=1 (ind)’,meanEind_L1
 write (22,’(a23,8x,i8)’) ‘Mean ext lambda=1 (cov)’,meanEcov_L1
 write (22,’(a26,5x,i8)’) ‘Mean ext lambda=calc (ind)’,
+      meanEind_Lcalc
 write (22,’(a26,5x,i8)’) ‘Mean ext lambda=calc (cov)’,
```

```
+      meanEcov_Lcalc
 write (22,’(a20,11x,f8.6)’) ‘Alpha (for lambda=1)’,adjAlpha

*Save 4 examples of population trajectories
*for cov=’y’ and cov=’n’ when lambda = lambda(calc)

 cov = ‘n’
 do i=1,4
       years = 0
       detDone = ‘n’
       write (28,’(a4,i1,i7,2i10)’) ‘ind’,i,0,nint(Nstart),
+            nint(Nstart)
       detNt = Nzero
       stoNt = Nzero
       detNtsum = Nstart
       stoNtsum = Nstart
       do while (stoNtsum.ge.Nextinct.and.stoNtsum.lt.50000000
+            .and.years.lt.5000)
             call fillMatrix(alpha)
             stoNt = matmul(M,stoNt)
             stoNtsum = 0
             do kj=0,ubound
                   stoNtsum = stoNtsum + stoNt(kj)
             end do
             if (detDone.eq.’n’) then
                   if (lambdaIsOne.eq.’n’) then
                         detNt = matmul(detM,detNt)
                         detNtsum = 0
                         do kj=0,ubound
                               detNtsum = detNtsum + detNt(kj)
                               if (detNtsum.gt.50000000) detDone = ‘y’
                         end do
                   else
                         detNtsum = Nstart
                   end if
             else
                   detNtsum = 0
             end if
             years = years + 1
             write (28,’(a4,i1,i7,2i10)’) ‘ind’,i,years,
+                  nint(stoNtsum),nint(detNtsum)
       end do
 end do

 cov = ‘y’
 do i=1,4
       years = 0
       detDone = ‘n’
       write (28,’(a4,i1,i7,2i10)’) ‘cov’,i,0,nint(Nstart),
+            nint(Nstart)
       detNt = Nzero
       stoNt = Nzero
       detNtsum = Nstart
       stoNtsum = Nstart
       do while (stoNtsum.ge.Nextinct.and.stoNtsum.lt.50000000
+            .and.years.lt.5000)
```

```
             call fillMatrix(alpha)
             stoNt = matmul(M,stoNt)
             stoNtsum = 0
             do kj=0,ubound
                   stoNtsum = stoNtsum + stoNt(kj)
             end do
             if (detDone.eq.’n’) then
                   if (lambdaIsOne.eq.’n’) then
                         detNt = matmul(detM,detNt)
                         detNtsum = 0
                         do kj=0,ubound
                               detNtsum = detNtsum + detNt(kj)
                               if (detNtsum.gt.50000000) detDone = ‘y’
                         end do
                   else
                         detNtsum = Nstart
                   end if
             else
                   detNtsum = 0
             end if
             years = years + 1
             write (28,’(a4,i1,i7,2i10)’) ‘cov’,i,years,
+                  nint(stoNtsum),nint(detNtsum)
       end do
 end do

 contains

       function rv()
             total = 0
             do k = 1,12
                   call random_number(y)
                   total = total + y
             end do
             rv = total-6
       end function

       subroutine fillMatrix(alpha_z)
             rvcov = rv()
             rvwinter = rv()
             rvsummer = rv()
             do a = delta,ubound
                   if (cov.eq.’y’) then
                         M(0,a) = alpha_z + (SDalpha*rvcov)
                   else
                         M(0,a) = alpha_z + (SDalpha*rvsummer)
                   end if
                   if (M(0,a).lt.0) M(0,a) = 0
                   if (M(0,a).gt.1.and.allowGTone.eq.’n’) M(0,a) = 1
             end do
             if (cov.eq.’y’) then
                   M(1,0) = b1 + (SDb1*rvcov)
                   M(2,1) = b2 + (SDb2*rvcov)
             else
                   M(1,0) = b1 + (SDb1*rvwinter)
```

```
                  M(2,1) = b2 + (SDb2*rvwinter)
            end if
            if (M(1,0).lt.0) M(1,0) = 0
            if (M(1,0).gt.1) M(1,0) = 1
            if (M(2,1).lt.0) M(2,1) = 0
            if (M(2,1).gt.1) M(2,1) = 1
            do a = 2,ubound-1
                  if (cov.eq.’y’) then
                        M(a+1,a) = gamma + (SDgamma*rvcov)
                  else
                        M(a+1,a) = gamma + (SDgamma*rvwinter)
                  end if
                  if (M(a+1,a).lt.0) M(a+1,a) = 0
                  if (M(a+1,a).gt.1) M(a+1,a) = 1
            end do
      end subroutine

      function sumNt()
            sum = 0
            do k=0,ubound
                  sum = sum + Nt(k)
            end do
            sumNt = sum
      end function

      subroutine calcTrends()
            do nn=0,28
                  span(nn) = span(nn+1)
            end do
            span(29) = Ntsum
            do lk=1,3
                  trends(lk) = ((span(10*lk-1) - span(0))/span(0))*100
            end do
            if (cov.eq.’n’) then
                  write (23,’(3(f10.1))’) (trends(il),il=1,3)
            else
                  write (24,’(3(f10.1))’) (trends(il),il=1,3)
            end if
      end subroutine

end program
```

This page left intentionally blank.

Appendix D. Current Population Estimates—British Columbia

by Alan E. Burger[1]

Burger (2002) summarized at-sea and radar counts for British Columbia to estimate the provincial population (table D1). Most of the vast coastline of British Columbia did not have count data and estimates were based on several methods of extrapolating from at-sea or radar counts covering portions of each of the six conservation regions established by the Canadian Marbled Murrelet Recovery Team (CMMRT) (see map of regions: fig. 7). More than 32,500 birds were actually counted, and the likely population was estimated to be 55,000–78,000 birds (median 66,000 birds; table D1). Burger (2002) stressed that there was much uncertainty in these estimates, because large areas of the British Columbia coast had not been censused, many of the census data were out of date and often based on single boat transects, and extrapolations from the patchy census data were necessarily crude.

There is little new information with which to update and improve the crude population estimates made by Burger (2002). Nevertheless, I have tried to improve the population estimates in two ways: first by updating, where possible, the information used by Burger (2002), and second by making a new estimate by applying densities derived from radar studies to estimates of total habitat area within British Columbia. Neither of these approaches is highly satisfactory and an accurate estimate of the British Columbia population remains elusive.

Table D1. Population estimates for British Columbia as reported by Burger (2002) and updated with new information (2006).

[See Appendixes for details. Birds, not breeding pairs or nests, are the measure of population used here. **Conservation region:** For details on the conservation regions see Bertram and others (2003; available at http://www.sfu.ca/biology/wildberg/bertram/mamurt/links.htm). **Population estimate made in 2002:** Range indicates the pessimistic and optimistic population estimates (Burger, 2002). Note that these estimates were often based on data from 10 to 25 years earlier than 2002. **Updated estimate:** See text for details on new population data and updated estimates. Note that these estimates remain relatively crude for most of the conservation regions.

Conservation region	Population estimate made in 2002 (birds)	Updated estimate (birds)
West and North Vancouver Island	19,400–24,500	18,700-23,600
East Vancouver Island	700–1,000	1,000-2,000
Southern Mainland Coast	6,000–7,000	6,000–7,000
Central Mainland Coast	10,000–21,000	10,000–21,000
Northern Mainland Coast	10,100–14,600	10,100–14,600
Haida Gwaii (Queen Charlotte Islands)	8,500–9,500	8,500 – 25,000
Total for British Columbia	54,700–77,600	54,300 – 92,600

Updated Regional Population Estimates

The only new data available to improve regional population estimates comes from radar studies. The CMMRT has recommended the use of radar to monitor population trends (Bertram and others, 2003), and radar also is widely used in British Columbia for identifying watershed populations and relationships with habitat (see for example, Burger, 2001, Burger and others, 2004). Radar counts cannot be directly compared with at-sea counts from boats. Most studies in British Columbia use radar at the mouths of watersheds to count birds heading into watersheds. Radar counts tend to reveal higher numbers of birds than at-sea counts in adjacent areas (Burger, 2001), but because murrelets can commute large distances (Whitworth and others, 2000; Hull and others, 2001), one cannot reliably link these radar counts with counts made at sea in marine foraging areas. In some cases, estimates based on incomplete at-sea counts (Burger, 2002) can be re-assessed using radar counts made in the same areas. Neither method provides a complete, accurate measure of local populations and uncertainty remains over all regional estimates, and mix of radar and at-sea counts had to be used in some regions.

West and North Vancouver Island.—The 2002 estimates were based on both at-sea and radar counts where appropriate (Burger, 2002). There are no new at-sea counts to include, but recent radar counts tend to support earlier estimated population ranges (table D2). Estimates made in the subregions on West and North Vancouver Island are discussed here.

Owen Point-Cape Beale (West Coast Trail coast).—The 2002 estimate was based on repeated at-sea counts made in 1994–2001 covering this entire coastline, and there was some confidence in the estimate (3,000–3,300 birds; table D2). The same transect data indicate declines in numbers in this area between 1994 and 2006 (see appendix E). Radar surveys covering 11 watersheds leading off this coast in 2002–05 gave pooled mean counts of 2,126 birds and pooled mean of the annual maximum counts of 2,593 birds (table D3; A.E. Burger, University of Victoria, unpub. data, 2006). The watersheds sampled included a substantial portion of the likely nesting areas off this coast, but did not cover some large areas of suitable forest, including the Nitinat Triangle, Cheewat, lower Walbran, Logan and Cullite drainages. Taking these unsurveyed areas into account, the radar counts seem consistent with the 2002 estimates.

---

[11] University of Victoria, British Columbia

Table D2. Counts and estimated populations of Marbled Murrelets breeding season (May through July) in the West and North Vancouver Island conservation region, British Columbia.

[See Burger (2002) for details on 2002 estimates]

Section within the region	2002 estimates		2006 estimates		Notes on new data
	Actual counts	Estimated range	Actual counts	Estimated range	
Victoria Harbour to Port San Juan	–	200–300	–	200–300	No new data
West Coast Trail (Owen Point to Cape Beale)	2,859	3,000–3,300	Mean: 2,126 Mean of max.: 2,593	3,000–3,300	Radar counts covered most but not all watersheds. Radar counts support previous estimate.
Barkley Sound + Alberni Inlet	3,618	3,200–3,900	Mean: 1949 Mean of max.: 2,182	2,500–3,000	Radar counts covered all major watersheds and most nesting habitat. Previous estimate reduced.
Clayoquot Sound and Long Beach	5,536	6,000–8,000	See text	6,000–8,000	Radar counts show no change.
NW Vancouver Island	5,930	6,500–8,000	See text	6,500–8,000	Radar counts at a four sites similar to previous.
NE Vancouver Island	418	500–1000	383	500–1,000	Radar counts at nine sites. Estimates possibly optimistic.
Total	18,361	19,400–24,500	-	18,700–23,600	

Barkley Sound and Alberni Canal.—The 2002 estimate for these areas (3,200–3,900 birds; table D2) was based on at-sea counts made in the 1980s and early 1990s (Burger, 2002). Repeated surveys on four transect routes in Barkley Sound all indicate declines since 1979 or 1980 (see appendix E). Radar surveys covering 19 watersheds leading off these waterways in 2002–05 gave pooled mean counts of 1,949 birds and pooled mean of the annual maximum counts of 2,182 birds (table D3; A.E. Burger, University of Victoria, unpub. data, 2005). The watersheds sampled covered all major drainages containing likely nesting habitat and a substantial portion of the total nesting habitat area here. It therefore seems unlikely that the 2002 estimate is correct, and a more likely population range here is 2,500–3,000 birds.

Clayoquot Sound and Long Beach.—The 2002 estimate of 6,000—8,000 birds (table D2) was based on radar counts at 20 watersheds in 1995–98 covering most of the likely habitat (Burger, 2002, appendix 2). Fourteen of these sites were resurveyed with radar in 2006, yielding similar total counts to 1995–98 (A.E. Burger, unpub. data). Consequently, there is no evidence to change the 2002 estimate.

NW Vancouver Island (Estevan Point to Cape Sutil).—At-sea counts were too sparse to derive estimates for this area, and Burger (2002) used Manley's (British Columbia Ministry of Environment, unpub. data, 2000) radar counts from 1999 and 2001 at 18 watersheds totaling 5,930 birds to reach an estimate of 6,500–8,000 birds (table D2; see also Burger, 2002, appendix 2). Radar counts made by W. Harper and J. Deal (Canadian Forest Products, Ltd., unpub. data, 2003–04) at four of Manley's coastal sites showed similar numbers to 1999–2001. There are no new at-sea counts in this area. Population estimates for this area therefore remain the same as in 2002 (table D2).

NE Vancouver Island.—Burger (2002) estimated 500–1,000 murrelets in the sector, based on very incomplete at-sea counts made in 1991 (table D2). Radar counts in 2003–04 at nine sites in this region, mostly inland, showed a total of 295 (sum of mean counts) to 383 birds (sum of the total counts; W. Harper and J. Deal, Canadian Forest Products, Ltd., unpub. data, 2003–04). There are no new at-sea counts. The estimate of 500–1,000 murrelets in this area might be optimistic, but in the absence of better data should remain (table D2).

The updated total for the West and North Vancouver Island region is 18,700–23,600 birds (table D1), which is slightly lower overall than the 2002 estimate (table D1).

Table D3. Radar counts at 30 watersheds on southwest Vancouver Island in 2002–05, grouped by the likely marine source of the incoming murrelets.

[Mean, SD, minimum and maximum pre-sunrise counts of incoming Marbled Murrelets entering watersheds. The mean of each year's maximum count also is shown. Data from A.E. Burger (University of Victoria, unpub. data, 2002–05)]

Marine source	Watershed code	Watershed	Pre-sunrise count of murrelets					Number of surveys
			Mean	SD	Min.	Max.	Mean of annual maximum	
A.—Birds likely to be coming from West Coast Trail coast								
	CAR	Carmanah Valley	114.5	61.0	63	196	196.0	4
	CAY	Caycuse River	195.7	86.7	124	292	231.5	3
	DAR	Darling River	91.5	65.1	15	150	75.0	4
	GOR	Gordon River	148.2	99.4	47	287	244.5	5
	KLA_BO	Bottard Creek	120.3	50.9	75	180	130.5	4
	KLA_GO	Gorge Creek	151.8	76.1	67	234	175.0	5
	KLA_KR	Klanawa River	231.8	97.4	121	317	268.7	4
	KLA_WK	West Klanawa	46.3	42.2	11	93	52.0	3
	NIT	Nitinat River	311.9	157.3	96	559	396.3	7
	SJN	San Juan River	320.3	215.7	87	609	444.5	4
	WAL	Mid and Upper Walbran Valley	393.5	125.7	233	532	378.7	4
Total West Coast Trail			2,125.6	–	939.0	3,449.0	2,592.6	47
B.—Birds likely to be coming from Barkley Sound or Alberni Inlet								
	CHI	China Creek	215.7	227.5	62	477	292.5	3
	EFI	Effingham River	21.3	20.0	6	44	25.0	3
	EFI_British Columbia	Brand Creek	29.7	25.1	6	56	31.0	3
	FRB	Franklin River	35.3	1.0	34	36	36.0	4
	HAN	Handy Creek	15.5	9.2	9	22	22.0	2
	LUC	Lucky Creek	292.8	75.0	191	350	311.3	5
	MAC	Macktush Creek	1.0	1.2	0	2	1.3	4
	MAG	Maggie River/Draw Creek	13.3	11.6	3	28	16.7	4
	NAH	Upper Nahmint River	34.0	12.5	26	55	39.3	5
	NUM_CC	Carnation Creek	54.3	24.5	37	90	65.0	4
	PAC	Pachena River	140.7	19.6	120	159	151.0	3
	PIP_BP	Black Peaks	26.5	27.6	7	46	26.5	2
	PIP_SL	Skull Lake	32.0	0.0	32	32	32.0	2
	RIT	Ritherdon Creek	25.3	1.5	24	27	25.5	3
	SAR	Sarita River	180.8	52.8	144	259	208.0	4
	SNO	Snow Creek	1.3	1.5	0	3	1.5	3
	SPE	Spencer Creek	65.8	32.4	40	111	78.0	4
	TOQ	Toquart River	436.9	129.7	272	636	458.3	7
	UC_HEN	Henderson Lake (Uchucklesit and Useless Inlets)	326.7	130.9	167	549	361.3	6
Total Barkley Sound and Alberni			1,948.6	–	1,180.0	2,982.0	2,182.3	71
Overall total			4,074	–	2,119	6,431	4,775	118

East Vancouver Island.—The 2002 estimate (700–1,000 birds; table D1) was based on at-sea counts totaling 437 birds but covering a small portion of the region (Burger, 2002). There are no new at-sea counts, but radar counts were undertaken by D. Lindsay (TimberWest, Ltd.; unpub. data, 2002–04) at nine sites in this region over 3 years (total of 95 surveys in 2004–06). The sum of the annual mean count at these sites was 435 ± 351 birds (SD), and the sum of the maximum count at each site was 1,194 birds. A few of the birds likely flew from the west coast of the island, but these radar counts indicate that the original estimate for this region was low because these sites did not cover all the likely flight paths. Until more detailed data are available, a more realistic population range is 1,000–2,000 birds.

Southern Mainland Coast.—The 2002 estimate (6,000–7,000 birds; table D1) was based on a combination of at-sea counts, radar counts and population estimates based on mark-recapture studies in Desolation Sound (Burger, 2002). There are no new data with which to update this estimate. Radar surveys were repeated in 2006 at some of the sites sampled in 2000–01, but these data are not yet available (D. Bertram, Canadian Wildlife Service). The 2002 estimate therefore remains unchanged.

Central Mainland Coast.—The 2002 estimate (10,000–21,000 birds; table D1) was based primarily on models that combined murrelet densities from radar counts done in 1998 with Geographic Information System (GIS) measures of likely habitat (Schroeder and others, 1999; see also Burger, 2002). Other estimates for parts of this coast indicated fewer birds (Burger, 2002). Some of the radar sites were resurveyed in 2006 but the data are not yet available (D. Bertram, Canadian Wildlife Service). In the absence of additional information, the crude population estimate from 2002 cannot be changed.

Northern Mainland Coast.—The 2002 estimate (10,100–14,600 birds; table D1) was based on extrapolations from radar counts at 26 watersheds in 2001 using a Habitat Suitability Index model (Steventon and Holmes, 2002; see also Burger, 2002). There have been very few at-sea counts in this area. Radar surveys at some of the 2001 sites were repeated in 2005 but these data are not available (D. Bertram, Canadian Wildlife Service). In the absence of additional information, the crude population estimate from 2002 cannot be changed.

Haida Gwaii (Queen Charlotte Islands).—The 2002 estimate from this archipelago was 8,500-9,500 birds (table D1) based on actual counts of 6,063 birds mostly made 10–25 years previously and covering only part of the coastline (Burger, 2002). There are no new at-sea counts covering previously uncounted areas.

Information available since 2002 provides conflicting evidence of what current populations might be. On the one hand, the analysis by Holt (2004) indicated that habitat areas have declined by an estimated 42 percent, mostly throughout the past 50 years, so that if murrelet numbers tracked habitat area as expected (Burger, 2001) then populations should be lower than 10–25 years ago. This is supported by the declines in numbers seen in the long-term data from Laskeek Bay in this region (see appendix E).

Densities (birds per hectare of apparently suitable habitat) made from recent radar counts applied to areas of habitat estimated from a management algorithm suggest that the population might be considerably higher than the 2002 estimate. Harfenist and Cober (2006) reported mean totals of 2,029 birds (sum of the annual mean of pre-sunrise incoming birds) or 2,492 birds (sum of annual maximum count of incoming or outgoing birds) from radar counts made in 2004–05 at 26 watersheds (table D4). It was difficult to determine the catchment areas (areas of inland suitable nesting habitat) into which these birds were flying. Using 14 watersheds with the most likely predicted catchment areas, Harfenist and Cober (2006) calculated mean densities of 0.157 ± 0.078 (SD) birds per hectare of nesting habitat derived from the algorithm used for land-use planning. When applied to the total area of this habitat in Haida Gwaii (Queen Charlotte Islands), this density predicted a total population of 41,000 birds. This figure seems unreasonably high, given the numbers of birds counted on the water (Burger, 2002) and in the radar counts (table D4). Habitat mapping that is now in progress (but incomplete) using interpretation of aerial photographs suggests that the planning algorithm did not reliably predict habitat areas (Harfenist and Cober, 2006; A. Cober, Environment Canada, oral commun., 2006). The radar-based density derived from this study was 74 percent higher than that derived using a similar method on western Vancouver Island (0.090 birds per hectare of nesting habitat; Burger and others, 2004b) where densities of murrelets on the water were higher than off Haida Gwaii (Queen Charlotte Islands) (Burger 1995, 2002). Applying the west Vancouver Island density to the estimated habitat area gives an estimated population of 23,500 birds.

Applying radar densities in Haida Gwaii (Queen Charlotte Islands) seems problematic, due in part to the topography. The mountain ranges generally are lower than on the British Columbia mainland and Vancouver Island, making it less likely that murrelets would be constrained to remain in the watersheds in which they were seen entering. In addition, the relatively narrow land area means that murrelets are likely to fly across the islands entirely. Both of these factors would lead to an overestimate of densities and hence estimated populations. It seems that the radar density method is overestimating the Haida Gwaii (Queen Charlotte Islands) population but it does suggest that the population is indeed larger than that estimated by Burger (2002). Given these uncertainties, it seems the most prudent approach is to estimate a wide range in the likely population taking into account both past and previous estimates. Until further

Table D4. Summary of radar counts of Marbled Murrelets from 26 radar stations on Haida Gwaii (Queen Charlotte Islands) in 2004 and 2005.

[Data from Harfenist and Cober, 2006. Surveys between May 28 and July 16 were included, and those with rain or technical problems were excluded]

Radar station	Mean pre-sunrise count of incoming birds	Mean of the annual maximum count	Number of surveys
Bigsby	98.0	130.0	2
Botany	86.8	130.5	4
Dawson Harbour	65.5	66.0	2
Dawson Inlet	95.0	110.0	3
Fairfax	90.3	123.0	3
Gregory	176.0	220.0	4
Harriet Harbour	42.5	43.0	2
Huston	96.8	127.0	4
Hutton	88.3	92.0	3
Jalun Lake	30.0	30.0	1
Kitgoro	47.0	57.0	1
Klunkwoi	48.0	98.0	3
Lagoon	79.0	79.5	2
Long	133.5	146.5	3
Mather’s Lake	10.0	11.0	1
Mitchell	32.8	40.0	4
Mt. Creek	30.0	48.0	2
Port Chanal	193.8	233.5	3
Security	82.3	154.0	3
Shields	36.0	37.0	1
Slatechuck	64.0	66.0	1
South Carmichael	19.0	20.0	1
South Louise	9.0	11.0	1
Tartu	109.3	127.0	3
Trounce	55.5	65.5	3
Windy Bay	210.8	226.5	4
Sum	2,029	2,492	64

information can refine the estimate, it should be considered to be 8,500–25,000 birds.

Population Estimated by Applying Radar-Derived Densities

Several studies have shown a significant positive correlation between the numbers of murrelets counted with radar as they enter watersheds before dawn and the area of likely habitat within those watersheds (Burger, 2001; Raphael and others, 2002; Bigger and others, 2006). Five studies in British Columbia, covering a 101 watersheds (more than 2 million hectares) showed this trend; linear regressions generally fit this relationship well although there were widely scattered data points in some studies (Burger and others, 2004).

In radar studies, murrelet populations are estimated as birds, not nests or pairs because birds are what the radar detects. The actual breeding status of birds detected by radar is not known, but a portion of the birds flying into the forests are known to be non-breeders or failed breeders (Peery and others, 2004). Because other measures of Marbled Murrelet population size (at-sea counts) also record birds of all ages and breeding condition, there is compatibility between radar counts and at-sea counts.

Areas of likely suitable habitat can be estimated by applying algorithms to forest cover, satellite imagery or other measures of forest composition using GIS. In the British Columbia-wide radar study (Burger and others, 2004), areas of likely suitable habitat were estimated using a simple algorithm based on the suggestions of the Canadian Marbled Murrelet Recovery Team (Bertram and others, 2003; see table 37); likely habitat was selected as forest with stand age class 8+ (>140 years), tree height class 4+ (>27.5 m), and distance from the sea <30 km. This same algorithm also was used to estimate the area and distribution of suitable habitat across the murrelet’s range in British Columbia (see below and also section, “Population Status and Trends”).

By dividing radar counts by the estimated areas of habitat within the “catchment areas” into which murrelets counted with radar are flying, one can estimate murrelet densities (expressed as birds per hectare of suitable habitat). The two largest sources of error in making these density calculations arise from estimating the extent of the catchment area and in estimating the area of suitable habitat within this area. Errors in defining catchment areas are less when the murrelets are entering well-defined valleys bounded by high mountains (Burger, 2001). Many of the radar studies in British Columbia were made in such areas, but murrelets are known to cross high mountain ridges and some catchment areas were not bounded by high mountains. Murrelets may therefore continue flying beyond the estimated catchment area (leading to overestimates of density) or may enter the catchment areas undetected (leading to underestimates of density). Errors in estimating likely habitat within the catchment area depend on the accuracy of the GIS data used.

Densities derived from the radar counts can be used in two ways: to estimate the areas of suitable forest needed to support a given population of murrelets; or conversely to estimate the number of birds that a given area of habitat is likely to support. Here, I apply the second approach to make a crude estimation of the possible population likely to be supported by the habitat area in British Columbia predicted from a simple algorithm (CMMRT) applied to the province-wide forest cover and biogeographic data.

Burger and others (2004) showed that there was a consistent statistically significant difference between densities on the British Columbia mainland (0.045 ± 0.039 SD birds per ha; data from 62 watersheds in three separate studies) and the west coast of Vancouver Island (0.090 ± 0.060 SD birds per ha; 36 watersheds in two studies). The reasons for these differences are not known but might include more favorable foraging conditions or nesting habitat on western Vancouver Island. A third reason seems to be differences in topography: the mainland coast has many long fjords and inlets. Murrelets tend to forage at the seaward ends of these and densities are lower in apparently suitable habitat accessible from these fjords (distance to open sea was a significant covariate with murrelet densities in the British Columbia mainland but not on Vancouver Island; Burger and others, 2004). The habitat mapping study has not released regional totals for likely suitable habitat. I was therefore unable to apply the regional densities to regional habitat areas, but used the two different regional densities instead as indicators of high (Western Vancouver Island density) or low (British Columbia Mainland density) estimators. The mean density from both regions in British Columbia was 0.061 ± 0.052 SD birds per hectare (Burger and others, 2004).

Areas of likely suitable habitat in each of the six regions in British Columbia have been estimated by the British Columbia Ministry of Environment (M. Mather and T. Chatwin, unpub. data, 2006) using GIS and applying the simple algorithm given above (age >140 years; tree height >27.5 m). The mapping is being done for both 0–30 km and 0–50 km distances from the ocean. I considered habitat <30 km from the coast to be the most likely to be used; this also matches the limits set on catchment areas used to derive the densities (Burger and others, 2004). The final maps and estimates of habitat area from this study are not yet available, but preliminary estimates suggest that the habitat areas comparable with the radar density estimates total about 1.6 million ha in British Columbia.

Estimates using these density and habitat area measures indicate that the total British Columbia population is in the range of 72,000–175,000 birds, with the extremes in this range being due to the application of low (British Columbia Mainland) and high (western Vancouver Island) densities (table D5). Using the mean density for all 98 radar sites, the total population is estimated at 97,600 birds (95 percent confidence limits (CL): 81,000–114,000). These estimates capture some of the uncertainty in the radar density estimates, but because the habitat mapping study is not complete, I was not able to incorporate effects of variance in habitat estimates. These estimates of the total British Columbia population therefore remain crude and unreliable.

Table D5. Estimates of the population of Marbled Murrelets in British Columbia made by applying radar-derived densities to the estimated total area of likely suitable habitat within 30 kilometers of the coast.

[The 95-percent confidence limits (CL) were derived from the variance in the density.]

	Mean	Lower CL	Upper CL
A.—Murrelet density (birds/ha)[1]			
Density 1: British Columbia Mainland watersheds	0.045	0.035	0.055
Density 2: Western Vancouver Island watersheds	0.090	0.070	0.110
Density 3: Mean of both areas	0.061	0.051	0.071
B.—Population estimate based on estimate habitat (birds)			
Habitat area = 1,600,000 ha[2]			
Density 1	72,000	56,467	87,533
Density 2	144,000	112,640	175,360
Density 3	97,600	81,127	114,073

[1] Densities from radar studies summarized by Burger and others (2004).

[2] Based on recent updates of the habitat estimates given by Deschesne-Mansiere (British Columbia Forest Practices Board, unpub. data, 2004)

Total Population in British Columbia

The total British Columbia population of Marbled Murrelets based on the most recent information is estimated to be in the range of 54,300–92,600 birds (median 73,000 rounded to the nearest thousand; table D1). This is slightly higher than the previous estimate (55,000–78,000 birds; median 66,000 birds; table D1; Burger, 2002). It must be emphasized that both the current and the previous estimates are crude, based on extrapolations from rather sparse information in most regions and with large margins for error. It also must be emphasized that the slightly higher population estimate produced in 2006 does not indicate that the numbers of murrelets in British Columbia have risen since the last estimate or since the original estimate made by Rodway (1990; 45,000–50,000 breeding birds or approximately 53,000–59,000 birds; see Burger, 2002). Rather the higher numbers reflect somewhat improved data and greater geographical coverage of surveys. All available evidence points to declining populations in British Columbia (see appendix E).

Population estimates from the central and northern mainland and the Haida Gwaii (Queen Charlotte Islands) probably are the least reliable. In the two mainland regions, the populations were estimated from a single year of radar counts extrapolated using correlates with areas of apparently suitable habitat. Radar surveys are underway, which will improve our knowledge of these populations and their trends (D. Bertram, Canadian Wildlife Service). In all three of these regions, the numbers of murrelets per 1,000 ha of suitable habitat varied considerably among the sampled watersheds, and the interpretation of suitable habitat from the GIS data also has considerable scope for error. GIS mapping to improved the estimates of areas of suitable habitat across British Columbia is nearing completion (T. Chatwin and M. Mather, British Columbia Ministry of Environment), which will help improve population estimates based on the radar densities.

References Cited

Bertram, D.F., Burger, A.E., Chatwin, T.A., Chutter, M.J., Guy, S., Cooke, F., Lank, D.B., Deal, J.A., Hay, D.E., Jones, T.L., Lindsay, D.J., Manley, I.A., Reader, B., Steventon, J.D., Waterhouse, F.L., and Williams, E., 2003, Canadian Marbled Murrelet Recovery Team advisory document on conservation and management, *Part B in* Marbled Murrelet conservation assessment 2003: Delta, British Columbia, CWS, Working Document 1, 31 p.

Bigger, D., Peery, M.Z., Baldwin, J., Chinnici, S., and Courtney, S.P., 2006, Power to detect trends in Marbled Murrelet populations using audio-visual and radar surveys: Journal of Wildlife Management, v. 70, p. 493-504.

Burger, A.E., 1995, Marine distribution, abundance, and habitats of Marbled Murrelets in British Columbia, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 295-312.

Burger, A.E., 2001, Using radar to estimate populations and assess habitat associations of Marbled Murrelets: Journal of Wildlife Management, v. 65, no. 4, p. 696-715.

Burger, A.E., 2002, Conservation assessment of Marbled Murrelets in British Columbia. Part A: Review of the biology, populations, habitat associations, and conservation: Delta, British Columbia, CWS, Pacific and Yukon Region, Technical Report 387, 194 p.

Burger, A.E., Chatwin, T.A., Cullen, S.A., Holmes, N.P., Manley, I.A., Mather, M.H., Schroeder, B.K., Steventon, J.D., Duncan, J.E., Arcese, P., and Selak, E., 2004, Application of radar surveys in the management of nesting habitat of Marbled Murrelets *Brachyramphus marmoratus*: Marine Ornithology, v. 32, no. 1, p. 1-11.

Harfenist, A., and Cober, A., 2006, Baseline radar inventory of Marbled Murrelets on Haida Gwaii/Queen Charlotte Islands, 2004-2005: Queen Charlotte City, British Columbia, Ministry of Environment.

Holt, R.F., 2004, Environmental conditions report for the Haida Gwaii/Queen Charlotte Islands land use plan: Victoria, British Columbia, Ministry of Sustainable Resource Management.

Hull, C.L., Kaiser, G.W., Lougheed, C., Lougheed, L.W., Boyd, W.S., and Cooke, F., 2001, Intraspecific variation in commuting distance of Marbled Murrelets (*Brachyramphus marmoratus*): Ecological and energetic consequences of nesting further inland: Auk, v. 118, no. 4, p. 1036-1046.

Peery, M.Z., Beissinger, S.R., Newman, S.H., Becker, B.H., Burkett, E., and Williams, T.D., 2004, Individual and temporal variations in inland flight behavior of Marbled Murrelets: Implications for population monitoring: Condor, v. 106, p. 344-353.

Schroeder, B.K., Mather, M.H., and Chatwin, T.A., 1999, Reconnaissance inventory of Marbled Murrelets on the central coast of British Columbia 1998: Nanaimo, British Columbia, Ministry of Environment, Lands, and Parks, 108 p.

Raphael, M.G., Evans Mack, D., and Cooper, B.A., 2002, Landscape-scale relationships between abundance of Marbled Murrelets and distribution of nesting habitat: Condor, v. 104, no. 2, p. 331-342.

Steventon, J.D., and Holmes, N.L., 2002, Radar-based inventory of Marbled Murrelets (*Brachyramphus marmoratus*), northern mainland coast of British Columbia: Smithers, British Columbia, Ministry of Forests, Prince Rupert Forest Region.

Whitworth, D.L., Nelson, S.K., Newman, S.H., van Vliet, G.B., and Smith, W.P., 2000, Foraging distances of radio-marked Marbled Murrelets from inland areas in southeast Alaska: Condor, v. 102, no. 2, p. 452-456.

This page left intentionally blank.

Appendix E. Population Trends of the Marbled Murrelet Evident from At-Sea Surveys in British Columbia

By Alan E. Burger[1], Bob Hansen[2], E. Anne Stewart[3], Danielle Bellefleur[2], Danielle Edwards[2], Harry R. Carter[4], Shay Howlin[5], and Anthony J. Gaston[6]

Abstract

This appendix summarizes multi-year trends in counts of Marbled Murrelets made at sea in British Columbia during the breeding season (late April–mid-July). Data were available from six transect routes, which were repeatedly sampled (but not in every year) within the period 1979 to 2006, and two routes sampled in 1996–2000. Most of the data cover the years 1995–2006. Seven of the transects were off southwest Vancouver Island (Clayoquot Sound, Barkley Sound, and the West Coast Trail) and one was in Laskeek Bay off Haida Gwaii (Queen Charlotte Islands). Methods varied somewhat among the studies but generally murrelets were counted on both sides of a small vessel running at constant speed along a fixed route and densities were estimated either using an unlimited distance transect (giving densities as birds per kilometer) or within 300 meter-wide strip transects (giving densities as birds per square kilometer). All six data sets with more than 10 years of data show declines in densities of Marbled Murrelets and these trends were statistically significant at four sites. Annual rates of change ranged between -5.8 and -14.6 percent. The two surveys in Clayoquot Sound showed significant or near-significant rates of decline (-21.3 and -31.2 percent) in 1996–2000. Four of the data sets with adequate sampling from 1999 to 2006 showed no significant change in densities through these years, indicating that the major declines happened prior to 1999. Other published sources on murrelet numbers or relative activity in British Columbia also indicate declines over the past century and particularly in the past 20 years. The causes of population declines are not known but are likely to involve a combination of loss of nesting habitat due to logging and changes in ocean conditions affecting foraging at sea. Mortality from fisheries bycatch also might be a factor in some areas.

Introduction

Marbled Murrelets were listed as Threatened in Canada on the basis of perceived reductions of nesting habitat in British Columbia in the absence of data on population trends. Information on population trends is therefore needed in order to assess the species status within British Columbia (Bertram and others, 2003), but there are no data covering the entire British Columbia range with which to assess population changes. For much of the province, population estimates are sketchy, based on extrapolations from a few at-sea surveys or radar counts which do not provide a long time series (Burger, 2002). Indications of population trends are therefore possible only from a few long-term data sets involving at-sea counts in relatively small prescribed areas. In this appendix, we collate available data from these studies, analyse trends in the sampled populations, and review other evidence for population change in British Columbia.

On the basis of the power analysis by Arcese and others (2005), radar counts have been identified by the Canadian Marbled Murrelet Recovery Team (CMMRT) as the most reliable method for monitoring population trends in British Columbia (Bertram and others, 2003). Several studies show that repeated radar counts at fixed stations have high power to detect trends in Marbled Murrelet counts (Arcese and others, 2005; Bigger and others, 2006; Cooper and others, 2006). Bi-annually repeated radar surveys are now being undertaken in all six Marbled Murrelet conservation regions in British Columbia, but repeated counts have not been done for long enough to report on trends, and the results of surveys done in 2006 to repeat those done in the late 1990s in Clayoquot Sound, and parts of the British Columbia mainland are not yet available.

The few at-sea surveys that cover 10 or more years provide the most reliable insights into population trends. We recognize that the available data have severe limitations in their geographical scope (five of the sites are close together in Barkley Sound and adjacent West Coast Trail and the sixth is in Laskeek Bay off Haida Gwaii (Queen Charlotte Islands); fig. E1). We also include a re-analysis of previously published data from the Tofino and Flores transects done in Clayoquot Sound more than 4 years (Mason and others, 2002), which help to explain the long-term trends seen in that area (Kelson and others, 1995; Burger, 2002). Although there are gaps

---

[1] Department of Biology, University of Victoria, Victoria, British Columbia.

[2] Parks Canada, Pacific Rim National Park Reserve, Ucluelet, British Columbia, V0R 3A0, Canada.

[3] Bamfield Marine Sciences Centre, Bamfield, British Columbia, V0R 1B0, Canada.

[4] Carter Biological Consulting, Victoria, British Columbia, V8S 4S8, Canada.

[5] Western EcoSystems Technology, Inc., Cheyenne, Wyoming.

[6] Canadian Wildlife SPervice, National Wildlife Research Centre, Hull, Quebec, K1A 0H3, Canada.

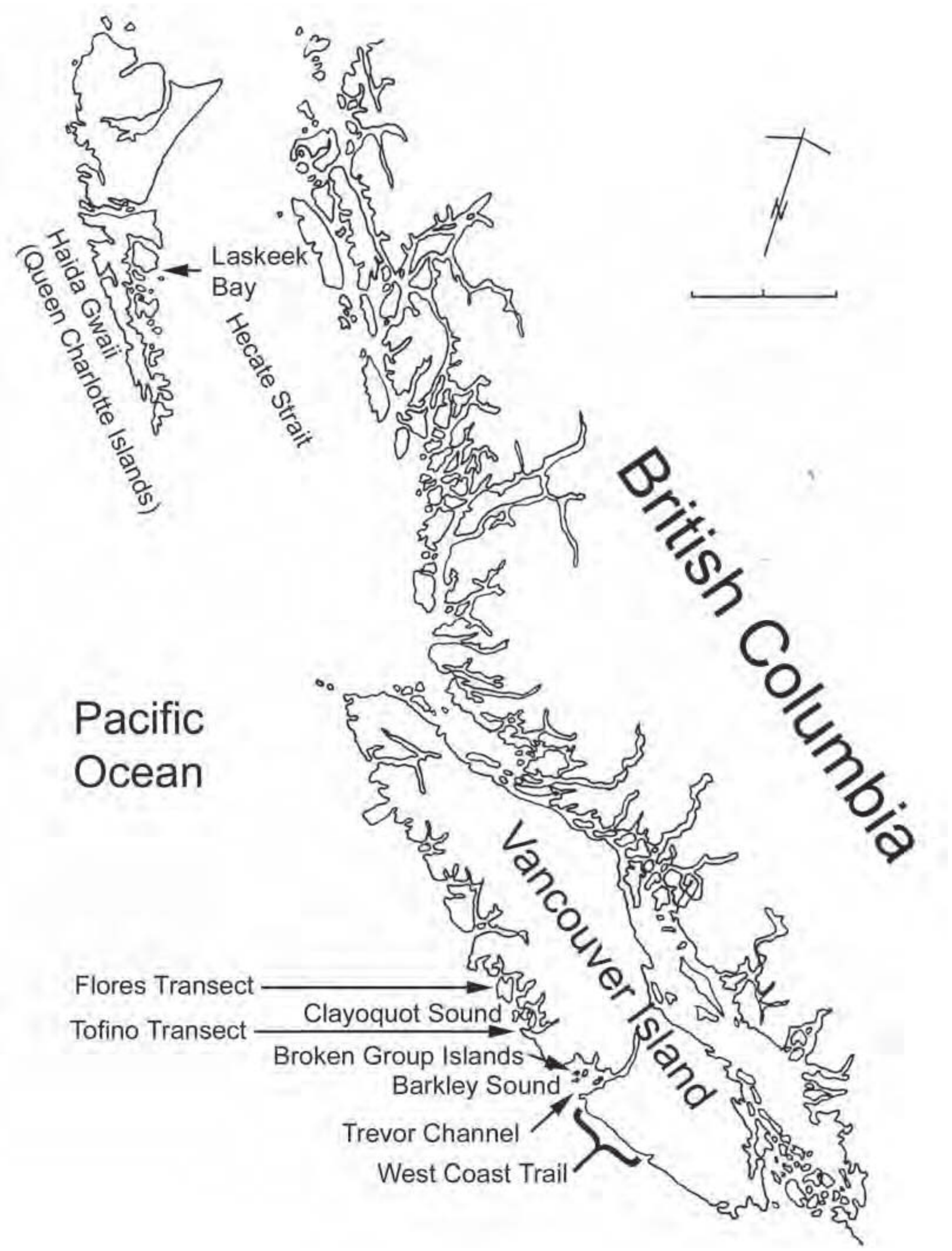


Figure E1. Location of sites where at-sea surveys were undertaken in British Columbia.

and inconsistent survey effort in all data sets, sampling effort was sufficient to reveal likely trends. Because all eight data sets were derived from fixed transect routes, spatial variation within study areas is not an issue when analysing long-term temporal variations in these data. Portions of these data sets have been used to summarize interannual variations in earlier reviews (Burger 1995, 2000, 2002; Bellefleur and others, 2005), but this appendix is the most complete analysis of these data.

In addition to analyzing the data from the at-sea transects, we also summarize other evidence for population trends in British Columbia, which has been previously published.

Methods

At-Sea Surveys.—The eight studies reviewed here were all established before provincial standards were in place for sampling Marbled Murrelets at sea. Nevertheless, all conform to these standards with minor deviations. Within each data set there were some inconsistencies in boat type, observer skills, sea and weather conditions, and other variables which confound boat surveys for seabirds, but we found no evidence that these variations were systematic and might have caused the trends which emerge from the data. We used data representative of the breeding season and all surveys fell within the period April 24–July 16, which covers the period that numbers of murrelets were highest and most consistent off Vancouver Island (Burger, 2000, 2001) and Haida Gwaii (Queen Charlotte Islands) (Harfenist and Cober, 2006). We examined each data set carefully to ensure that there was no bias caused by including or excluding data at either extreme in this seasonal range.

Laskeek Bay.—Laskeek Bay on the east side of Moresby Island in the Haida Gwaii (Queen Charlotte Islands) archipelago has been surveyed by boat annually by the Laskeek Bay Conservation Society since 1991 (2005 and 2006 data not yet available), using a protocol established by A.J. Gaston of the Canadian Wildlife Service (Gaston, 1996). The 53.8-km route covers both nearshore sheltered waters and open water between islands. All murrelets on the water on either side of the boat were reported and we therefore report densities as birds on the water per kilometer.

Trevor Channel.—In 1980, Carter (1984) undertook repeated surveys of murrelets within a 23.7-km^2 grid in lower Trevor Channel, Barkley Sound, which he had previously identified as an area with high densities of murrelets. Alan E. Burger and E. Anne Stewart censused murrelets in the same area between 1992 and 2000. Initially, they used the same grid pattern as Carter but in July 1994 switched to a looping 43-km long strip-transect route covering the same area in order to facilitate habitat analyses and hydroacoustic sampling of prey (see Carter, 1984: fig. 15 for the grid map and Burger, 2000 for the overlapping transect route). For this analysis, Carter (1984) provided the raw data for each survey, which were not available in his thesis. To accommodate the change in method, we analysed total counts of birds (in and out of transect strips) made in each survey and hence report numbers of murrelets seen on the water within the entire grid area.

Trevor-Beale-Seabird Rocks.—In 1979, Carter (1984) did repeated surveys along a 17.2-km L-shaped line transect running down the centre of Trevor Channel past Cape Beale, then turning to run parallel with the outer coast to Seabird Rocks (see Carter, 1984: fig. 6, sectors 1–4 for the route map). Part of this transect crosses the area sampled in the Trevor Channel grid area. Alan E. Burger and E. Anne Stewart sampled a 19.5-km route (slightly different start and turning points to Carter) sporadically between 1987 and 2006. Both survey teams recorded birds ahead and to both sides of the vessel, but Carter (1984) recorded all birds to 750 m while Alan E. Burger and E. Anne Stewart recorded murrelets within and beyond a 300-m strip (150 m on either side of the vessel). To accommodate these different methods, we analyzed all birds reported inside or outside the transect strips and hence report densities as birds on the water per kilometer.

Broken Group Islands Inner and Outer (BGI Inner and BGI Outer).—These data sets come from two non-overlapping routes within Barkley Sound (see Bellefleur and others, 2005, for maps), which were sampled by trained Parks Canada staff, under the supervision of Bob Hansen. Broken Group Islands (BGI) Inner (9.2 km) runs through the center of the BGI and BGI Outer (14.6 km) runs from the mouth of Ucluelet Harbour across Loudon Channel to end at Turtle Island in the Broken Group. Both routes were sampled using a 300-m wide strip transect (150 m on either side of the boat) from 1995 to 2006, but murrelets outside the transect also were recorded. The BGI Inner route was previously sampled as an unlimited distance line transect in 1991–93. To cover the longest time period, we therefore considered all birds seen on the water (in or out of the transect strip) in the BGI Inner data set and hence report density as birds on the water per kilometer. For BGI Outer, we used birds on the water within the transect and report densities as birds per square kilometer.

West Coast Trail.—This transect runs parallel to the coastline for 64.6 km (vessel approximatley 200 m offshore) between Seabird Rocks and Owen Point (map in Burger, 2000), covering the nearshore area with the highest known density of Marbled Murrelets in British Columbia (Burger 1995, 2002). Surveys were initially done by Alan E. Burger working with Parks Canada staff (1994–96) and subsequently by the park staff. Birds were counted in a 300-m-wide strip (150 m on either side of the vessel) and we report densities as birds per square kilometer.

Tofino and Flores transects. —We re-analyzed the data from these two transect routes in Clayoquot Sound recorded in 1996–2000 and previously published by Mason and others (2002; see this reference for maps and details). Both transects covered large areas of exposed inshore waters and sheltered channel waters in areas of high murrelet densities previously identified from grid surveys (Sealy and Carter, 1984; Kelson and others, 1995). The Tofino transect (49.8 km), sampled annually in 1996–2000, covered exposed waters off the Tofino peninsula and both exposed and sheltered waters around Vargas Island. The Flores transect (82.1 km), sampled annually in 1997–2000, covered exposed and sheltered waters around Flores Island and off the Catface Peninsula.

Statistical Analysis.—To analyze trends across years, we first calculated the annual mean murrelet response (density or count) across the replicate surveys for each transect. In order to apply linear regression, we log transformed the mean value, and because there were no zero values, we did a simple transformation using the natural logarithm, i.e. ln (mean) (Zar, 1996, p. 279). area. We plotted graphs showing the log transformed data on the *y*-axis, but to make the scale more readily understandable, we show the actual densities or numbers of birds and not the log values on these axes. The variance of the log-transformed annual means was calculated using a first order Taylor Series expansion (Seber, 1982). This approximation equates to the variance of the annual mean divided by the product of the sample size and the square of the annual mean. Linear regression of the logged mean response was conducted with year as the independent variable and the inverse of the variance as the weight. From the regression, we derived the slope of the trend in the log-transformed data and the amount of variance explained by the regression line (*R*-squared value). The annual rate of change (percent change) was then calculated from the slope using the formula: $1\text{-}e^{slope}$, where *e* is the base of natural logarithms (2.71828). Moran's I was calculated to estimate the autocorrelation of the model residuals (Moran, 1948). The model for Trevor Channel included an indicator variable for survey method, given as 0 for grid surveys (during and before 1994) and 1 for looped transect surveys (during and after 1995).

Because there was evidence of changing trends before and after 1999 (see section, "Results"), we also calculated linear regressions of the log-transformed mean responses for four survey areas using data after and including 1999. Again, year was the independent variable and the inverse of the variance was the weight in the model.

Results

Trends in At-Sea Densities—All survey areas had negative trends in murrelet counts or densities across years; six areas had significant negative trends (table E1). The parameter estimate on survey method for the Trevor Channel model was not significantly different from zero ($P = 0.507$). The estimate for the indicator variable was 0.235, which represents the difference in the predicted means for the looped transect surveys, where the grid surveys are the reference level.

Moran's I indicated negative serial autocorrelation for the West Coast Trail area model. The error estimate for this model may be underestimated resulting in decreased confidence in the significance of the trend estimate. There was no serial autocorrelation indicated in the residuals of the remaining models.

The Laskeek Bay data show a decline in annual mean density over the 14-year period 1991–2004 (fig. E2). This trend was statistically significant and indicated an annual rate of decline of -14.6 percent (table E1).

Off southwest Vancouver Island, both the Trevor Channel and the Trevor-Beale-Seabird Rocks data show declining trends in the period 1979–2006 (fig. E3) but sampling over the years was inconsistent and only the Trevor Channel survey was statistically significant (table E1). Similarly the three survey routes covered by Parks Canada (Broken Group Inner and Outer within Barkley Sound and the West Coast Trail on the outer coast) showed declines in 1990–2006 (fig. E4) and these trends were significant for the BGI Inner (annual decline of -8.3 percent) and West Coast Trail (annual decline -6.1 percent; table E1).

At-sea surveys using a grid pattern covering most of Clayoquot Sound, west Vancouver Island (fig. E1) were done in 1982 (Sealy and Carter, 1984) and repeated using the same method in 1992, 1993, and 1996 (Kelson and others, 1995; Kelson and Mather, 1999). This area supports one of the highest concentrations of murrelets in British Columbia (Burger, 1995, 2002). The grid survey data show declines in populations of between 22 and 40 percent since 1982 (fig. E5), attributed to the effects of logging (Kelson and others, 1995). Closer examination of these data, however, revealed that the only significant change occurred in the exposed inshore zone, and there was no evidence of change in the protected channels (fig. E5; Burger, 2000). Burger (2000) also suggested that the changes in the exposed inshore zone might have been linked with exceptionally warm ocean conditions in the 1990s, but there are insufficient data to statistically separate the effects of temperature and years.

The Flores and Tofino transects in Clayoquot Sound offer a much shorter time span to measure trends (4 and 3 years, respectively in 1996–2000), but both transects sampled both exposed inshore waters and sheltered channel waters. A significant decline was evident in the Flores data and the Tofino trend was close to significant (fig. E6; table E1). The annual rates of decline in these years were -21.3 and –31.2 percent in the Flores and Tofino transects, respectively (table E1).

Trends Since 1999 – There are indications that the long-term Pacific Decadal Oscillation (PDO) shifted from a warm to a more mixed phase in 1999, and large-scale logging practices affecting murrelets changed in the mid-1990s. We therefore tested for trends in the data for 1999–2006 in the four data sets that adequately covered this period (figs. E2 and E4). There were no significant trends in any of the data sets (table E2) and none of these data sets showed evidence of autocorrelation. Most of the changes in densities in these areas therefore occurred prior to 1999.

Table E1. Summary of trends of Marbled Murrelet counts and densities at eight marine transect routes in British Columbia.

[Linear regressions were derived from log transformed annual means using annual variance as the regression weighting. Statistically significant trends (*P*<0.05) are shown in **bold**. Sites are listed from north to south]

Site or transect route	Region	Range of years	Number of years sampled	Number of surveys	Regression of log transformed data					
					Slope	Rate of change percent per year	*R*-squared	*F*	df	*P*
Laskeek Bay	Haida Gwaii (Queen Charlotte Islands)	1992–2004	14	56	**-0.158**	**-14.6**	**0.394**	**7.790**	**1,12**	**0.016**
Flores transect	West Vancouver Island	1997–2000	4	15	**-0.240**	**-21.3**	**0.977**	**86.030**	**1,2**	**0.011**
Tofino transect	West Vancouver Island	1996–2000	4	19	-0.375	-31.2	0.892	16.580	1,2	0.055
BGI Inner	West Vancouver Island	1991–2006	14	65	**-0.087**	**-8.3**	**0.720**	**30.850**	**1,12**	**0.000**
BGI Outer	West Vancouver Island	1995–2006	10	41	-0.062	-6.0	0.173	1.670	1,8	0.232
Trevor Channel	West Vancouver Island	1980–2000	10	61	**-0.060**	**-5.8**	**0.585**	**4.930**	**1,7**	**0.046**
Trevor/Beale/SBR	West Vancouver Island	1979–2005	6	20	-0.097	-9.3	0.482	3.720	1,4	0.126
West Coast Trail	West Vancouver Island	1994–2006	10	32	**-0.063**	**-6.1**	**0.530**	**9.020**	**1,8**	**0.017**

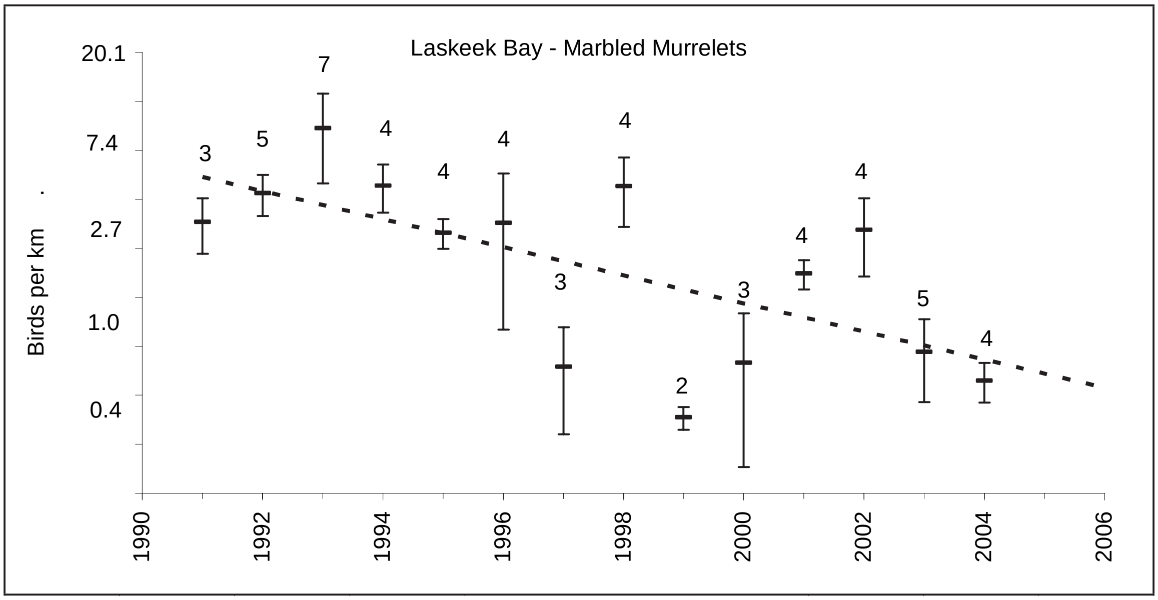


Figure E2. Mean plus or minus SE linear densities (birds per kilometer of transect) of Marbled Murrelets along a 54-km boat transect in Laskeek Bay, Haida Gwaii (Queen Charlotte Islands). (Data from Laskeek Bay Conservation Society). Note that the y-axis has a logarithmic scale but the labels are actual densities and not the log values. Sample size (number of days surveyed) is shown for each year.

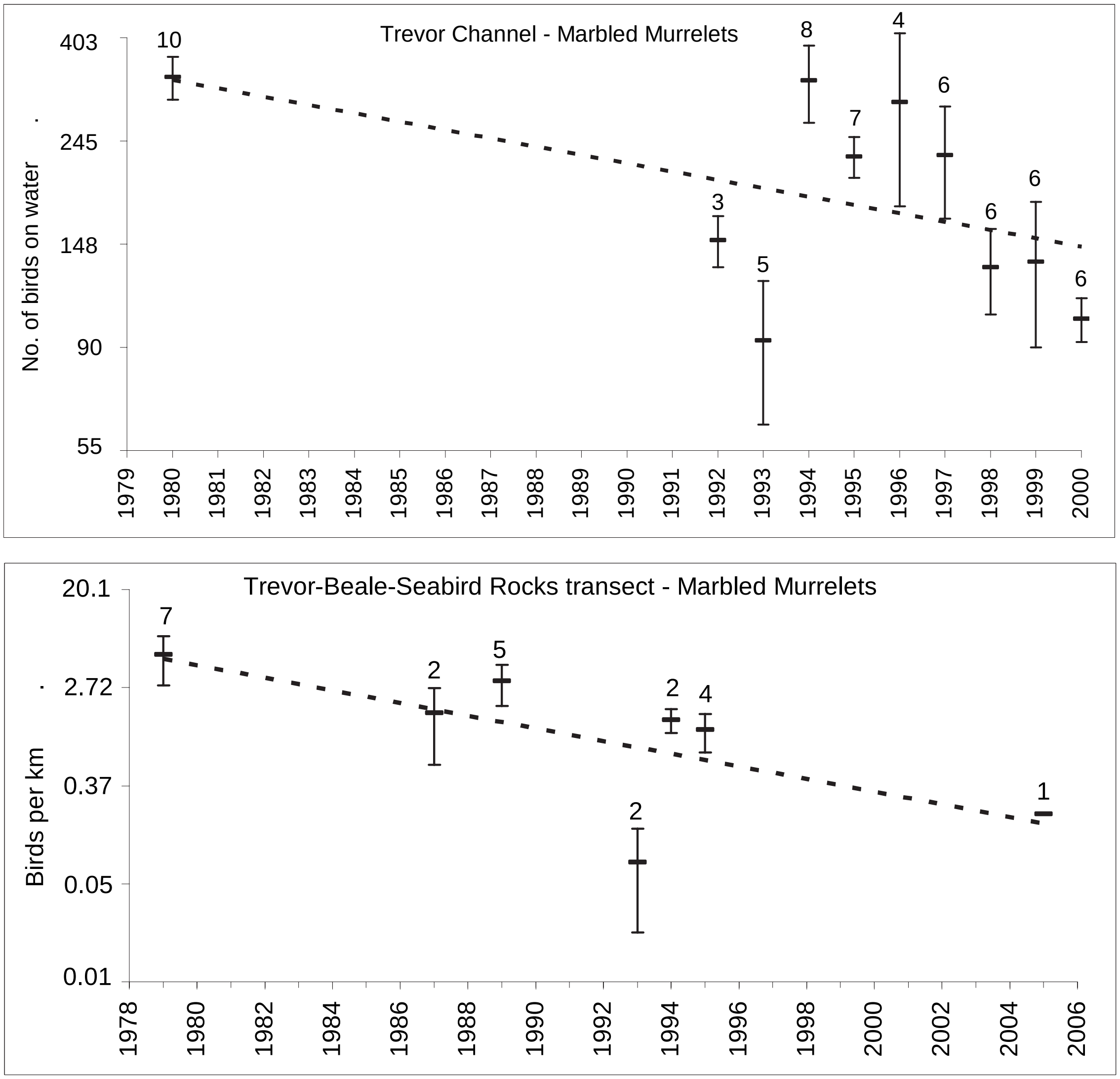


Figure E3. Mean (plus or minus SE) counts of Marbled Murrelets made in two overlapping census routes (Trevor Channel, upper graph; Trevor Channel-Cape Beale-Seabird Rocks, lower graph) in Barkley Sound, southwest Vancouver Island, between late April and mid-July. (Updated from Burger, 2000, 2002; Burger and Stewart, University of Victoria, unpub. data). Note that the *y*-axes have logarithmic scales but the labels are actual densities and not the log values. The sample size (number of days surveyed) is shown for each year.

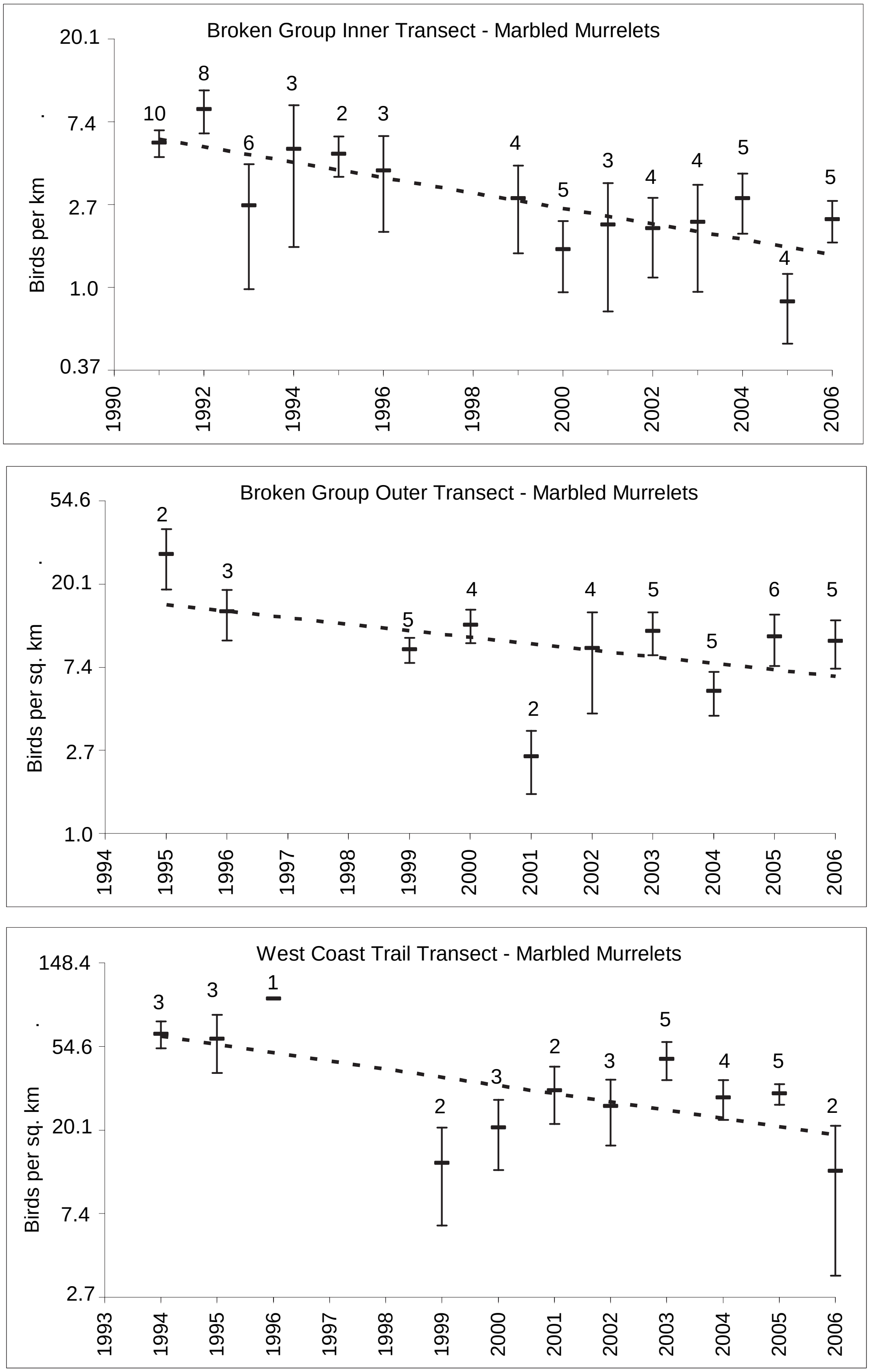


Figure E4. Trends in densities of Marbled Murrelets in three transects surveyed by Parks Canada in Barkley Sound (Broken Group Islands Inner, Broken Group Islands Outer) and the West Coast Trail. Annual means (plus or minus SE) shown for counts made between April 24 and July 16. Linear density (birds per kilometer) is used for the Broken Group Islands Inner transect to cover a wider range of years. The *y*-axes have log scales but labels are actual densities and not log values. Sample size (*n* days surveyed) is shown for each year.

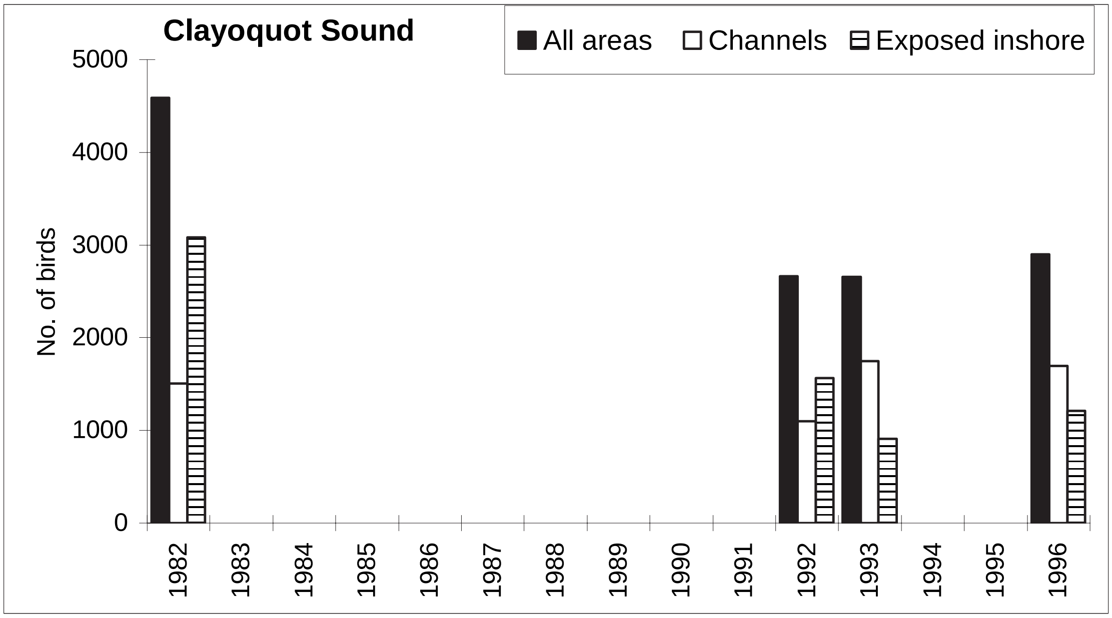


Figure E5. Counts of Marbled Murrelets in a grid-survey census in Clayoquot Sound, broken down by habitat type. (Data from Sealy and Carter, 1984; Kelson and others, 1995; Kelson and Mather, 1999). See Burger (2002) for further details.

Table E2. Summary of regressions testing for trends in counts of Marbled Murrelets in the years 1999-2006.

[Linear regressions were applied to log transformed annual means. None of the tests was significant]

Site or transect route	Regression of log transformed data				
	Slope	**R-squared**	***F***	**df**	***P***
Laskeek Bay	0.156	0.175	0.85	1,4	0.409
BGI Inner	-0.014	0.008	0.05	1,6	0.833
BGI Outer	-0.010	0.004	0.03	1,6	0.879
West Coast Trail	0.037	0.060	0.38	1,6	0.559

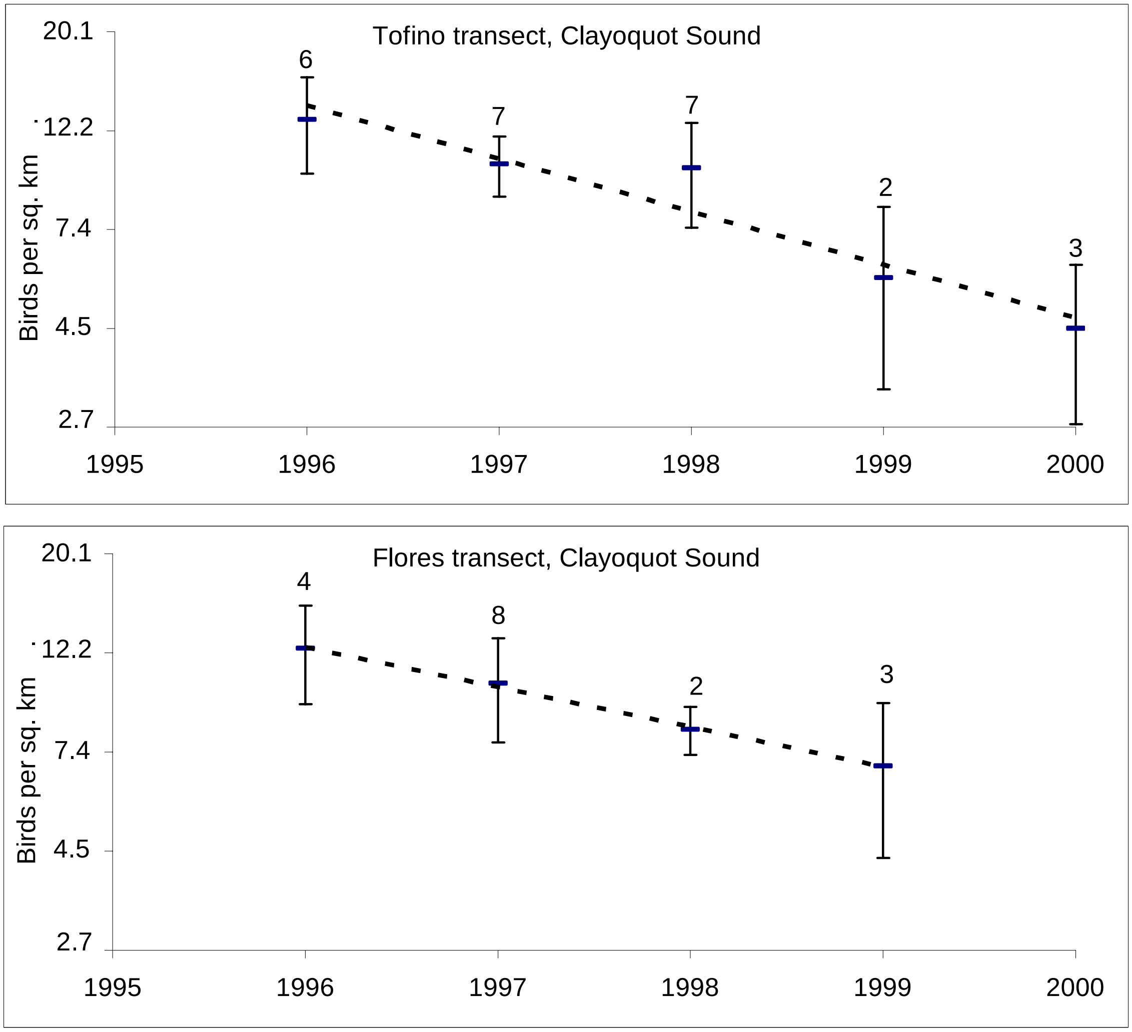


Figure E6. Mean (plus or minus SE) counts of Marbled Murrelets made in two census routes (Tofino, upper graph; Flores, lower graph) in Clayoquot Sound, southwest Vancouver Island, between May 14 and July 13. (Updated from Mason and others, 2002). Note that the *y*-axis has a logarithmic scale but the labels are actual densities and not the log values. The sample size (number of days surveyed) is shown for each year.

Discussion

Trends within the transect data.—Overall, we found declines in densities or counts of Marbled Murrelets in all six data sets covering 1979–2006, and the two data sets covering much shorter periods 1996–2000. Despite considerable within- and among-year variations in densities, these trends were statistically significant in five data sets (table E1). Statistically significant trends emerged from the three data sets with the most consistent sampling (Laskeek Bay, BGI Inner, and West Coast Trail) and we feel the lack of significant trends in three data sets might be due to insufficient sample sizes needed to overcome the natural variation in these at-sea data. The annual rates of decline in these data covering more than 10 years ranged from -5.8 to -14.6 percent (6.1–14.6 percent in the statistically significant data sets; table E1), and was much higher in the Flores and Tofino transects covering 1996–2000 (table E1). These estimated rates of decline are not precise and the addition of another year or two of data would undoubtedly change the calculated rate. Nevertheless, these are high rates of decline for any population and indicate a potentially serious problem for the populations that they represent. In the four data sets with adequate sampling in recent years, we found no significant trends in densities since 1999 suggesting that the major changes occurred prior to this year.

Although some of the survey sites (Trevor Channel, Trevor-Beale-Seabird Rocks) were chosen as study areas because of high densities of murrelets (Carter, 1984), there is no evidence that selection of sites with initial high densities produced a biased measure of trend. The high densities in the Trevor Channel area were well known to local residents for many years prior to Carter’s (1984) study and Harry R. Carter’s unpublished data shows consistent high densities in both 1979 and 1980. Most of the other transects were long enough that they encompassed a wide range of habitats and murrelet densities (see Gaston, 1996; Mason and others, 2002; Bellefleur and others, 2005), reducing the likelihood that high counts in early years were spatial anomalies. Furthermore, the large spatial coverage of seven transect routes on the west coast of Vancouver Island, all of which show declines, reduces the likelihood that the trends observed were due to local movements. We cannot, however, rule out larger-scale emigration to other parts of the murrelet’s range.

Other evidence of change in British Columbia.—Burger (2002) reviewed evidence for population trends of murrelets in British Columbia and the main points are briefly summarized here. Rodway and others (1992) found no clear trends in Christmas Bird Count data from 1957 through 1988. This analysis has not been expanded to include more recent data, because few count areas overlap with significant wintering populations in British Columbia and Christmas Bird Count data seem to be poor indicators of widespread population trends in this species (Piatt, 1998; Hayward and Iverson, 1998).

There is anecdotal evidence that populations of Marbled Murrelets in the Strait of Georgia declined significantly in the early 1900s. Brooks (1926) commented on the scarcity of Marbled Murrelets along the east coast of Vancouver Island in 1925–26 compared with numbers observed in 1920 and earlier. Pearse (1946) reported a decline in numbers around Comox between 1917 and 1944, concomitant with the loss of large tracts of the surrounding coniferous forests. In more recent times, counts of birds along a 6 km stretch of shoreline at Boundary Bay, south of Vancouver, between November and August showed a decline from an average of 66 Marbled Murrelets in 1980–81 to 2 in 1994–95 and no birds in 1996 and 1997 (Cooke, 1999). Murrelets appear to have disappeared from Burrard Inlet near Vancouver since 1990 (G. Kaiser quoted by Hull, 1999).

Burger (2002) analyzed data from audio-visual surveys made from 1991 through 1999 at 11 stations within the forest nesting habitat in the Carmanah and Walbran watersheds adjacent to the West Coast Trail on southwest Vancouver Island. A sub-set of the audio-visual detections which indicate site occupancy provided indirect measures of relative murrelet abundance. Mean frequencies of occupied detections showed a significant negative correlation with sea temperature (Burger ,2000), but Burger’s (2002) analysis, using analysis of covariance (ANCOVA) with sea temperature as a covariant, showed a significant negative trend over the 9 years (fig. E7; adjusted $r^2 = 0.347$, $P<0.001$). Since 1990, there has been no logging in the Carmanah valley, but parts of upper Carmanah were logged in the late 1980s and logging continued in the upper Walbran close to the observation stations.

Radar counts made during the breeding season at the mouth of the Bedwell-Ursus watershed in Clayoquot Sound showed a significant decline in 1995–98, which corresponded to declines in annual mean detections in audio-visual surveys made in same drainage (Burger, 2000). This could not be attributed to logging because there had not been any logging in that drainage for 40 years. There was a weak non-significant negative correlation with local sea temperatures in both the radar and audio-visual detections (Burger, 2000).

Overall, these published data and reviews show a consistent pattern of decline in numbers of Marbled Murrelets wherever there are reasonable data to test trends in British Columbia.

Causes of change.—There are no obvious explanations for the declining trends seen in the at-sea surveys made in two widely separate regions in British Columbia, and in the other data reviewed here. The two most likely causes are the impacts of logging causing reductions in nesting habitat and unfavorable conditions in the ocean foraging environment. It is most probable that both factors contribute to the declines.

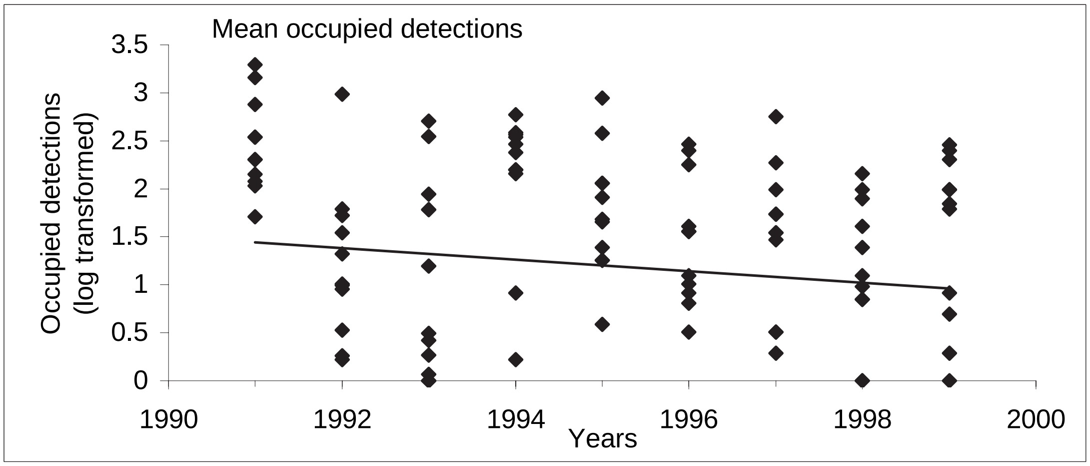


Figure E7. Trends in occupied detections of Marbled Murrelets in Carmanah-Walbran. Each point represents the mean frequency of occupied detections from three or more surveys at each station per year. The trend line was determined from ANCOVA analysis, with local sea temperatures as a covariate (see Burger, 2002).

There have been significant reductions in areas of nesting habitat for Marbled Murrelets in many areas of their British Columbia range and in particular on Vancouver Island and Haida Gwaii (Queen Charlotte Islands) (details given elsewhere in this review). Given that there is a strong relationship between area of habitat and numbers of murrelets entering watersheds (Burger, 2001; Burger and others, 2004), loss of habitat is expected to result in population reductions, although these might be delayed by many years in these long-lived birds. Reduction in nesting habitat prior to 2000 was estimated to be 46 percent in the Alberni Forest District, adjacent to the Barkley Sound and West Coast Trail at-sea surveys and the Clayoquot Sound grid surveys (Burger, 2002, using data from Demarchi and Button, 2001a, 2001b) and 42 percent in Haida Gwaii (Queen Charlotte Islands), adjacent to the Laskeek Bay survey area (Holt, 2004). Logging was particularly intense in the 1970s through to the mid-1990s in both of these regions, but was reduced as the new provincial Forest Practices Code came into effect in the late 1990s and large tracts of suitable habitat were protected (Gwaii Haanas National Park Reserve on Haida Gwaii (Queen Charlotte Islands); Carmanah-Walbran Park and large parks adjacent to Clayoquot Sound on southwestern Vancouver Island). It is possible that the trends seen in the six data sets, i.e., declines overall but with less change after 1999, could be explained by loss of nesting habitat, which was more intense prior to the mid-1990s than afterwards.

Changes in ocean conditions affecting murrelets are another possible explanation. Many seabirds in the Pacific Northwest respond to changes associated with varying sea temperatures, either generated by periodic El Niño (ENSO) events (Hodder and Greybill, 1985; Wilson, 1991; Ainley and Boekelheide, 1990), or longer-term PDO cycles (Piatt and Anderson, 1996; Anderson and Piatt, 1999). Generally warm ocean conditions reflect reduced upwelling in nearshore waters resulting in reduced productivity. Other alcids are known to be negatively impacted by warm ocean conditions in British Columbia (Bertram and others, 2000, 2001; Gjerdrum and others, 2003).

Impacts of such ocean and climatic changes are poorly known for Marbled Murrelets and it is uncertain whether warm ocean conditions have negative, neutral or positive effects. In central California, Peery and others (2004) reported fewer murrelets flying inland to breeding sites in warm years, which was linked with improved adult survival in those years (Peery and others, 2006). Burger (2000) reported weak negative effects of the warm 1992–93 El Niño events in British Columbia, inconsistent correlations between sea temperatures and annual averages of at-sea, audio-visual and radar counts, but some indications that warm sea temperatures had negative effects on these measures.

Bellefleur and others (2005) compared the densities of murrelets within the BGI Inner, BGI Outer, and West Coast Trail transects with mean sea surface temperatures recorded in spring at Amphitrite Point in Barkley Sound. They found no significant correlations in the BGI Outer and West Coast Trail data. There was a weak but significant interaction in the BGI Inner data, primarily due to high counts in the El Nino year of 2002, but when possible effects of sea temperature were statistically controlled, the significant long-term decline remained significant (details in Bellefleur and others 2005). Note that the temperature effect here was the opposite of what is expected with seabirds: numbers were higher in BGI Inner some warm years. The prolonged warm conditions in 1993, however, coincided with exceedingly low densities in Barkley Sound (see figs. E3 and E4; also Burger, 2000). Conversely, the densities at Laskeek Bay were the highest recorded in 1993. Clearly there is no simple relationship between murrelet densities and local sea temperatures, and ocean conditions directly associated with sea temperatures do not explain the long-term trends in these data. Cooper and others (2006) examined the effects of oceanic and climatic factors on radar counts of murrelets on the Olympic Peninsula, Washington in 1996–2004. They found no significant effects of sea surface temperature, Northern Oscillation Index (a measure of upwelling strength) or the 1998 El Niño, and suggested that oceanic effects off northern Washington might have less severe impacts on murrelets and other seabirds than in the upwelling systems off California.

In 1999, there was evidence of a weak regime shift in the broad-scale ocean conditions in the eastern North Pacific associated with the PDO (Bond and others, 2003; Curchitser and others, 2005). Off British Columbia, ocean temperatures tended to be cooler than in the previous 1977–99 period (Department of Fisheries and Oceans: satellite and lighthouse temperature data at http://www-sci.pac.dfo-mpo.gc.ca/osap/data/default_e.htm) and breeding success improved for some seabirds (Gjerdrum and others, 2004). This large-scale shift coincided with the change in density trends reported in four of our murrelet data sets, which showed no significant declines in 1999–2006 (table E2). Interestingly, this was seen in data from both southwestern Vancouver Island and Laskeek Bay even though these fall into different oceanic zones. Southwest Vancouver Island is within the Coastal Upwelling Domain influenced by the California Current and wind-driven summer upwelling, whereas Laskeek Bay is in the Transition Zone separating the upwelling domain from the Coastal Downwelling Domain of Southeast Alaska (Ware and McFarlane, 1989). There are hints therefore that the large scale changes in ocean conditions experienced across the eastern North Pacific might be influencing Marbled Murrelets in British Columbia, although we are a long way from understanding and explaining these possible links.

Marbled Murrelets are known to be killed as bycatch in gillnet and sports fishing (Carter and Kuletz 1995). Carter and Sealy (1984) reported significant mortality caused by gillnet fishing in Barkley Sound in the 1980s, but this fishery has been greatly curtailed since then (Smith and Morgan 2005). In the 1980s and early 1990s, the Barkley Sound salmon gillnet fishery had an active fleet of 300 to 400 vessels, each fishing 2-3 days per week, and 24 hours a day between late June and early August (when murrelet numbers were highest in Barkley Sound). This effort decreased greatly after the mid-1990s, with a reduction in the number of vessels, daylight fishing only and single-day openings in July and August. Sports fishing has, however, greatly increased in the Barkley Sound and West Coast Trail waters and small boats are known to disrupt feeding of Marbled Murrelets there (Hentze 2006, Bellefleur and others in prep.). Murrelets might therefore still be negatively impacted by human fishing activities in these waters but in a different manner. Gillnet fishing has not been identified as a problem for Marbled Murrelets off Haida Gwaii (Queen Charlotte Islands) (Smith and Morgan, 2005), although gillnetting and collisions with fishing vessels were known to impact Ancient Murrelets Synthliboramphus antiquus in these waters in the 1950s–1970s (Bertram, 1995; Vermeer and Sealy, 1984).

We cannot rule out a role of fisheries bycatch in the declining trends of Marbled Murrelets some areas of British Columbia given the paucity of data available, but the available evidence suggests that these impacts could not explain the consistent declining trends seen in many areas of British Columbia. A new study is underway to elucidate possible impacts of fisheries on this species (D. Bertram and K. Charleton, Canadian Wildlife Service).

Conclusions

It is striking that nearly all of the quantitative or anecdotal evidence for population trend of Marbled Murrelets in British Columbia consistently indicates a decline. The multi-year series of data that we analysed from six transect sources in two widely separated regions show quite startling rates of declines, which were statistically significant in those data sets with the largest and most consistent sampling. We are frustrated in trying to interpret and explain these trends by the paucity of comparable data from other regions in British Columbia and the lack of information of factors that affect the distribution and densities of murrelets at sea. Nevertheless we believe that our data and the other evidence that we reviewed are symptoms of widespread and biologically significant adverse conditions experienced by murrelets in this province. Loss of nesting habitat caused by logging and unfavorable foraging conditions in the ocean remain the two most likely explanations for the changes. It is heartening to note that there is evidence that declines seem to have leveled off since 1999, but until we understand the underlying causes of population changes in this species there is no room for complacency.

Acknowledgments

We thank the many volunteers, students at Bamfield Marine Sciences Centre and University of Victoria, and staff of Parks Canada, Laskeek Bay Conservation Society, Canadian Wildlife Service who contributed hundreds of hours in collecting these data. At-sea surveys were funded by Parks Canada, Canadian Wildlife Service, Laskeek Bay Conservation Society, and grants to AEB from NSERC Canada, the Nestucca Trust Fund, British Columbia Forest Science Program, and Endangered Species Recovery Fund (World Wildlife Fund Canada and CWS).

References Cited

Ainley, D.G., and Boekelheide, R.J., 1990, Seabirds of the Farallon Islands: Ecology, dynamics, and structure of an upwelling-system community: California, Stanford University Press.

Arcese, P., Bertram, B., Burger, A.E., Cullen, S.A., Deal, J.A., Gibbs, J., Fall, A., Harfenist, A., Harper, W.L., Jones, G., Lank, D.B., Lindsay, D.J., Manley, I.A., Selak, E., Runyan, S., Schroeder, B.K., Staudhamer, C., Steventon, J.D., and Sutherland, G.D., 2005, Monitoring designs to detect population declines and identify their causes in the Marbled Murrelet: Vancouver, University of British Columbia, Centre for Applied Conservation Research, Report to Ministry of Water, Land, and Air Protection.

Bertram, D.F., Jones, I.L., Cooch, E.C., Knechtel, H.A., and Cooke, F., 2000, Survival rates of Cassin's and Rhinoceros auklets at Triangle Island, British Columbia: Condor, v. 102, p. 155-162.

Bertram, D.F., Mackas, D.L., and McKinnell, S.M., 2001, Seasonal cycle revisited: Interannual variation and ecosystem consequences: Progress in Oceanography, v. 49, p. 283-307.

Bellefleur, D., Edwards, D., Hansen, B., and Burger, A.E., 2005, Marine distribution and abundance of Marbled Murrelets in Pacific Rim National Park Reserve of Canada, 1995-2004: Ucluelet, British Columbia, Parks Canada, Pacific Rim National Park Reserve.

Bertram, D.F., Burger, A.E., Chatwin, T.A., Chutter, M.J., Guy, S., Cooke, F., Lank, D.B., Deal, J.A., Hay, D.E., Jones, T.L., Lindsay, D.J., Manley, I.A., Reader, B., Steventon, J.D., Waterhouse, F.L., and Williams, E., 2003, Canadian Marbled Murrelet Recovery Team advisory document on conservation and management, *Part B in* Marbled Murrelet conservation assessment 2003: Delta, British Columbia, CWS, Working Document 1, 31 p.

Bigger, D., Peery, M.Z., Baldwin, J., Chinnici, S., and Courtney, S.P., 2006, Power to detect trends in Marbled Murrelet populations using audio-visual and radar surveys: Journal of Wildlife Management, v. 70, p. 493-504.

Brooks, A., 1926, Scarcity of the Marbled Murrelet: Murrelet, v. 7, p. 39.

Burger, A.E., 1995, Marine distribution, abundance, and habitats of Marbled Murrelets in British Columbia, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 295-312.

Burger, A.E., 2000, Bird in hot water: Responses by Marbled Murrelets to variable ocean temperatures off southwestern Vancouver Island, *in* Darling, L.M., ed., Biology and Management of Species and Habitats at Risk Conference, Kamloops, British Columbia, 1999, v. 2, p. 723-732.

Burger, A.E., 2001, Using radar to estimate populations and assess habitat associations of Marbled Murrelets: Journal of Wildlife Management, v. 65, no. 4, p. 696-715.

Burger, A.E., 2002, Conservation assessment of Marbled Murrelets in British Columbia. Part A: Review of the biology, populations, habitat associations, and conservation: Delta, British Columbia, CWS, Pacific and Yukon Region, Technical Report 387, 194 p.

Carter, H.R., 1984, At-sea biology of the Marbled Murrelet (*Brachyramphus marmoratus*) in Barkley Sound, British Columbia, Thesis: Winnipeg, University of Manitoba.

Cooke, F., 1999, Population studies of Marbled Murrelets (*Brachyramphus marmoratus*) in British Columbia, *in* Nettleship, A.W., and Diamond, D.N., eds., Biology and conservation of forest birds [Proceedings], Fredericton, New Brunswick, 1999, Special Publication 1, p. 43-51.

Cooper, B.A., Raphael, M.G., and Peery, M.Z., 2006, Trends in radar-based counts of Marbled Murrelets on the Olympic Peninsula, Washington, 1996-2004: Condor, v. 108, p. 936-947.

Gaston, A.J., 1996, Seabird distributions in Laskeek Bay, *in* Gaston, A.J., ed., Laskeek Bay Conservation Society: Queen Charlotte City, British Columbia, Annual Scientific Report, 1995, p. 2-28.

Kelson, J.D., Manley, I.A., and Carter, H.R., 1995, Decline of the Marbled Murrelet in Clayoquot Sound, British Columbia: 1982-1993: Northwestern Naturalist, v. 76, no. 1, p. 90-98.

Harfenist, A., and Cober, A., 2006, Baseline radar inventory of Marbled Murrelets on Haida Gwaii/Queen Charlotte Islands, 2004-2005: Queen Charlotte City, British Columbia, Ministry of Environment.

Mason, A., Burger, A.E., and Hansen, B., 2002, At-sea surveys of Marbled Murrelets in Clayoquot Sound, 1996-2000, *in* Burger, A.E. and Chatwin, T.A., eds., Multi-scale studies of populations, distribution and habitat associations of Marbled Murrelets in Clayoquot Sound, British Columbia: Victoria, British Columbia, Ministry of Water, Land and Air Protection, p. 15-33.

This page left intentionally blank.

Appendix F. Comparison of Two Large-Scale Surveys for *Brachyramphus* Murrelets in Southeast Alaska

By John Piatt[1], Gary Drew[1], Mayumi Arimistu[1], Shay Howlin[2], and Lyman McDonald[2]

Southeast Alaska hosts the largest concentration of Marbled Murrelets (*Brachyramphus marmoratus*) found anywhere throughout their range from California to the Bering Sea (Piatt and Naslund, 1995; Nelson, 1997). A regional-scale survey of Southeast Alaska in 1994 suggested that between 486,000 and 888,000 *Brachyramphus* murrelets resided in Southeast Alaska during summer (Agler and others, 1998). This survey has not been repeated, and we do not know the size of the present-day murrelet population in Southeast Alaska. However, between 1997 and 2001, the U.S. Fish and Wildlife Service conducted aerial surveys of the entire shoreline of Southeast Alaska, and conducted small boat surveys over about 16 percent of the shoreline to provide correction factors for numbers of birds observed on aerial surveys. We compiled and analyzed the boat-based survey data and compared them with the previous area-wide survey conducted by Agler and others (1998). These data suggest a decline in murrelet populations during the short period between surveys. Estimated populations diminished by approximately 45 percent during a period of 7 years and at an approximate overall rate of -11.5 percent per year. Owing to differences in timing and methodology between surveys, these estimated changes should be considered tentative and part of the overall assessment of populations in Southeast Alaska.

Methods

Agler Survey Methods.—Agler and others (1998) used small boats to survey murrelets throughout Southeast Alaska. These methods have been widely used and reported in detail elsewhere (e.g., Klowieski and Laing, 1994; Agler and others, 1998, 1999; Irons and others, 2000). In summary, 631 randomly selected transects (fig. F1) were surveyed between June 9 and July 27, 1994. The study area was divided into two strata: (1) coastal (all waters <200 m from shore), and (2) offshore (all waters >200 m from shore). Potential transects were created by using Geographic Information System (GIS) to overlay a grid of 1.9 km (1 nmi) square blocks over the entire southeast area, and selecting at random from those that had no land closer than 200 m from shore (offshore block) and those that did (coastal block). Transects in offshore blocks simply cut straight through blocks and averaged 1.7 km in length. Coastal transects followed any shoreline falling within the block and averaged 3.9 km in length. In all surveys, observers surveyed a sampling window 100 m on either side and ahead of the boat. All flying birds and birds on the water were recorded continuously and binoculars were used to aid in identification of species. Because of the difficulty in distinguishing Marbled from Kittlitz's Murrelet, most birds were recorded simply as *Brachyramphus* murrelets.

We obtained the original data from this survey from the U.S. Fish and Wildlife Service (Migratory Bird Management, Anchorage). Given the importance of this area-wide survey, we also located the original field data sheets containing raw data and we verified that the computer files were accurate with respect to murrelet observations. We found a few minor discrepancies, and we adjusted the number of murrelets observed on four transects. The total number of murrelets observed was adjusted to 5,702 from 5,714 reported in Agler and others (1998). No adjustments were necessary for the 631 transect distances or calculated areas. We used this data set for all statistical comparisons with Hodges data (see below).

Hodges Survey Methods.—A complete aerial survey of the shoreline and boat sample survey of the shoreline was conducted for marine birds in Southeast Alaska during the summers of 1997–2001 (Jack Hodges and Debbie Groves, U.S. Fish and Wildlife Serfice, Migratory Bird Management, Juneau Field Office, unpub. data, 1997–2001). The primary aerial survey was conducted using fixed wing aircraft and standardized methods for aerial surveys in Alaska (e.g., Conant and others, 1988). The plane was flown parallel to all shores and birds were counted in a 400-m strip from the beach outward. The survey was conducted over a 5-year period in which successive blocks of shoreline were sequentially flown until the entire study area was completely covered. Surveys were conducted during the last week of July or the first 2 weeks of August. Aerial surveys are known to have measurement bias with respect to identification of species and counting of numbers (Briggs and others, 1985). Owing to their relatively small size and drab plumage, murrelets are not always detected under poor viewing conditions (e.g., glare, white-caps) on aerial surveys (Piatt and others, 1991; Varojean and Williams, 1995; Nysewander and others, 2005). Therefore, counts of murrelets obtained on the Southeast Alaska aerial survey were not considered reliable for evaluating murrelet distribution or estimating population size of murrelets. The aerial survey data are not considered further in this report.

However, subareas of Southeast Alaska shoreline were also surveyed by boat in order to obtain visibility correction ratios for the aerial survey data. Areas were subjectively selected (fig. F2) to be logistically practical and representative of all habitat types. Boat surveys were conducted over a 5-year period, with similar effort (table F1) in each of 4 of those

---

[1] U.S. Geological Survey.

[2] WEST, Inc., Cheyenne, Wyoming.

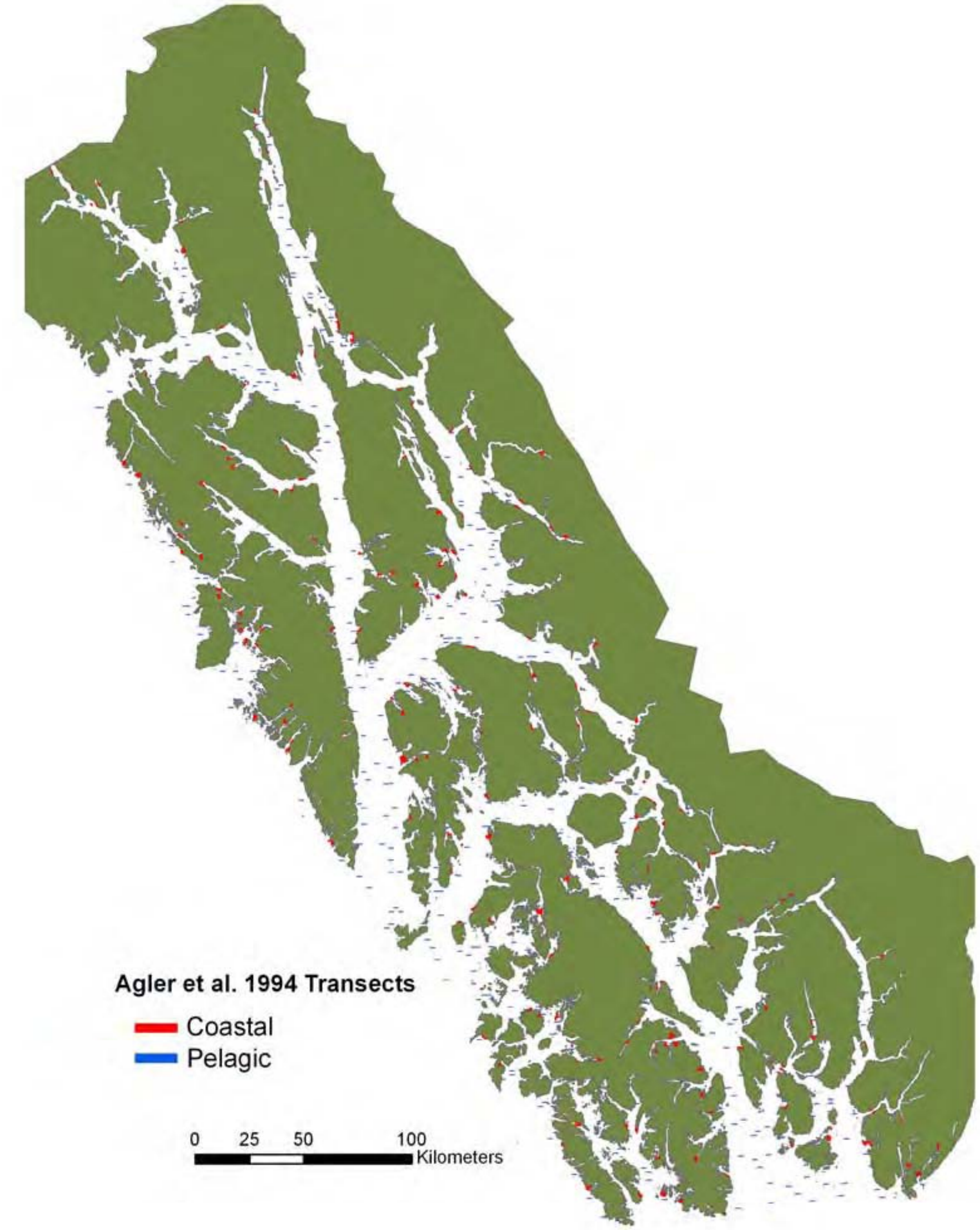


Figure F1. Survey of Southeast Alaska conducted by Agler and others (1998) in 1994. The survey comprised 631 randomly selected transects in coastal and pelagic waters.

Table F1. Details of effort on Agler and Hodges surveys and a comparison of population size estimated from those surveys.

Comparison	Survey	Sampling area	Transect effort		Number of birds	Density (No./km^2)	Total area	Population estimate	95 percent confidence limit		Prob. A = H	Percent change per annum
			n	Area (km^2)					Lower	Upper		
All SE Alaska	Agler, 1994	Coastal, Offshore	631	297	5,702	19.22	35,468	681,741	485,678	877,804		
	Hodges, 1997–2001	Coastal	1,704	748	7,795	10.42	35,468	369,708	284,333	500,370	*$p<0.01$	-11.5
	Agler, 1994	Coastal	191	150	2,799	18.66	4,690	87,498	65,403	109,593		
	Hodges, 1997–2001	Coastal	1,704	748	7,795	10.42	4,690	48,887	37,598	66,165	$p<0.10$	-11.0

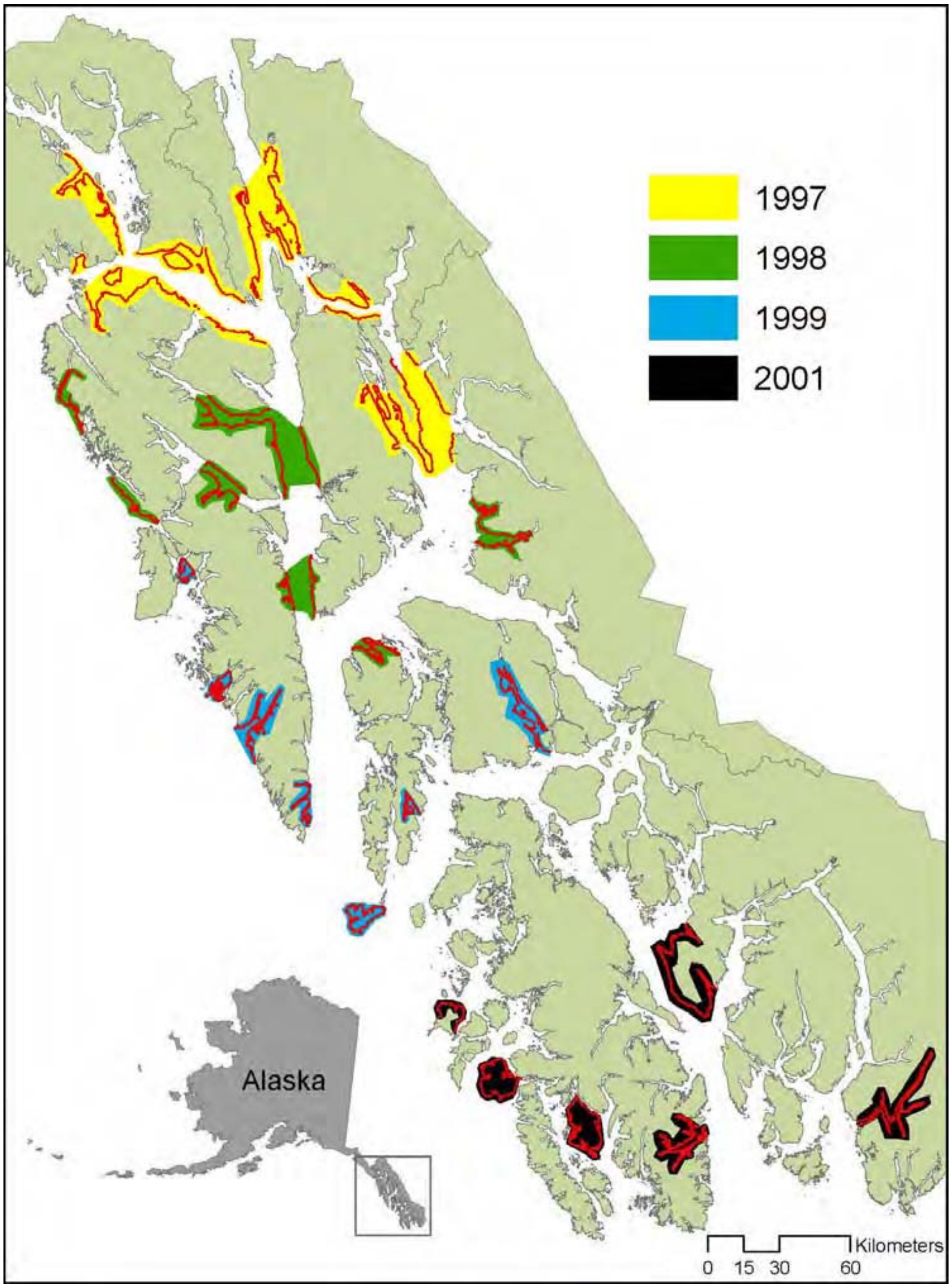


Figure F2. Location of coastal small-boat surveys for marine birds in Southeast Alaska conducted by U.S. Fish and Wildlife Service (J. Hodges and others) during four years (1997, 1998, 1999, 2001). Colored polygons indicate what year surveys were conducted, and the red lines indicate the survey tracks.

years (1997: 1,015 km; 1998: 743 km; 1999: 705 km; 2001: 894 km). Effort was distributed over a different geographic range of Southeast Alaska in each year (fig. F2). On boat surveys, two observers with binoculars rode in stable skiffs with outboard motors. Skiffs were driven about 100 m from shore and all birds observed between the boat and shore were counted. On the offshore side of the boat, birds were surveyed out to 300 m. All marine birds flying or on the water within the transect zone were identified and counted on boat surveys. Laptop computers, housed in protected cases, allowed Global Positioning System (GPS) locations to be tagged with each observation. Because the purpose of the boat surveys was to provide a correction factor for aerial surveys, the vessel was slowed or stopped when necessary in order to count flocks or identify species. The evasive behavior of birds ahead of the boat was carefully monitored and the path of the skiff adjusted to help prevent roll up of flocks ahead of the skiff that might have resulted in double counting.

The skiffs were driven in a similar fashion as the airplane track, that is, distance from shore was optimized to best census coastal birds such as harlequin ducks (*Histrionicus histrionicus*), mergansers and gulls. Murrelets can be observed as much as 1 km from shore under optimum conditions (Speckman and others, 2000). In field trials, observers traveling in small skiffs detected 60–80 percent of murrelets at distances of as much as 200 m even when the water surface was choppy (Mack and others, 2002). However, we assume that under average conditions, counts of murrelets beyond 100 m from the boat were biased low because some individuals were not detected (Ralph and Miller, 1995; Strong and others, 1995), but most murrelets as much as 100 m distance were detected—which is why this distance is frequently used as a truncation distance on line transects for murrelets (Bentivoglio and others, 2002). Therefore, to be conservative in comparisons to the Agler data, and to keep these transect tracks comparable to others conducted by USFWS, we assume an effective transect width of 200 m (100 m either side of boat) for Marbled Murrelets and we use this distance in all calculations of density. Correspondingly, all density and population estimates from Hodges' shoreline survey probably are biased upwards because the counts included individuals detected at greater than 100 m. These surveys were never intended to collect population assessment data for Marbled Murrelets and observers are not confident that they observed all murrelets on boat-based surveys (J. Hodges, U.S. Fish and Wildlife Service, oral commun., 2006). We compared estimates of murrelet densities with those of other seabird species observed on both Agler and Hodges surveys to get some idea of the magnitude of errors arising from the use of different methods among surveys.

All of Hodge's boat surveys were conducted between August 1–13 over all years (1997–2001), and this constitutes another source of error in the data. Bird numbers observed in early August tend to be elevated by ca. 20–40 percent relative to counts earlier in the season (DeGange, 1996; Speckman and others, 2000; Kuletz, 2005). This corresponds to the late chick-rearing and fledging period when foraging adults are highly mobile (Whitworth and others, 2000), and large numbers of failed breeders and subadults contribute to the size of local populations in the surveyed area (Speckman and others, 2000). For these reasons, we assume that counts of murrelets on the 1997–2001 boat-based shoreline surveys would be biased high relative to counts conducted in June and July (Speckman and others, 2000), and hence conservative when compared to the Agler surveys that were conducted during June and July 1994. No adjustments were made for this potential source of error.

Data Analysis.–Agler data were collected in 631 randomly placed transects. Hodges data were collected over stretches of continuous shoreline. In order to compare data sets at similar spatial scales of analysis, we used the same 1 nmi (1.9 km) square grid overlay used by USFWS to create and select the original Agler transects (see above) and binned the Hodges survey track into 1,704 coastal transects with an average length of 4.4 km (fig. F2). Agler estimated the mean and variance of population size in Southeast Alaska using a ratio estimator (Cochran, 1977) applied to the two strata; coastal and offshore (Agler and others, 1998). Because the Hodges transects were not randomly selected and were continuous with potential autocorrelation among adjacent transects, we used a bootstrap procedure to estimate the variance and confidence intervals on density for each survey data set. The population density was estimated from the ratio of total birds observed on all transects to the total area surveyed on all transects (Cochran, 1977). The total population size of Southeast Alaska was estimated by extrapolation from the estimate of density to the total area of Southeast Alaska (table F1). The bootstrap procedure resampled the original transects with replacement, assuming the variance in the sample was equivalent to the variance of the universe of all possible transects in the area of interest (Manly, 1997). The ratio estimator of density (total murrelets observed to total area surveyed) was calculated for each resampled dataset. These steps were repeated 2,000 times. The mean, standard deviation, variance, and percentile confidence intervals were calculated for the 2,000 bootstrapped ratios. Potential mathematical bias was calculated for each survey as the difference between the bootstrap mean and the observed ratio of totals. Density estimates are reported as the ratio estimator of density, because mathematical bias was insignificant, being less than 0.6 percent in all comparisons.

Agler conducted surveys in both coastal and offshore waters, and Hodges surveyed coastal waters only (figs. F1 and F2). First, we considered whether comparisons of these surveys would be biased by the unequal spatial distribution of transects among studies. Although offshore densities (19.8 birds/km^2) were slightly higher than coastal densities (18.7 birds/km^2 0.196, p>0.25, df = 395 using Welch's correction for unequal variance; Zar, 1999). We observed a similar tendency for murrelet densities to be about 20 percent higher in offshore waters of Glacier Bay, but densities did not vary consistently among 6 years of study (J. Piatt, U.S.Geological Survey, unpub. data, 1991–2003). Therefore, in contrast to the methods and results reported by Agler and others (1998), we combined transects from the coastal and offshore strata and calculated a single ratio estimate of density. The fact that our estimate differs by less than 0.8 percent from Agler's indicates in itself how evenly distributed murrelets were in both habitats.

We have observed that murrelets move rapidly between offshore and coastal habitats over daily, weekly and monthly time scales (Romano and others, 2004), but data collected over many weeks (Agler) and years (Hodges) should reflect average use of both habitats. There is evidence, however, that murrelets in some areas move away from coastal habitats and toward offshore habitats in August (Matt Kirchhoff, Alaska Department of Fish and Game. oral commun., 2006).

Therefore we also compared Agler's subset of coastal transects with Hodges coastal-only dataset. Differences between studies in the density of murrelets were tested using a 2-tailed *t*-test with Welch's correction for unequal variance (Zar, 1999). Because Hodges data were collected over 4 years (1997, 1998, 1999, 2001), we compared Agler data to the entire 4-year dataset of Hodges as a group, and estimate trend by assuming a year mid-point of 1999 for the Hodges data.

Results and Conclusions

These data indicate that a sharp decline in murrelet populations occurred during the short period between surveys. Comparing the region-wide data of Agler and Hodges (table F1), and using all of Agler's survey data (coastal and offshore transects), and conservative estimates for 1997–2001, we found a significant decline (t=2.71, corrected df=1,060, p<0.01) in the population between 1994 and the 1997–2001 sampling period. This comparison indicates that the population diminished by approximately 46 percent. If we use 1999 as a mid-point for date of the later surveys, the change occurred at an estimated rate of about -11.5 percent per year (table F1). If we compare only Agler's coastal transects to those of Hodges, we observe about the same decline (44 percent) and about the same rate (-11.0 percent per year) of decline (t=1.70, corrected df=239, p<0.10).

We have concerns that differences in the purpose, methods, and timing of each survey could affect the outcome of the survey comparison. One way to cross-check these results is to examine other species of seabirds observed on both surveys, and contrast changes in their estimated numbers with those of murrelets. Results suggest that the density of all other seabirds remained similar or increased markedly between the Agler and Hodges surveys (table F2). The "increase" in density of some species may be due to the conservative assumption of a 200-m transect width on Hodge's survey, or to the inherent variability in temporal-spatial abundance of some species that tend to aggregate (e.g., kittiwakes, gulls, murres, and puffins), or because populations actually increased. Perhaps the best species to compare with murrelets is the pigeon guillemot, a widely distributed, dispersed and coastal relative of the murrelet. Data indicated almost no change in pigeon guillemot densities and murrelet densities decreased by 44 percent. This comparison eliminates some concerns about the comparability of methods, but does not resolve the issue of timing.

Table F2. Comparison of estimated seabird densities on shoreline surveys conducted in SE Alaska by Agler (1994) and Hodges (1997–2001).

Taxa	Density (birds/km^2)		Direction of change
	Agler	Hodges	
Arctic Tern	0.41	0.37	Down
Kittiwake	0.73	12.34	Up
Bonaparte's Gull	7.17	10.18	Up
Common Loon	0.13	0.18	Up
Common Murre	0.13	2.42	Up
Cormorant (spp)	0.36	3.39	Up
Larus gulls (spp)	3.03	18.03	Up
Mew Gull	5.67	47.40	Up
Murrelet	18.70	10.42	Down
Pacific Loon	0.02	0.07	Up
Pigeon Guillemot	1.79	1.88	Up
Rhinoceros Auklet	0.68	4.15	Up
Red-throated Loon	0.05	0.08	Up
Tufted Puffin	0.05	0.25	Up

In summary, the weight of evidence supports a conclusion that murrelet populations have declined markedly in Southeast Alaska. The comparison of Agler and Hodges data suffers from at least three major sources of potential bias (timing of surveys, effective transect width, and location of transects), but on average these biases should lead to a conservative comparison. Conclusions based on the Agler-Hodges data should be considered tentatively, and results should be viewed more as a corroboration of trends suggested by better and completely independent data sets in Icy Strait (-12.7 percent per year) and Glacier Bay (-11.7 percent per year) (see appendixes G and H for details). The Agler-Hodges comparison provides compelling evidence that the changes observed in Glacier Bay and Icy Strait were not restricted to this area, but were in fact observed widely in Southeast Alaska.

References Cited

Agler, B.A., Kendall, S.J., Seiser, P.E., and Irons, D.B., 1998, Abundance and distribution of Marbled and Kittlitz's murrelets in south central and southeast Alaska: Condor, v. 100, no. 2, p. 254-265.

Agler, B.A., Kendall, S.J., Irons, D.B., and Klosiewski, S.P., 1999, Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift: Waterbirds, v. 22, no. 1, p. 98-103.

Bentivoglio, N., Baldwin, J., Evans Mack, D., Max, T., Miller, S., Nelson, S.K., Ralph, C.J., Raphael, M., Strong, C., Thompson, C., Ostrom, K., and Wilk, R., 2002, Northwest Forest Plan Marbled Murrelet effectiveness monitoring: Portland, Oregon, U.S. Fish and Wildlife Service, 2000 Annual Report, 72 p.

Briggs, K.T., Tyler, W.B., and Lewis, D.B., 1985, Comparison of ship and aerial surveys of birds at sea: Journal of Wildlife Management, v. 49, no. 2, p. 405-411.

Cochran, W.G., 1977, Sampling techniques: New York, John Wiley and Sons, 428 p.

Conant, B., King, J.G., Trapp, J.L., and Hodges, J.I., 1988, Estimating populations of ducks wintering in Southeast Alaska, *in* Weiler, M.W., ed., Waterfowl in winter: Minneapolis, University of Minnesota Press, p. 541-551.

DeGange, A.R., 1996, Conservation assessment for the Marbled Murrelet in southeast Alaska: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, General Technical Report 388, 72 p.

Irons, D.B., Kendall, S.J., Erickson, W.P., and McDonald, L.L., 2000, Nine years after the *Exxon Valdez* oil spill: Effects on marine bird populations in Prince William Sound, Alaska: Condor, v. 102, no. 4, p. 723-737.

Klosiewski, S.P., and Laing, K.K., 1994, Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, State / Federal Natural Resource Damage Assessment Final Report, Bird Study 2, 88 p.

Kuletz, K.J., 2005, Foraging behavior and productivity of a non-colonial seabird, the Marbled Murrelet (*Brachyramphus marmoratus*), relative to prey and habitat: Dissertation, British Columbia, University of Victoria.

Mack, D.E., Raphael, M.G., and Laake, J., 2002, Probablility of detecting Marbled Murrelets at sea: effects of single versus paired observers, Journal of Wildlife Management, v. 66, p. 865-873.

Manly, B.F.J., 1997, Randomization, bootstrap and Monte Carlo methods in biology: London, Chapman and Hall.

Nelson, S.K., 1997, Marbled Murrelet (*Brachyramphus marmoratus*), *in* Poole, A., and Gill, F., eds., Birds of North America: Philadelphia, Pennsylvania, Academy of Natural Sciences and American Ornithologists' Union, p. 276.

Nyeswander, D.R., Evenson, J.R., Murphie, B.L., and Cyra, T.A., 2005, Report of marine bird and mammal component, Puget Sound Ambient Monitoring Program, for July 1992 to December 1999 period: Olympia, Washington State Department of Fish and Wildlife, Wildlife Management Program.

Piatt, J.F., and Naslund, N.L., 1995, Abundance, distribution, and population status of Marbled Murrelets in Alaska, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 285-294.

Piatt, J.F., Conant, B., and Iverson, C.G., 1991, Comparison of aerial and boat-based surveys for Marbled Murrelets in southeast Alaska, July 23-28, 1991: Anchorage, Alaska, U.S. Fish and Wildlife Service, 14 p.

Ralph, C.J., and Miller, S.L., 1995, Offshore population estimates of Marbled Murrelets in California, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 353-360.

Romano, M.D., Arimitsu, M.L., Piatt, J.F., Agness, A.A., and Drew, G.S., 2004, At-sea density and distribution of Kittlitz's Murrelets (*Brachyramphus brevirostris*) and Marbled Murrelets (*Brachyramphus marmoratus*) in Glacier Bay, Alaska, Summer 2003: Anchorage, U.S. Geological Survey Alaska Science Center, Annual Report to U.S. National Park Service, Glacier Bay National Park and Preserve.

Speckman, S.G., Springer, A.M., Piatt, J.F., and Thomas, D.L., 2000, Temporal variability in abundance of Marbled Murrelets at sea in southeast Alaska: Waterbirds, v. 23, no. 3, p. 364-377.

Strong, C.S., Keitt, B.S., McIver, W.R., Palmer, C.J., and Gaffney, I., 1995, Distribution and population estimates of Marbled Murrelets at sea in Oregon during the summers of 1992 and 1993, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 339-352.

Varoujean, D.H. II, and Williams, W.A., 1995, Abundance and distribution of Marbled Murrelets in Oregon and Washington based on aerial surveys, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 327-338.

Whitworth, D.L., Nelson, S.K., Newman, S.H., van Vliet, G.B., and Smith, W.P., 2000, Foraging distances of radio-marked Marbled Murrelets from inland areas in southeast Alaska: Condor, v. 102, no. 2, p. 452-456.

Zar, J.H., 1996, Biostatistical analysis: Upper Saddle River, New Jersey, Prentice Hall, ed. 3.

Appendix G. Population Trend of the Marbled Murrelet in Icy Strait, Southeast Alaska

By John Piatt[1], Gary Drew[1], John Lindell[2], Lyman McDonald[3], Shay Howlin[3], and Kirsten Bixler[1]

Summary

Throughout its range in North America, the largest concentration of Marbled Murrelets is found in Southeast Alaska (Piatt and Naslund, 1995; Nelson, 1997). The entire region was sampled with randomly selected transects in 1994 in order to estimate the size of marine bird populations (Agler and others, 1998). This survey suggested that between 486,000 and 888,000 *Brachyramphus* murrelets resided in Southeast Alaska during the summer. This survey has not been repeated, and we do not know the size of the present-day murrelet population in Southeast Alaska. However, we can examine trends for Icy Strait, an east-west waterway in northern Southeast Alaska (fig. G1) that is an important staging and foraging area for thousands of murrelets in the region (DeGange, 1996; Whitworth and others, 2000). This large strait was surveyed repeatedly between 1993 and 2003 using the same survey track and protocols in each year (Robards and others, 2003; Lindell, 2005). Here we analyze the data and report on the observed trend. The estimated total population size of murrelets in Icy Strait shows a statistically significant decrease from approximately 37,000–53,000 birds in 1993 to approximately 16,000–17,000 birds in 2002–03. Linear modeling also suggests a decline since 1993 of 11.4 percent per year. These approaches support the projection of an 80 percent decline in total numbers between 1993 and 2006.

Methods

Beginning in 1993, the U.S. Fish and Wildlife Service initiated a systematic survey of Icy Strait (Lindell, 2005). This survey was comprised of a grid of 12 north-south legs separated by 2.5 nmi and set perpendicular to Icy Strait, running from the head of Chatham Strait in the east to the mouth of Glacier Bay in the west (fig. G2). The cross-strait

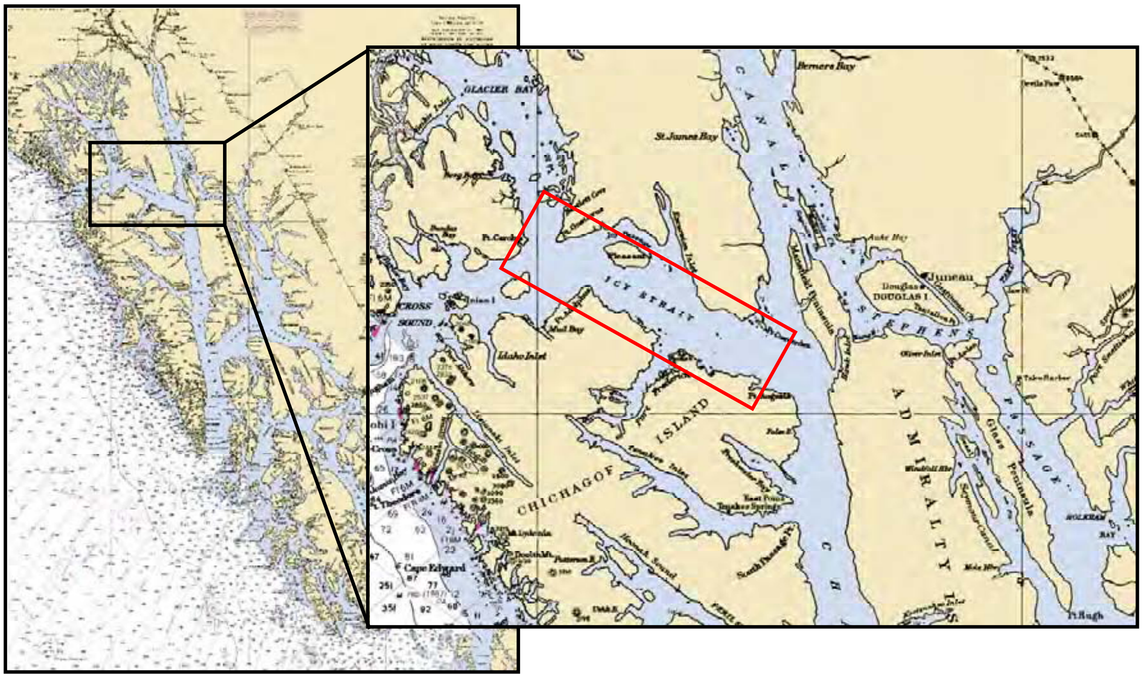


Figure G1. Location of Icy Strait study area in the northern half of Southeast Alaska. Area outlined in red is where surveys were conducted.

---

[1] U.S. Geological Survey.

[2] U.S. Fish and Wildlife Service.

[3] WEST, Inc., Cheyenne, Wyoming.

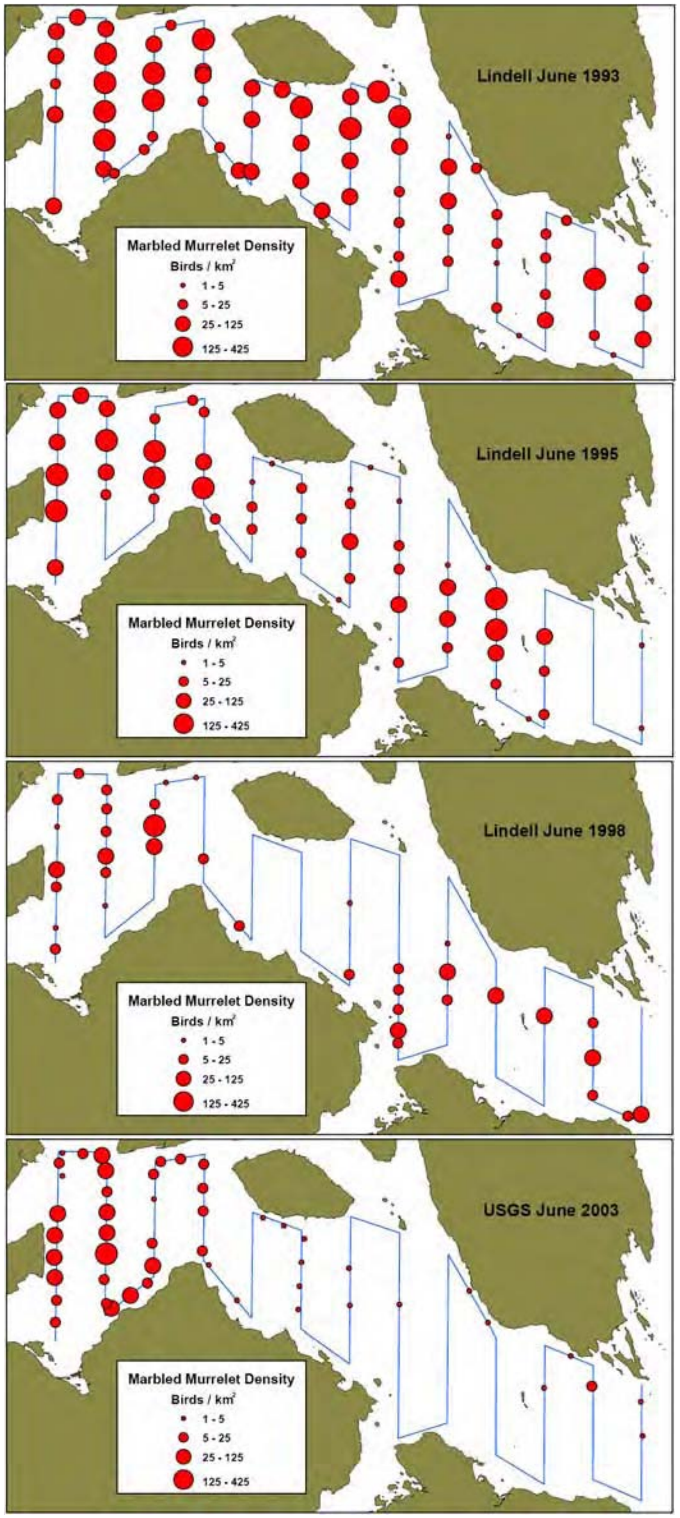


Figure G2. Selection of Icy Strait surveys to illustrate the change in murrelet population abundance and distribution over time.

transects were joined by 13 east-west legs that ran parallel to the coast on both sides of the Icy Strait. The total distance surveyed comprised 240 km or about 70 km^2 within an area of about 1,000 km^2. This grid was surveyed repeatedly within and between the years of 1993 to 1999 by Lindell (2005) and then once a year between 1999 and 2003 by the U.S. Geological Survey (Robards and others, 2003).

Lindell's Survey Methods—The end of each Icy Strait segment was fixed with latitude and longitude waypoints, and these were used by Lindell (2005) as start and stop positions for each segment of the Icy Strait survey. All surveys were completed using the U.S. Fish and Wildlife Service motor vessel *Curlew*, a 65-foot ship. When he established near-shore segments, Lindell placed transects as near as possible to the adjacent shore without compromising survey vessel safety. These along-shore segments were straight-line transects and did not often venture within 200 m of shore. In this respect, they differ from small-boat protocols used by other researchers (Agler and others, 1998) where vessels closely followed shorelines at 100 m distance offshore, and where offshore (≥ 200 m) areas were segregated as different strata for statistical analysis.

Lindell (2005) conducted 15 complete surveys of Icy Strait during the summers of 1993–99. In some years, he replicated surveys in June, July, and August. However, surveys conducted by U.S. Geological Survey (USGS) in 1999–2003 were only conducted in June, raising concerns about comparability with some of Lindell's surveys. Bird numbers observed in early August also tend to be elevated and more variable (DeGange, 1996). This corresponds to the late chick-rearing period when foraging adults are highly mobile (Whitworth and others, 2000), and large numbers of failed breeders and subadults also contribute to volatility in size of local populations (Speckman and others, 2000). For all these reasons, then, we excluded all of Lindell's surveys that were conducted in the month of August, leaving seven surveys that were conducted between June 14 and July 16, in 1993, 1995, 1998, and 1999. Out of concern that the August survey might still provide some useful trend information, or at least a different perspective, we analyzed those data separately.

USGS Survey Methods.—Beginning in 1999, surveys were conducted by USGS in Icy Strait, using the same protocols as Lindell (Gould and Forsell, 1989). Again, all flying birds were counted continuously (e.g., Agler and others, 1998) rather than on periodic scans. In 1999, surveys were conducted using a 300-m strip transect, counting birds on 150 m either side of the *R/V Pandalus*, (22-m length, 5-m viewing height). In 2000–03, observations were made from several vessels including the *R/V Alaskan Gyre* (17 m, 5-m viewing height, 300–m transect width) and the smaller vessels *Lutris II*, (8 m, 2-m viewing height) and *David Grey* (10 m, 2.5-m viewing height) from which we reduced the strip width from 300 to 200 m. Although the total linear distance surveyed (240 km) did not change among years, the total area surveyed changed from about 72 km^2 during 1993–99 to about 52 km^2 during 2000–03 because of the difference in vessel type and strip widths.

Most other USGS methods were similar to those used by Lindell and described above. Birds were identified to species whenever possible, and again, only 19 Kittlitz's were observed out of 2,188 birds identified, so we are essentially analyzing trends for Marbled Murrelets in this report. We used exactly the same waypoints and segments as Lindell. All surveys were conducted between June 11 and June 23, so seasonal variability is not a significant issue. Surveys were not conducted when seas exceeded 1 m. Bird and mammal sightings were recorded by entering them directly into a real-time computer data-entry system (Glenn Ford, R.G. Ford Consulting Inc.) that plots sighting positions continuously using Global Positioning System (GPS) coordinates. GPS locations were obtained from a Rockwell Precision Lightweight Global-Positioning Receiver (PLGR). PLGR units have a worst-case horizontal position accuracy of ±10 m at speeds less than 36 kph.

Data Analysis.—Data were collected using protocols established for 10 minute transects. This is a robust scale for collection of marine bird data, and widely used for pelagic observation programs in the Pacific and Atlantic oceans (Gould and Forsell, 1989; Huettmann and Diamond, 2006). Serial correlation of birds along continuously recorded survey lines can be a problem in data analysis (Schneider, 1990), but binning of data into 10-15 min or 3-5 km transect lengths reduces substantially or eliminates autocorrelation effects for most species (Fauchald and others, 2000; Yen and others, 2004; Huettmann and Diamond, 2006) perhaps because it matches the typical scale of aggregation of seabirds and their prey (Schneider and Piatt, 1986; Piatt, 1990; Fauchald and others, 2000), including Marbled Murrelets (Burger and others, 2004). Autocorrelation of adjacent 10- min survey periods and 20-min survey periods were investigated using Moran's I statistic (Moran, 1948). We calculated Moran's I for each survey and day. Autocorrelation was indicated for adjacent 20-min survey lengths for only 2 of 27 survey days. We proceeded with statistical analysis to estimate variances of density estimates using a bootstrapping procedure (described below) on 20-min survey periods.

Population density of murrelets on each survey was calculated as the ratio (number per square kilometer) of total murrelets observed to total area surveyed (Cochran, 1977, table 1). The total population size of Icy Strait was estimated by extrapolation from the ratio estimator of density to the total Icy Strait study area (1,063 km^2). A bootstrap procedure (Manly, 1997) was used to estimate the variance of the density estimate for every survey. The bootstrap procedure resampled the original data with replacement, assuming the variance in the sample was equivalent to the variance of the universe of all possible sample units in the study area (Manly, 1997). The bootstrap procedure was conducted separately for each survey. For each replication of the bootstrap procedure, 20-min survey periods were resampled with replacement until the resampled sample size was equal to the original sample size. The ratio estimator of density (total murrelets observed to total area surveyed) was calculated for each resampled dataset. These steps were repeated 2,000 times. The mean, standard deviation, variance, and percentile confidence intervals were calculated for the 2,000 bootstrapped ratios. We also computed the bootstrapped variance of log-transformed estimates of density. Potential mathematical bias was estimated for each survey as the difference between the bootstrap mean and the observed ratio of totals. Density estimates are reported as the ratio estimator of density, because mathematical bias was insignificant, being less than 1 percent in all comparisons.

Trend was estimated by weighted linear regression of natural log of murrelet densities on time where the weights were the inverse of the estimated variance of log-transformed density (Sokal and Rohlf, 1981). Potential autocorrelation in the time series was investigated by computing Moran's I on the residuals in the weighted regression analysis.

Results and Conclusions

There was a large change in estimated total numbers of murrelets in Icy Strait between 1993 and 2003, declining from a high of more than 50,000 birds in 1993 to about 16,000 birds in recent years (table G2). The areal extent of distribution contracted as well, with birds retaining high densities near the entrance to Glacier Bay but diminishing in areas to the east (fig. G3). This represents a significant change in abundance over time, as indicated by the lack of overlap in 95-percent confidence limits surrounding population estimates during the early versus late years of sampling (table G2, fig. G3). Weighted linear regression of log-transformed densities indicates a significant decline over the time period of 1993 through 2003 (F=8.52, df=1,10, p=0.015, r^2 =0.46), at a rate of -12.7 percent per year (fig. G3). All 95-percent confidence intervals on Moran's I contained zero indicating no significant serial autocorrelation among the residuals over time. Separate regression of Lindell's August data (1993–98 only) provided corroboration of the magnitude of the trend (-8.5 percent per year) although the amount of explained variation was low and insignificant (r^2 = 0.14, F=1.02, df=1,6, p=0.35). Because of the shorter time span, higher variability among counts, lack of significance, and less certainty about the source of variability during this part of the season, we place no confidence in these results from August, nor use them for further analyses.

Table G1. Survey effort, area surveyed (km²), and total number of murrelets observed on Icy Strait surveys.

Date	No. of transects	Area surveyed	Percent total area	No. murrelets counted
06/21/1993	71	71.1	6.7	3,555
07/15/1993	71	72.5	6.8	2,510
07/09/1995	69	71.6	6.7	2,631
07/11/1995	74	71.6	6.7	2,038
06/22/1998	77	74.8	7.0	1,221
06/24/1998	84	71.6	6.7	803
06/11/1999	88	73.0	6.9	336
06/14/1999	77	71.6	6.7	944
06/21/2000	79	46.4	4.4	638
06/21/2001	79	48.3	4.5	1,073
06/13/2002	90	57.6	5.4	899
06/11/2003	82	55.0	5.2	822

Table G2. Estimated density (birds/km²) and total number of Marbled Murrelets occupying Icy Strait during summer with 95-percent confidence limits on the total.

Date	Density	Population estimate	95-percent confidence limits	
			Lower	Upper
06/21/1993	50.0	53,171	36,107	72,817
07/15/1993	34.6	36,815	23,957	50,792
07/09/1995	36.7	39,042	21,216	60,719
07/11/1995	28.5	30,243	15,753	49,052
06/22/1998	16.3	17,340	8,407	26,990
06/24/1998	11.2	11,916	5,429	22,470
06/11/1999	4.6	4,892	3,045	7,084
06/14/1999	13.2	14,009	6,309	23,608
06/21/2000	13.7	14,615	7,850	22,497
06/21/2001	22.2	23,594	13,980	35,306
06/13/2002	15.6	16,589	7,939	26,617
06/11/2003	14.9	15,880	8,966	23,654

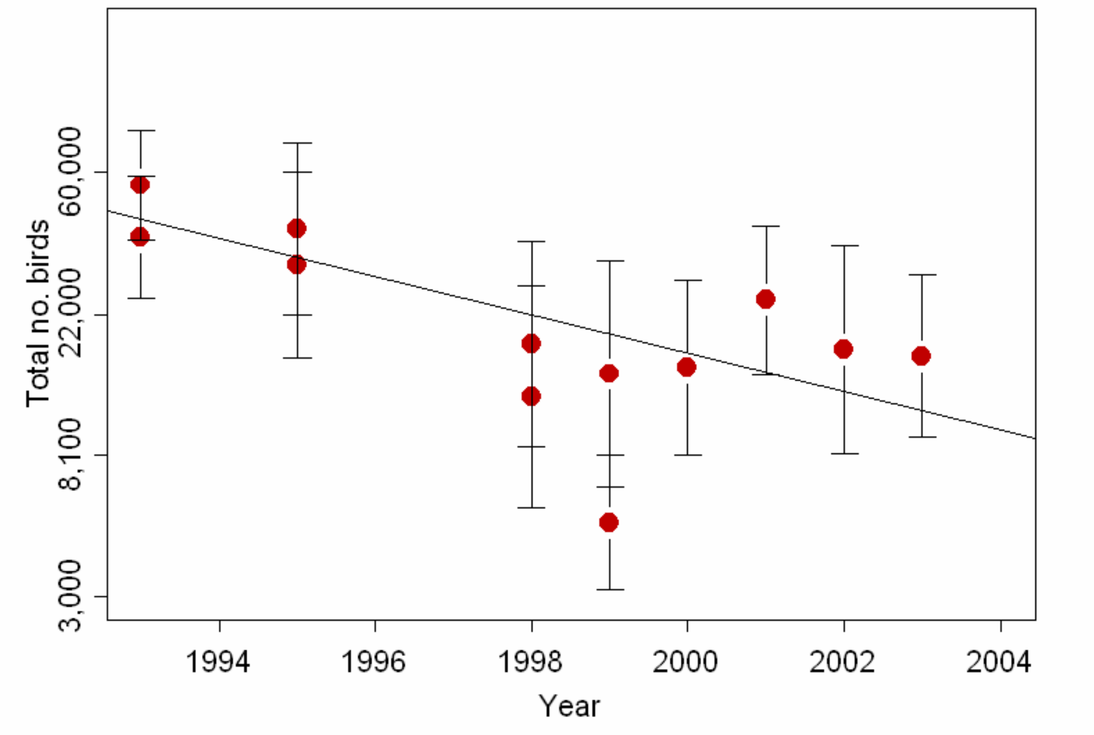


Figure G3. Population trend for Marbled Murrelets in Icy Strait, 1993–2003. Note log scale for population size. Each point represents a different survey of Icy Strait. Weighted linear regression indicates a decline of -12.7 percent per year (*p*=0.015).

The relationship of log-transformed density and time may not be strictly linear over the period from 1993 through 2003. Estimated population declines exhibited in this data set may have occurred mostly between 1993 and 1999, as indicated by a conjectured stronger negative trend in log-transformed counts during this period, followed by a period of little change during 2000 through 2003 when the trend is relatively flat. The estimated decrease per annum during 1993 through 1999 is -25.9 percent per year (r^2 =0.84, F=30.47, df=1,6, p=0.002) and the slope during 2000 through 2003 is not statistically different from zero, although this conjectured break in the data was not defined a-priori and the results must be viewed as tentative.

There is evidence for a weak North Pacific climate regime shift in 1999 (Bond and others, 2003; Curchitser and others, 2005; Overland and Wang, 2005) and evidence that climate-related physical changes (e.g., winds, SST) have had pervasive biological effects on marine animals (Springer, 2004; Grebmeier and others, 2006; but see Litzow, 2006). Under this scenario, the long period of decline in murrelet numbers that began after the 1976 regime shift (Agler and others, 1999) could have been slowed or halted by a later regime shift in 1999. In the absence of a longer time series of data, or any data after 2003, or any clear understanding of the mechanism by which regime shifts influence seabirds (Springer, 2004), the conservative conclusion based on the best available information should be that (1) murrelet numbers in Icy Strait have declined at a very high rate since 1993, and (2) we have insufficient data to establish whether or not the decline is continuing.

References Cited

Agler, B.A., Kendall, S.J., Irons, D.B., and Klosiewski, S.P., 1999, Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift: Waterbirds, v. 22, no. 1, p. 98-103.

Agler, B.A., Kendall, S.J., Seiser, P.E., and Irons, D.B., 1998, Abundance and distribution of Marbled and Kittlitz’s murrelets in south central and southeast Alaska: Condor, v. 100, no. 2, p. 254-265.

Bond, N.A., Overland, J.E., Spillane, M., and Stabeno, P., 2003, Recent shifts in the state of the North Pacific: Geophysical Research Letters, v. 30, p. 2183-2187.

Burger, A.E., Hitchcock, C.L., and Davoren, G.K., 2004b, Spatial aggregations of seabirds and their prey on the continental shelf off southwest Vancouver Island: Marine Ecology Progress Series, v. 283, p. 279-292.

Cochran, W.G., 1977, Sampling techniques: New York, John Wiley and Sons, 428 p.

Curchitser, E., Haidvogel, D.B., Hermann, A.J., Dobbins, E.L., Powell, T.M., and Kaplan, A., 2005, Multi-scale modeling of the North Pacific Ocean: Assessment and analysis of simulated basin-scale variability (1996-2003): Journal of Geophysical Research, v. 110, p. 11021-11042.

DeGange, A.R., 1996, Conservation assessment for the Marbled Murrelet in southeast Alaska: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, General Technical Report 388, 72 p.

Fauchald, P., Erikstad, K.E., and Skarsfjord, H., 2000, Scale-dependent predator-prey interactions: Hierarchical spatial distribution of seabirds and prey: Ecology, v. 81, p. 772-783.

Gould, P.J., and Forsell, D.J., 1989, Techniques for shipboard surveys of marine birds: Washington, D.C., U.S. Fish and Wildlife Service Technical Report 25, 22 p.

Fauchald, P., Erikstad, K.E., and Skarsfjord, H., 2000, Scale-dependent predator-prey interactions: Hierarchical spatial distribution of seabirds and prey: Ecology, v. 81, p. 772-783

Grebmeier, J.M., Overland, J.E., Moore, S.E., Farley, E.V., Carmack, E.C., Cooper, L.W., Frey, K.E., Helle, J.H., McLaughlin, F.A., and McNutt, S.L., 2006, Major ecosystem shift in the northern Bering Sea: Science, v. 311, p. 1461-1464.

Huettmann, F., and Diamond, A.W., 2006, Large-scale effects on the spatial distribution of seabirds in the Northwest Atlantic: Landscape Ecology, v. 21, p. 1089-1108.

Lindell, J.R., 2005, Results of at-sea *Brachyramphus* murrelet surveys in Icy Strait and other selected areas of southeast Alaska, 1993-1999: Juneau, Alaska, U.S. Fish and Wildlife Service, Unpublished Report, 17 p.

Litzow, M.A., 2006, Climate regime shifts and community reorganization in the Gulf of Alaska: How do recent shifts compare with 1976/1977?: Journal of Marine Sciences, v. 63, p. 1386-1396.

Manly, B.F.J., 1997, Randomization, bootstrap and Monte Carlo methods in biology: London, Chapman and Hall.

Nelson, S.K., 1997, Marbled Murrelet (*Brachyramphus marmoratus*), *in* Poole, A., and Gill, F., eds., Birds of North America: Philadelphia, Pennsylvania, Academy of Natural Sciences and American Ornithologists’ Union, p. 276.

Sokal, R.R., and Rohlf, F.J., 1981, Biometry: New York, W.H. Freeman.

Moran, P.A.P., 1948, Interpretation of statistical maps: Royal Statistical Society B Journal, v. 10, p. 243-251.

Overland, J.E., and Wang, M., 2005, Arctic climate paradox: Recent decrease of the Arctic Oscillation: Geophysical Research Letters, v. 32, p. L06701-L06706.

Piatt, J.F., 1990, Aggregative response of Common Murres and Atlantic Puffins to their prey: Studies in Avian Biology, v. 14, p. 36-51.

Piatt, J.F., and Naslund, N.L., 1995, Abundance, distribution, and population status of Marbled Murrelets in Alaska, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 285-294.

Robards, M., Drew, G.S., Piatt, J.F., Anson, J.M., Abookire, A., Bodkin, J.L., Hooge, P., and Speckman, S.G., 2003, Ecology of selected marine communities in Glacier Bay: Zooplankton, forage fish, seabirds and marine mammals: Anchorage, USGS Alaska Science Center, Final Report to USNPS, GBNPP, 156 p.

Schneider, D.C., 1990, Spatial autocorrelation in marine birds: Polar Biology, v. 8, p. 89-97.

Schneider, D., and Piatt, J.F., 1986, Scale-dependant aggregation and correlation of seabirds with fish in a coastal environment: Marine Ecology Progress Series, v. 32, p. 237-246.

Speckman, S.G., Springer, A.M., Piatt, J.F., and Thomas, D.L., 2000, Temporal variability in abundance of Marbled Murrelets at sea in southeast Alaska: Waterbirds, v. 23, no. 3, p. 364-377.

Springer, A.M., 2004, Changing relationships between climate and biological indices in the eastern Bering Sea, *in* Macklin, S.A. and Hunt, G.L. Jr., eds., Southeast Bering Sea ecosystem: Implications for marine resource management: Silver Springs, Maryland, National Oceanic and Atmospheric Administration Coastal Ocean Program Decision Analysis Series 24 Final Report, p. 112-125.

Whitworth, D.L., Nelson, S.K., Newman, S.H., van Vliet, G.B., and Smith, W.P., 2000, Foraging distances of radio-marked Marbled Murrelets from inland areas in southeast Alaska: Condor, v. 102, no. 2, p. 452-456.

Yen, O.P.W., Sydeman, W.J., and Hyrenbach, K.D., 2004, Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: Implications for trophic transfer and conservation: Journal of Marine Systems, v. 50, p. 79-99.

Appendix H. Population Trend of *Brachyramphus* Murrelets in Glacier Bay, Alaska

By John Piatt[1], Gary Drew[1], John Lindell[2], Shay Howlin[3], and Lyman McDonald[3]

Recent concerns over the population status of Marbled Murrelets (*Brachyramphus marmoratus*) and Kittlitz's Murrelets (*B. brevirostris*) led us to examine murrelet population trends in Glacier Bay, Alaska. Glacier Bay is located in the northern end of Southeast Alaska, a region that hosts the largest concentration of Marbled Murrelets found anywhere throughout their range from California to the Bering Sea (Piatt and Naslund, 1995; Nelson, 1997). A regional-scale survey of Southeast Alaska in 1993 suggested that between 486,000 and 888,000 *Brachyramphus* murrelets resided in Southeast Alaska during summer (Agler and others, 1998). This survey has not been repeated, and we do not know the size of the present-day murrelet population in Southeast Alaska. However, we can examine trends for Glacier Bay, a large, protected body of water at the northern end of Southeast Alaska (fig. H1) and an important breeding and foraging area for thousands of murrelets in the region (DeGange, 1996; Whitworth and others, 2000). Glacier Bay was surveyed for marine birds in 1991 (Piatt and others 1991), 1993 (Lindell, 2005) and in 1999–2003 (Robards and others, 2003). Here we analyze these data and report on the observed trend. The estimated total population size of *Brachyramphus* murrelets in Glacier Bay shows a statistically significant decrease from approximately 75,000 birds in 1991 to approximately 16,000 birds in 2003. In contrast, no other bird species in Glacier Bay appear to have declined during this period. Linear modeling of log-transformed density estimates suggests a decline since 1991 of 11.7 percent per year. These approaches support the projection of approximately an 85 percent decline in total numbers between 1991 and 2006.

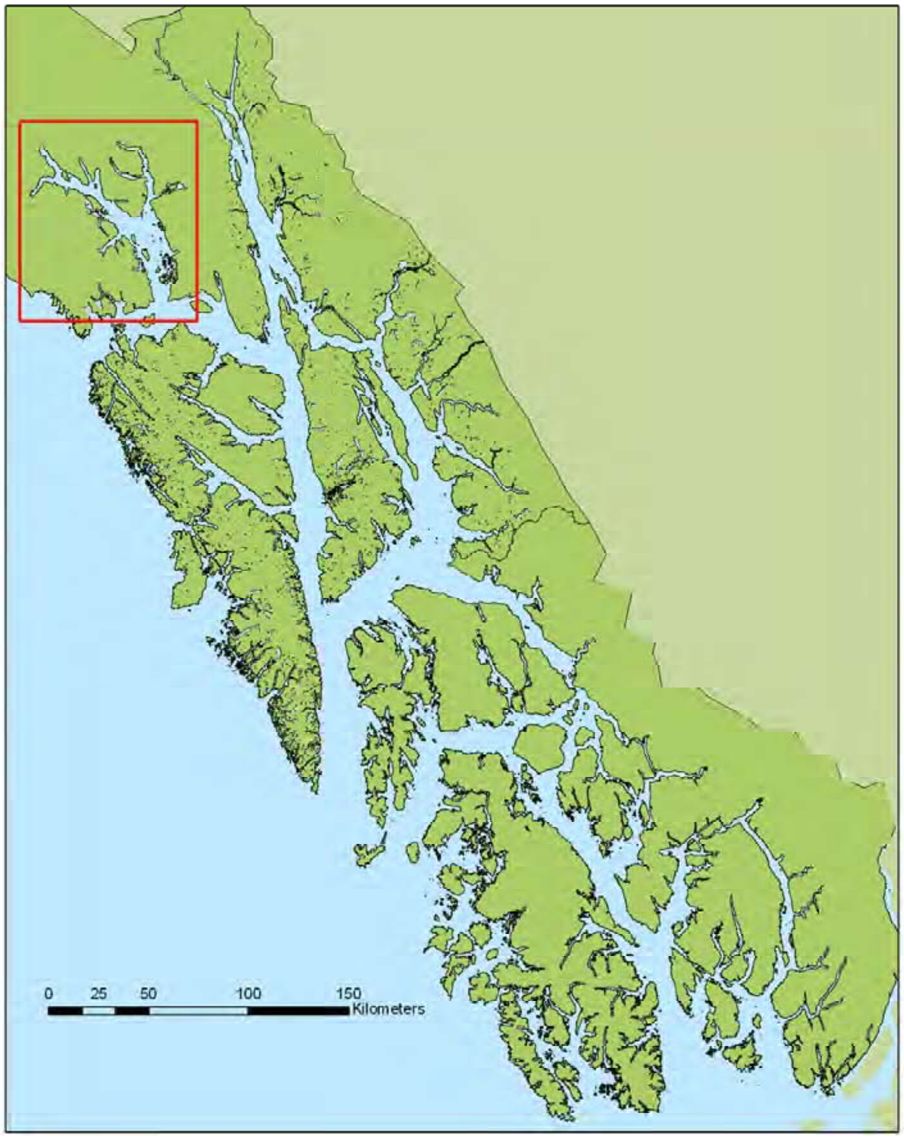


Figure H1. Location of Glacier Bay in the northern end of Southeast Alaska. Area outlined in red is where surveys were conducted.

Methods

Outside of a few partial or localized surveys of Glacier Bay (e.g., Conant, 1991; Duncan and Climo, 1991; Agler and others, 1998; Eckert, 2005), this region has been the object of extensive, bay-wide surveys for marine birds on eight occasions between 1991 and 2003 (Piatt and others, 1991; Robards and others, 2003; Lindell, 2005; Drew and others (U.S. Geological Survey, unpub. data, 2006). Methods for all surveys were similar, but in the following, we review them individually.

---

[1] U.S. Geological Survey.

[2] U.S. Fish and Wildlife Service.

[3] WEST, Inc., Cheyenne, Wyoming.

U.S. Fish and Wildlife Service 1991 Methods.—In 1991, biologists with the U.S. Fish and Wildlife Service, Glacier Bay National Park and University of Alaska, Fairbanks, conducted a systematic survey of Glacier Bay Alaska (Piatt and others, 1991). The purpose of these surveys was to conduct a preliminary reconnaissance for both Marbled and Kittlitz's Murrelets in Glacier Bay, as well as to collect baseline data on other marine bird and mammal species in the park. Using small, open skiffs, observers set out to survey the entire coastline and opportunistically sampled 15 offshore segments as well (fig. H2). Transect lengths ranged from 0.88 to 11.98 km with a total length of 723.36 km (table H1) and a surveyed area of 144.76 km^2 (about 10 percent of which was offshore).

Observers used standard sampling protocols developed for small-boat surveys of Prince William Sound shoreline following the *Exxon Valdez* oil spill (Klowsiewski and Laing, 1994). All flying birds were counted continuously (e.g., Agler and others, 1998) rather than on periodic scans (Gould and Forsell, 1989). Observers viewed birds from about 2 m above the water surface and two observers were on duty during all surveys. Observers surveyed continuously along transects and binoculars were used to aid in identification of species. All swimming birds and mammals within 100 m on either side or 200 m forward of the boat were identified to species. For more details on methods, see Klosiewski and Laing, 1994; Agler and others, 1998, 1999; Robards and others, 2003).

Lindell's Survey Methods.— In 1993, the U.S. Fish and Wildlife Service conducted systematic surveys of Glacier Bay, Alaska (Lindell, 2005). The survey consisted of 38 strip transects laid out in a zig-zag fashion to broadly cover the full length of Glacier Bay (fig. H3). Transect lengths ranged from 1.4 to 14.35 km with a total length of 278.6 km and a surveyed area of 83.6 km^2 (table H1). Surveys were conducted using the U.S. Fish and Wildlife Service motor vessel *Curlew*, a 65-foot ship. The survey was conducted once in June 1993 and replicated later in mid-August 1993. However, surveys for murrelets in late July and August may detect higher densities and greater variability within and between years (DeGange, 1996; Speckman and others, 2000). This corresponds to the late chick-rearing period when foraging adults are highly mobile (Speckman and others, 2000; Whitworth and others, 2000), and large numbers of failed breeders and subadults also contribute to the size and volatility of local populations (Speckman and others, 2000). For these reasons, the best time period for monitoring population change in murrelets is during June and early July when adults are still tied to nesting areas and attendance at sea is most stable (Speckman and others, 2000). Because of this, and because all other survey data were collected in June or early July, we excluded Lindell's survey data from August (even though murrelet densities [31.0 birds per square kilometer] were similar to those observed in June).

Lindell (2005) used shipboard survey methods described by Gould and Forsell (1989), with the exception that all flying birds were counted continuously (per Klosiewski and Laing, 1994) rather than on periodic scans. All surveys were completed using the *M/V Curlew* at a cruising speed of about 10 nmi/h (knots) (18.5 km/h). Observers were stationed approximately 5 meters above the water surface atop the ship's wheel house.

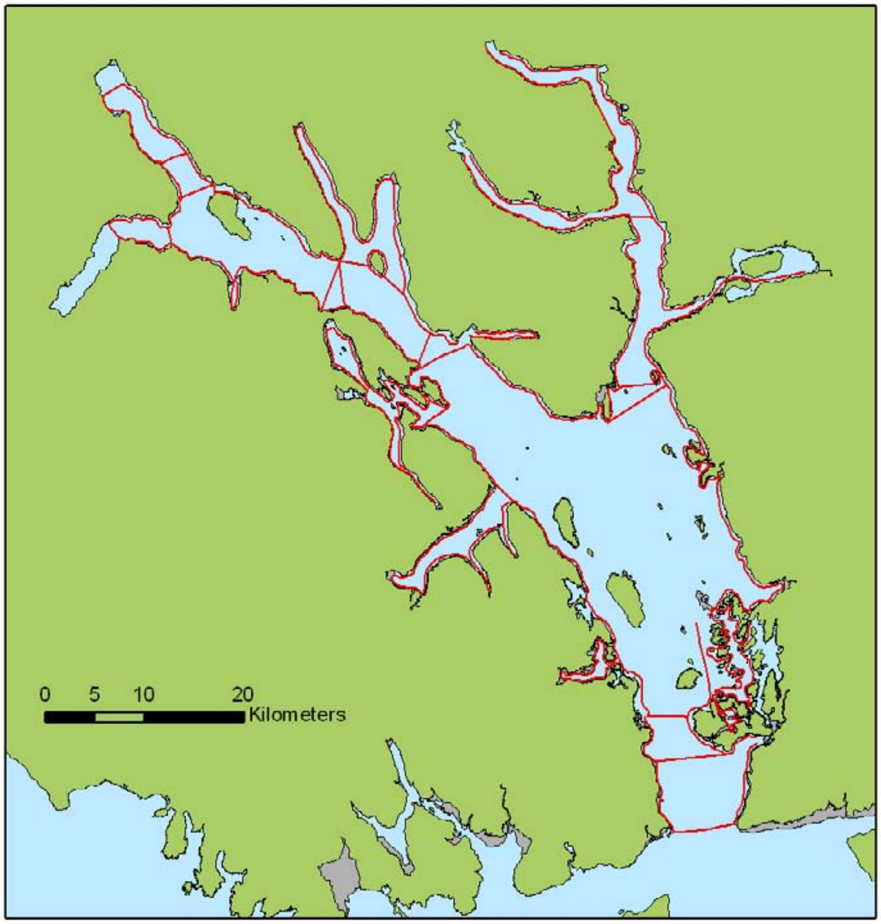


Figure H2. Route of surveys in Glacier Bay conducted in 1991 by U.S. Fish and Wildlife Service and National Park Service. (Piatt and others 1991).

Table H1. Survey effort, distance and area surveyed, and total number of *Brachyramphus* murrelets observed on Glacier Bay surveys.

[**Abbreviations**: n, number; km^2, square kilometer]

Year	Month	No. of transects	Amount surveyed		Percent total area	No. murrelets counted
			km	km^2		
1991	June-July	173	723.6	144.7	11.2	8,474
1993	June	37	278.6	83.6	6.5	3,017
1999	June	110	1,138.9	316.4	24.5	5,972
2000	June	109	1,169.1	270.1	21.0	3,879
2001	June	105	1,175.7	276.0	21.4	4,545
2002	June	109	1,218.5	258.5	20.1	3,302
2003	June	109	1,164.8	263.5	20.4	3,300

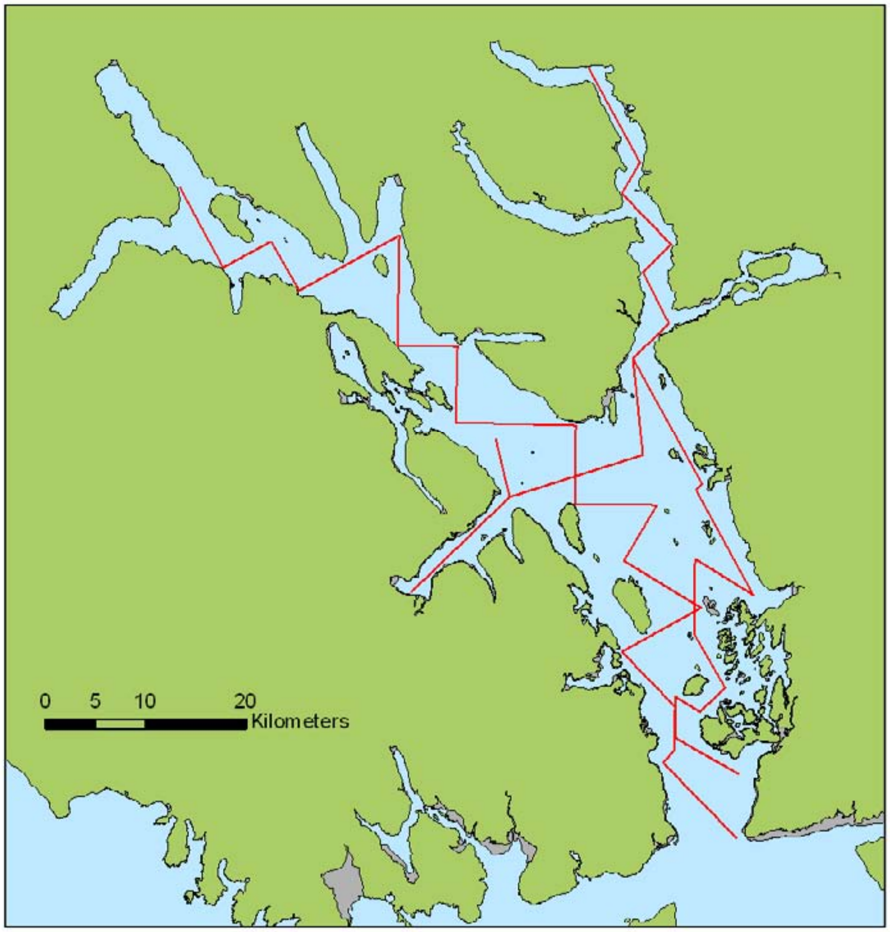


Figure H3. Route of surveys in Glacier Bay conducted in 1993 by U.S. Fish and Wildlife Service.

At least two observers were on duty during all surveys. A third observer was added when large numbers of birds were encountered. They identified and recorded all birds and mammals encountered within 150 m either side and ahead of the survey vessel. Observers estimated this distance using sight boards installed on the vessel and by calibrating against duck decoys or similarly sized buoys placed at a known distance from the vessel. Observers sampled continuously along transects, and binoculars were used to aid in identification of species. Surveys typically were conducted when wave heights were less than 0.6 m (2 ft), with few, if any, white caps. Surveys were conducted during all phases of the tide and throughout daylight hours, which would tend to reduce the variability associated with those factors (Speckman and others, 2000). Observers recorded the time of each *Brachyramphus* murrelet observation by hour and minute. Positions for each minute were calculated from time between waypoints obtained from the Differential Global Positioning System.

USGS Survey Methods.—Beginning in 1999, U.S. Geological Survey (USGS) biologists collected data along the entire coastline of Glacier Bay and on offshore transects that were perpendicular to the coastline and spaced at 2.5 nmi intervals (fig. H4). Methodologies were those recommended in Gould and Forsell (1989) for ship-based surveys except that all flying birds were counted continuously in order to be comparable with previous surveys of Glacier Bay (Piatt and others, 1991; Lindell, 2005). Transect lengths varied from 1.2 to 12.7 km with a total length of more than 1,100 km and a surveyed area of more than 250 km^2 each year (table H1), about 35 percent of which was offshore habitat.

During the years of study (1999–2003), several vessels were used to collect survey data. Observers on the *R/V Pandalus* (22 m length, 5-m viewing height, 300-m transect width) and Alaskan Gyre *R/V Alaskan Gyre* (17 m, 5-m viewing height, 300-m transect width) counted and identified birds and mammals within 150 m on either side or 150 m forward of the boat. Several smaller vessels also were used in these surveys. Due to the lower viewing angles from these boats, we limited the transect window to 100 m on either side and 100 m forward of the boats *Lutris II*, (8 m, 2-m viewing height), *David Grey* (10 m, 2.5-m viewing height), *Capeli*n (8 m, 2.5-m viewing height), and *Sigma-t* (9.5 m, 2-m viewing height). Observers actively scanned ahead of and alongside the survey vessel, and species identifications were confirmed using 7–10 power binoculars. Standard guides were used for identifications.

All surveys were conducted between June 11 and June 23, so seasonal variability is not an issue. Surveys were not conducted when seas exceeded 1 m. Bird and mammal sightings were recorded by entering them directly into a real-time computer data-entry system (DLOG; Glenn Ford, ECI) that plots sighting positions continuously using Global Positioning System (GPS) coordinates. GPS locations were obtained from a Rockwell Precision Lightweight Global-Positioning Receiver (PLGR). PLGR units have a worst-case horizontal position accuracy of ± 10 m at speeds less than 36 kph.

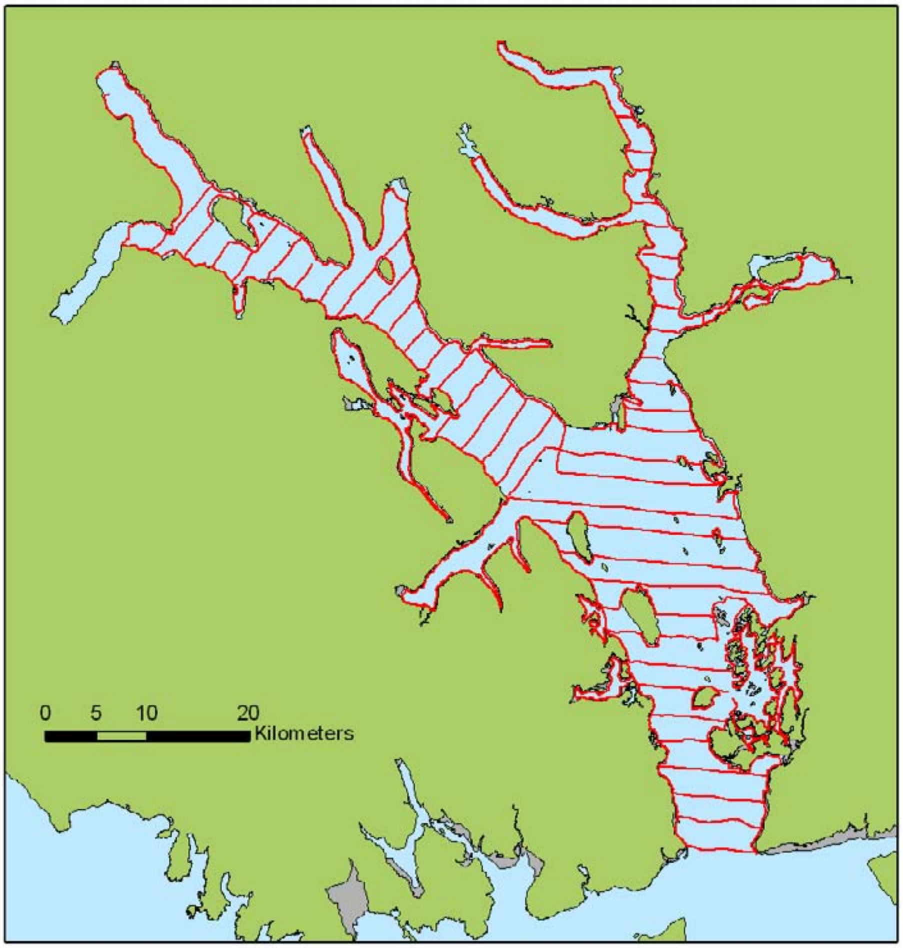


Figure H4. Route of surveys in Glacier Bay established in 1999 by the U.S. Geological Survey and conducted annually in 1999–2003. (Robards and others, 2003; U.S. Geological Survey, unpub. data, 1999–2003).

Data Analysis.**—**Murrelets were identified to species when possible, but a significant proportion were recorded as unidentified on all surveys. Identification of murrelets in the field can be difficult, even for experienced observers. Lighting conditions, distance, visibility, sea conditions, plumage variation, and willingness of observers to persist in efforts to verify identification, also contribute to variability in categorizing birds to species. For the seven surveys compiled here, the fraction of birds on survey that were categorized as unidentified *Brachyramphus* ranged from 22 to 58 percent of all birds observed. For those birds that were identified, the fraction that were Kittlitz's murrelet ranged from 7.2 to 25 percent, and averaged 15 percent. Ideally, we could prorate the unidentified *Brachyramphus* birds into species, but this would add uncertainty to our conclusions about trends for Marbled Murrelets. Therefore, for purposes of analyses here, all Marbled, Kittlitz's and Unidentified Murrelets were combined as *Brachyramphus* murrelets. On average, only about 15 percent of these are Kittlitz's Murrelets, and so the overall trends are still mostly attributable to those of Marbled Murrelets.

Data were collected and organized at spatial scales ranging between about 1–14 km in length and transects averaged about 4–10 km in length on all surveys. This is a robust scale for analysis of marine bird data. Serial correlation of birds along continuously recorded survey lines can be a problem in data analysis (Schneider, 1990), but binning of data into 1–10 km transect lengths reduces or eliminates autocorrelation effects for many species (Fauchald and others, 2000; Yen and others, 2004; Huettmann and Diamond, 2006) perhaps because it matches the typical scale of aggregation of seabirds and their prey (Schneider and Piatt, 1986; Piatt, 1990; Fauchald and others, 2000; Burger and others, 2004).

The design of surveys varied considerably among years. The 1991 survey was designed to sample shoreline habitat, and only about 10 percent of transects sampled offshore habitat haphazardly. In contrast, the survey conducted in 1993 sampled mostly offshore waters, and ventured near shore only near the end of pelagic transects or when surveying long, narrow arms of Glacier Bay. Finally, the 1999–2003 surveys sampled both shoreline and offshore habitats extensively, with about 35 percent of effort directed to offshore habitat. It is important to consider whether comparisons among studies are likely to be biased by this unequal distribution of effort among habitats. Preliminary analyses of habitat use by marine birds in Glacier Bay (G. Drew, U.S. Geological Survey, unpub. data, 2006) suggests that while some species exhibit markedly higher densities in shallow (0–60 m) waters (e.g., Common Mergansers *Mergus merganser*, Harlequin Duck *Histrionicus histrionicus*) or deeper (>60 m) offshore waters (e.g., Black-legged Kittiwake *Rissa tridactyla*), neither Marbled nor Kittlitz's Murrelet exhibited any persistent differences in their at-sea densities among habitats and years. Furthermore, birds move rapidly between offshore and coastal habitats over daily, weekly and monthly time scales (Romano and others, 2004). A simple comparison (using *t*-test) of shoreline and pelagic transect densities suggests some difference in distribution, with higher densities offshore in 3 of 6 years analyzed (1991, 1999–2000). A similar analysis of Agler and others (1998) survey data for all of Southeast Alaska revealed no difference in murrelet densities between shoreline and offshore transects. On average among these surveys, offshore densities were about 20 percent higher than coastal densities, but this difference was not apparent in all years, nor significant (t = 2.20, p=0.51, df = 11 using Welch's correction for unequal variance; Zar, 1996). Therefore, we proceeded with the comparison of murrelet densities among studies and years.

A bootstrap procedure was used to estimate the mean density (number per square kilometer) and variance for every survey. The population was estimated from the ratio of total birds observed on all transects to the total area surveyed on all transects (Cochran, 1977). The total population size of Glacier Bay was estimated by extrapolation from the bootstrap estimate of density to the total area of Glacier Bay (1288.7 km^2). The bootstrap procedure resampled the original data with replacement, assuming the variance in the sample was equivalent to the variance of the population (Manly, 1997). The bootstrap procedure was conducted separately for each survey. For each replication of the bootstrap procedure, transects were resampled with replacement. The resampled sample size was the original sample size. The ratio estimator of density (total murrelets observed to total area surveyed) was calculated for each resampled dataset. These steps were repeated 2,000 times. The mean, standard deviation, variance, and percentile confidence intervals were calculated for the 2,000 bootstrap ratios. We also computed the bootstrapped estimate of the variance of the log-transformed estimate of density.

Potential mathematical bias was calculated for each survey as the difference between the bootstrap mean and the observed ratio of totals. Density estimates are reported as the ratio estimator of density, because mathematical bias was insignificant, being less than 0.4 percent in all comparisons. Trend was estimated by weighted linear regression of natural log of murrelet densities on time where the weights were the inverse of the estimated variance of log-transformed density (Sokal and Rohlf, 1981). Potential autocorrelation in the time series was investigated by computing Moran's I on the residuals in the weighted regression analysis.

Results and Conclusions

There was a large change in total numbers of *Brachyramphus* murrelets observed in Glacier Bay between 1991 and 2003, declining from an estimated high of more than 75,000 birds in 1991 to about 16,000 birds in 2003 (table H2). This represents a significant change in abundance over time, as indicated by the lack of overlap in 95-percent confidence limits surrounding population estimates during the early versus late years of sampling (table H2, fig. H5). Weighted linear regression of log-transformed densities indicates a significant decline over time (F=128.5, df=1,6; p<0.0001, r^2=0.96), at a rate of -11.8 percent per year (fig. H5). All 95-percent confidence intervals on Moran's I contained zero indicating no significant serial autocorrelation among the residuals over time.

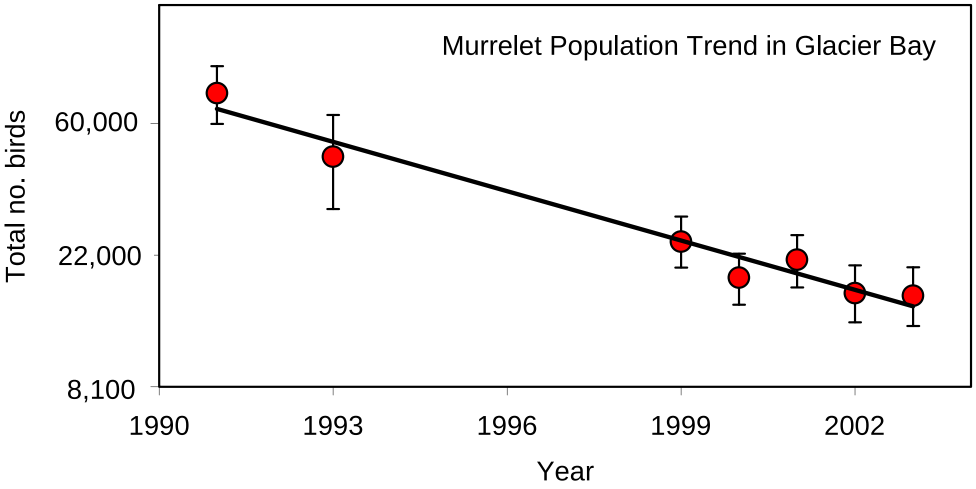


Figure H5. Population trend for *Brachyramphus* murrelets in Glacier Bay, 1991–2003. Note log scale for population size. Weighted linear regression indicates a decline of -11.8 percent per annum (p<0.0001, r^2 =0.96).

Table H2. Estimated density (birds/km²) and total number of *Brachyramphus* murrelets occupying Glacier Bay during summer with 95-percent confidence limits on the total.

Date	Density	Population estimate	95-percent confidence limits Lower	95-percent confidence limits Upper
1991	58.6	75,486	59,721	92,627
1993	36.1	46,552	31,275	63,928
1999	18.9	24,397	20,034	29,509
2000	14.4	18,550	15,120	22,254
2001	16.5	21,294	17,231	25,612
2002	12.8	16,485	13,221	20,380
2003	12.5	16,178	12,851	20,070

References Cited

Agler, B.A., Kendall, S.J., Irons, D.B., and Klosiewski, S.P., 1999, Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift: Waterbirds, v. 22, no. 1, p. 98-103.

Agler, B.A., Kendall, S.J., Seiser, P.E., and Irons, D.B., 1998, Abundance and distribution of Marbled and Kittlitz's murrelets in south central and southeast Alaska: Condor, v. 100, no. 2, p. 254-265.

Burger, A.E., Hitchcock, C.L., and Davoren, G.K., 2004, Spatial aggregations of seabirds and their prey on the continental shelf off southwest Vancouver Island: Marine Ecology Progress Series, v. 283, p. 279-292.

Conant, B., 1991, Marbled Murrelet population estimates for southeast Alaska: Anchorage, Alaska, U.S. Fish and Wildlife Service.

DeGange, A.R., 1996, Conservation assessment for the Marbled Murrelet in southeast Alaska: Portland, Oregon, U.S. Forest Service, Pacific Northwest Research Station, General Technical Report 388, 72 p.

Duncan, T., and Climo, L., 1991, Beardslee Island bird and mammal survey: Gustavus, Alaska, Glacier Bay National Park and Preserve, 14 p.

Eckert, G., 2005, Southeast Alaska synthesis of marine biology and oceanography: Juneau, University of Alaska Southeast, Report to the North Pacific Research Board.

Fauchald, P., Erikstad, K.E., and Skarsfjord, H., 2000, Scale-dependent predator-prey interactions: Hierarchical spatial distribution of seabirds and prey: Ecology, v. 81, p. 772-783.

Gould, P.J., and Forsell, D.J., 1989, Techniques for shipboard surveys of marine birds: Washington, D.C., U.S. Fish and Wildlife Service Technical Report 25, 22 p.

Huettmann, F., and Diamond, A.W., 2006, Large-scale effects on the spatial distribution of seabirds in the Northwest Atlantic: Landscape Ecology, v. 21, p. 1089-1108.

Klosiewski, S.P., and Laing, K.K., 1994, Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, State / Federal Natural Resource Damage Assessment Final Report, Bird Study 2, 88 p.

Lindell, J.R., 2005, Results of at-sea *Brachyramphus* murrelet surveys in Icy Strait and other selected areas of southeast Alaska, 1993-1999: Juneau, Alaska, U.S. Fish and Wildlife Service, Unpublished Report, 17 p.

Nelson, S.K., 1997, Marbled Murrelet (*Brachyramphus marmoratus*), *in* Poole, A., and Gill, F., eds., Birds of North America: Philadelphia, Pennsylvania, Academy of Natural Sciences and American Ornithologists' Union, p. 276.

Piatt, J.F., Conant, B., and Iverson, C.G., 1991, Comparison of aerial and boat-based surveys for Marbled Murrelets in southeast Alaska, July 23-28, 1991: Anchorage, Alaska, U.S. Fish and Wildlife Service, 14 p.

Piatt, J.F., 1990, Aggregative response of Common Murres and Atlantic Puffins to their prey: Studies in Avian Biology, v. 14, p. 36-51.

Piatt, J.F., and Naslund, N.L., 1995, Abundance, distribution, and population status of Marbled Murrelets in Alaska, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 285-294.

Romano, M.D., Arimitsu, M.L., Piatt, J.F., Agness, A.A., and Drew, G.S., 2004, At-sea density and distribution of Kittlitz's Murrelets (*Brachyramphus brevirostris*) and Marbled Murrelets (*Brachyramphus marmoratus*) in Glacier Bay, Alaska, Summer 2003: Anchorage, U.S. Geological Survey Alaska Science Center, Annual Report to U.S. National Park Service, Glacier Bay National Park and Preserve.

Sokal, R.R., and Rohlf, F.J., 1981, Biometry: New York, W.H. Freeman.

Robards, M., Drew, G.S., Piatt, J.F., Anson, J.M., Abookire, A., Bodkin, J.L., Hooge, P., and Speckman, S.G., 2003, Ecology of selected marine communities in Glacier Bay: Zooplankton, forage fish, seabirds and marine mammals: Anchorage, USGS Alaska Science Center, Final Report to USNPS, GBNPP, 156 p.

Schneider, D.C., 1990, Spatial autocorrelation in marine birds: Polar Biology, v. 8, p. 89-97.

Schneider, D., and Piatt, J.F., 1986, Scale-dependant aggregation and correlation of seabirds with fish in a coastal environment: Marine Ecology Progress Series, v. 32, p. 237-246.

Speckman, S.G., Springer, A.M., Piatt, J.F., and Thomas, D.L., 2000, Temporal variability in abundance of Marbled Murrelets at sea in southeast Alaska: Waterbirds, v. 23, no. 3, p. 364-377.

Whitworth, D.L., Nelson, S.K., Newman, S.H., van Vliet, G.B., and Smith, W.P., 2000, Foraging distances of radio-marked Marbled Murrelets from inland areas in southeast Alaska: Condor, v. 102, no. 2, p. 452-456.

Yen, O.P.W., Sydeman, W.J., and Hyrenbach, K.D., 2004, Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: Implications for trophic transfer and conservation: Journal of Marine Systems, v. 50, p. 79-99.

Zar, J.H., 1996, Biostatistical analysis: Upper Saddle River, New Jersey, Prentice Hall, ed. 3.

This page left intentionally blank.

Appendix I. Change in Abundance of *Brachyramphus* Murrelets Along the Outer Gulf of Alaska Coast, Adjacent to Malaspina Glacier

Summary of information by Michelle Kissling[1]

Summary

The U.S. Fish and Wildlife Service (USFWS) has been surveying areas of Southeast Alaska for Marbled and Kittlitz's Murrelets since 2002. Some results have reported elsewhere (e.g., Kissling, 2006). This is a synopsis of a USFWS survey of an area along the Malaspina Forelands that was previously surveyed in 1992 (Kozie, 1993). This is the only data from the outer coast of the Gulf of Alaska that can be used to assess changes in murrelet populations in this region. Results of other population surveys in the region are tabulated here (table I1), but for details on those contact Michelle Kissling.

Table I1. Marbled Murrelet population estimates by area.

[Data from M. Kissling, U.S. Fish and Wildlife Service, unpub. data, 2005]

Area	Populaton (N)			
	Estimate	Percent CV	95-percent confidence interval	
Icy Bay	199	51.39	0	399
Malaspina Forelands	5,367	38.1	1,359	9,375
Exposed North	2,720	21.57	1,570	3,870
Mouth of Lituya Bay	1,390	22.48	778	2,002
Lituya Bay	145	27.19	68	222
Exposed South	5,902	15.95	4,057	7,747
Icy Point	1,000	9.09	821	1,178
Outer Coast Bays	62	21.55	36	88

Methods

Kissling conducted broad-scale surveys to describe distribution and abundance of *Brachyramphus* murrelets in Southeast Alaska. The Icy Bay and Malaspina study areas were surveyed in 2002, and the Outer Coast study area was surveyed in 2003 and 2004 (fig. I1). Only the Malaspina survey is discussed here.

The following protocols were adopted by both Kissling (this report) and Kozie (1993). Shoreline transects ran parallel to shore and covered waters less than 200 m offshore. Along the Malaspina Forelands, boats maintained a distance of approximately 1 km from shore, roughly following the 10 fathom contour. Surveys were conducted from July 25–26, 1992 by Kozie and July 7–14, 2002 by Kissling using strip transect survey methods (Gould and Forsell, 1989) and all flying birds were counted continuously. Two observers recorded all birds 100 m either side of and ahead of the vessel. In 1992, observations were recorded on data sheets and in 2002 using a Global Positioning System (GPS)-integrated voice recording system (Program SURVEY, J. Hodges, U.S. Fish and Wildlife Service, Juneau). Information recorded included number of birds, behavior (on water, flying, foraging) and various environmental parameters (e.g., sea and ice conditions, wind speed, etc.).

The identification of murrelets in the field is often difficult. In 1992, 27–31 percent of murrelets were not identified, and Marbled Murrelets comprised 33–48 percent of those identified on replicate transects. In 2002, about 5–22 percent of birds were not identified to species on replicate transects, and about 7–18 percent of identified birds were Marbled Murrelets. With such high variability among transects and observers in the fraction of birds identified to species, and in the ratio of Marbled to Kittlitz's, the data have been lumped simply into *Brachyramphus* species.

---

[1] 3000 Vintage Blvd., Suite 240, Juneau, Alaska 99801-7100.

Results

The Malaspina survey basically consisted of running 127 km in 1-day from a point mid-way along the north coast of Yakutat Bay, around the Malaspina Forelands, and into Icy Bay (fig. I1). The survey was replicated on the second day by returning on the same track from Icy Bay to Yakutat Bay The total area surveyed was 25.4 km^2 on each trip, except on the first replicate in 2002 when a recorder malfunction resulted in loss of data from one side of the vessel (reducing transect width to 100 m). The transect still yielded data on murrelet densities, but only over a 100-m strip-width.

The average density of *Brachyramphus* murrelets declined by about one-half from 1992 to 2002 (table I2). Regression of the natural log of bird density versus date suggests (r^2=0.97, F=111.4, df=1,2, p<0.009) a rate of change equal to -5.4 percent per year.

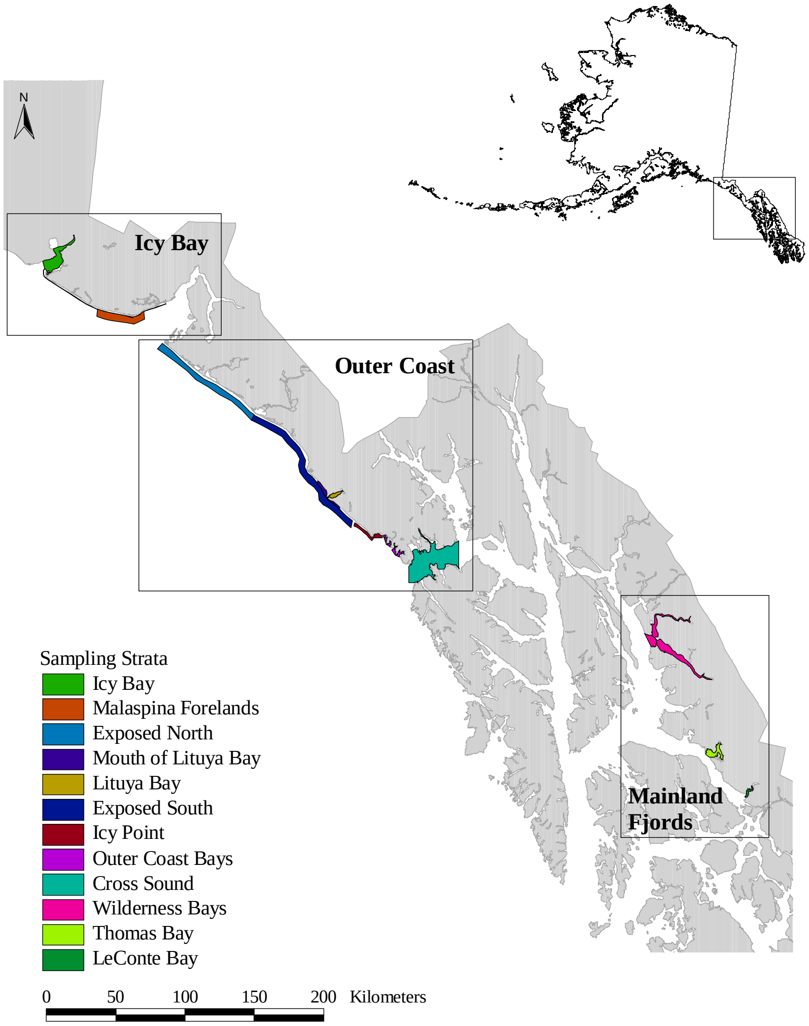


Figure I1. Study areas and 12 sampling strata delineated for estimation of *Brachyramphus* murrelet densities and populations in July 2002–04. Icy Bay and Malaspina Forelands study areas were surveyed in 2002, and the Outer Coast study area was surveyed in 2003 and 2004.

Table I2. Counts of *Brachyramphus* murrelets on the Malaspina transect in 1992 and 2002.

Year	Survey		Number of birds	Density number per square kilometer
	Replicate	Area, square kilometers		
1992	1	25.4	1,029	40.5
1992	2	25.4	1,070	42.1
2002	1	12.7	286	22.5
2002	2	25.4	631	24.8

References Cited

Gould, P.J., and Forsell, D.J., 1989, Techniques for shipboard surveys of marine birds: Washington, D.C., U.S. Fish and Wildlife Service Technical Report 25, 22 p.

Kissling, M., Kuletz, K.J., and Brockmann, S., 2006, Distribution and abundance of Kittlitz's Murrelets along the outer coast of Glacier Bay National Park and Preserve, *in* Piatt, J.F., and Gende, S.M., eds., Glacier Bay Science Symposium 4, 2004, p. 116-120.

Kozie, K., 1993, Coastal wildlife survey - Seabirds and marine mammals along the Malaspina Forelands 1992: Glenallen, Alaska, Wrangell-St. Elias National Park and Preserve, Research and Resource Management Report 92-07.

Appendix J. Population Trend of Kittlitz's and Marbled Murrelets in Prince William Sound

By Kathy Kuletz[1], Bryan Manly[1], Chris Nations[1], and David Irons[1]

[This analysis appears as an appendix in: Kuletz, K.J. 2005, Foraging behavior and productivity of a non-colonial seabird, the Marbled Murrelet (*Brachyramphus marmoratus*), relative to prey and habitat, Ph.D. Dissertation, University of Victoria, British Columbia.]

Abstract

Monitoring population trends of rare species can be difficult if the species are not distinguished in the field from closely related, abundant species. We faced this problem in Prince William Sound, Alaska for two seabirds, the Marbled Murrelet (*Brachyramphus marmoratus*) and the Kittlitz's Murrelet (*B. brevirostris*), both of which are surveyed at sea because they are non-colonial. As a group, *Brachyramphus* murrelets showed declines, but Marbled Murrelets (2004 population = 35,657 ± 7,809 birds; 95 percent CI greatly outnumbered Kittlitz's (2004 population = 778 ± 516), and murrelets were not always identified to species in the field. Using data from nine summer surveys (1972 and 1989–2004), we developed models that incorporated unidentified murrelets and predicted trends for each species. Model predictions reasonably fit field survey estimates, and substantiated observed trends of identified birds. Based on July (mid-breeding season) surveys, the Marbled Murrelet population declined at a rate of about 5 percent per year, a total of 85 percent since 1972, or 63 percent since 1989; predicted quasi-extirpation (<100 birds) is in year 2120. Kittlitz's have declined 17.7 percent per annum since 1972 (a total of 99 percent), or by 30.8 percent per year since 1989 (a total of 88 percent); predicted quasi-extirpation is year 2006, although the 2004 field estimate was about 700 birds. The decline in July estimates in both species is of concern, but the Kittlitz's is at greater risk because of its low numbers and faster rate of decline. For Kittlitz's, the decline may be exacerbated by dependence on foraging habitat that is undergoing rapid change due to glacial recession. For both species, the ability to identify species-specific trends will be important in forming policy decisions and conservation efforts.

Introduction

Identifying and interpreting trends in populations is a critical aspect of conservation and management, and the task is complicated by uncertainties in survey data (Harwood and Stokes, 2003). For rare species, detection of statistically significant trends is difficult, due to large errors in population estimates, often exacerbated by an insufficient number of years of data (Taylor and Gerrodette, 1993). Inaction due to inconclusive or compromised results hampers status designations and thus management and conservation by affecting legal and policy making decisions (Reed and Blaustein, 1997; Ralls and Taylor, 2000; Harwood and Stokes, 2003). For closely related species that are difficult to distinguish, another source of uncertainty is species identification (Hey and others, 2003). Incomplete species-specific data can result in trends of rare species being masked by trends in the more abundant species (Ludwig and others, 1993; Roberts and Hawkins, 1999; Dulvy and others, 2000). We faced these problems in attempts to determine the population status of two seabirds, the rare Kittlitz's Murrelet (*Brachyramphus brevirostris*) and the relatively abundant Marbled Murrelet (*B. marmoratus*). These closely related and phenotypically similar murrelets are sympatric in Prince William Sound, Alaska, with the Kittlitz's Murrelet found almost exclusively in fjords with tidewater glaciers (Kendall and Agler, 1998; Day and others, 2003; Kuletz and others, 2003), and the Marbled Murrelet occurring throughout coastal areas and outnumbering other seabird species in summer (Agler and others, 1998). The combined population of *Brachyramphus* murrelets was declining in Prince William Sound at least since 1989, and probably since 1972 (Lance and others, 2001). However, inconsistencies in species identification reduced confidence in interpretation of possible trends. The goal of this study was to substantiate and distinguish the trends of the two murrelet species.

Brachyramphus murrelets are small, diving, fish-eating seabirds (family Alcidae) found only in the North Pacific. Most of the world population of Kittlitz's Murrelets breed along Alaska's coastlines, but some occur off eastern Russia (Day and others, 1999). In 2004, Kittlitz's Murrelet became a candidate for listing under the Endangered Species Act (U.S. Fish and Wildlife Service, 2004). Concerns about possible declines in the Kittlitz's Murrelet spurred us to examine the best available data on their population trends, to insure that timely management actions could be implemented for this uniquely Alaskan species. Marbled Murrelets breed from the Aleutian Archipelago in Alaska to central California (Nelson, 1997) and are listed as threatened from British Columbia (Burger, 2002 to California (McShane and others, 2004). Most of the world population of Marbled Murrelets breed in Alaska (McShane and others, 2004), and Prince William Sound has a

---

[1] U.S. Fish and Wildlife Service.

relatively large population (Agler and others, 1998). Recently the U.S. Fish and Wildlife Service (USFWS) has proposed to eliminate the ‘Distinct Population Segment’ status of Marbled Murrelets in California, Oregon, and Washington (News Release, USFWS Pacific Regional Office, Portland, OR., September 1, 2004), which by inclusion with the Alaska population could lead to delisting. Thus, knowing the current status and trends of Marbled Murrelets in Alaska is important for determining the future legal status of this species. Because Prince William Sound is one of the few regions in Alaska with long-term data, it provides a valuable record of trends in the northern portion of the Marbled Murrelet’s range.

To evaluate the status of both murrelet species and assist future management decisions, we used at-sea survey data for Prince William Sound, which has data for the longest time span (9 years within the period, 1972–2004) for any region in Alaska. This level of coverage was unique for marine birds at sea in Alaska, but trends analysis was complicated by wide confidence intervals in the estimates for Kittlitz’s Murrelets, variable proportions of unidentified murrelets among years, and unusual spikes in the estimates in 2 years. To address these issues, we used the Prince William Sound population estimates in a modeling technique that incorporated unidentified birds, to estimate the size and trend of populations of each species.

Methods

Study Site— Our study site was Prince William Sound, a ca. 10,000 km^2 protected body of water in the northern Gulf of Alaska (Gulf of Alaska). Most of the shoreline is highly convoluted and includes deep fjords, shallow bays, deltas, large and small islands. There are several large icefields with more than 20 tidewater glaciers entering coastal waters (Molnia, 2001). The high freshwater input from rain and snow or glacial melt influences the strong cyclonic circulation that generally runs east to west (Niebauer and others, 1994). Surface waters from the Gulf of Alaska pulse into Prince William Sound primarily during winter months, via the Alaska Coastal Current, and in summer Prince William Sound waters become warmer and stratified (Niebauer and others, 1994).

Data Collection.— Between 1989 and 2004, surveys were conducted in 8 years (1989–91; 1993; 1996; 1998; 2000; 2004) during July, which is mid-breeding season (chick-rearing) for *Brachyramphus* murrelets in Prince William Sound (Kuletz and Kendall, 1998; Day and others, 1999). The USFWS surveys were designed for collecting data on all marine birds and mammals using randomly selected strip transects, (n = 325–350 per year, including 187–212 shoreline and 138 offshore) of varying length and 200 m wide, including shoreline, coastal pelagic, and pelagic. Crews on three 7.7 m fiberglass boats operated daily and simultaneously to complete the survey over a 3-week period. The USFWS conducted similar surveys, with different transects and slightly different design, in July 1972 (reanalyzed in Klosiewski and Laing, 1994). The 1972 survey used vessels and transect widths similar to the later surveys, but the randomly selected transects of the 1972 survey used a different grid system and included a ‘bay’ stratum along with shoreline and pelagic strata.

For surveys since 1989, 187 shoreline transects were randomly selected in 1989, with an additional 25 transects randomly selected in 1990. Shoreline transects were defined by geographical features, and ranged from 1 to 30 km and averaged 5.6 km in length (fig. J1; details in Agler and others, 1998; Irons and others, 2000; Lance and others, 2001); these were surveyed by piloting the boat parallel to and 100 m from shore. For offshore areas, a grid with 5-minute latitude-longitude blocks was overlaid on a nautical chart, and 69 blocks were randomly selected. Blocks that intersected the shoreline were categorized as ‘coastal-pelagic’ (n = 44), and those that did not touch land were ‘pelagic’ (n = 25). Within each block, two parallel lines running north-south were surveyed, for a total of 138 pelagic transects. For each block, bird density (birds/km^2) was averaged from the two lines, and this density was assumed to apply to the entire block, with the block density used to extrapolate to total area within its strata. Except for the lower number of shoreline transects in 1989, the same transects in all strata were surveyed every year. The surveyed area amounted to 4.6 percent of the surface area of Prince William Sound waters (Agler and others, 1998).

All birds and marine mammals were recorded continuously within 100 m either side of and 100 m ahead of the boat, with two observers and a driver. Observers identified all birds to the highest possible taxon, using 10× binoculars for species identification where necessary. Because the two murrelet species were difficult to distinguish at sea, a portion of them were recorded as ‘unidentified *Brachyramphus*’. More problematic, among years there was unequal emphasis on distinguishing between these two species, and the proportion of unidentified murrelets ranged from 2 to 89 percent.

Data Analysis.—The study design used for these surveys was well-suited to abundant and widely dispersed species such as Marbled Murrelets, but not for the rare and patchily-distributed Kittlitz’s Murrelet. For the latter species, population estimates had wide confidence intervals. Analysis of long-term trends also was complicated by the fact that the population estimates in 1972 and 1993 for both murrelet species were considerably higher than in other years. In summary, the analysis of trend data was complicated by large error in the estimates for the Kittlitz’s Murrelet, variable proportions of unidentified murrelets, and large population estimates in 1972 and 1993. Consequently, we analyzed three subsets of the data from Prince William Sound in July (table J1): (1) including all years; (2) excluding 1972; and, (3) excluding both 1972 and 1993.

The original population estimates (hereafter, ‘field estimates’) and variances were calculated using a ratio estimator (Cochran, 1977) on the densities for each stratum (shoreline, coastal-pelagic, and pelagic; see Stephensen and

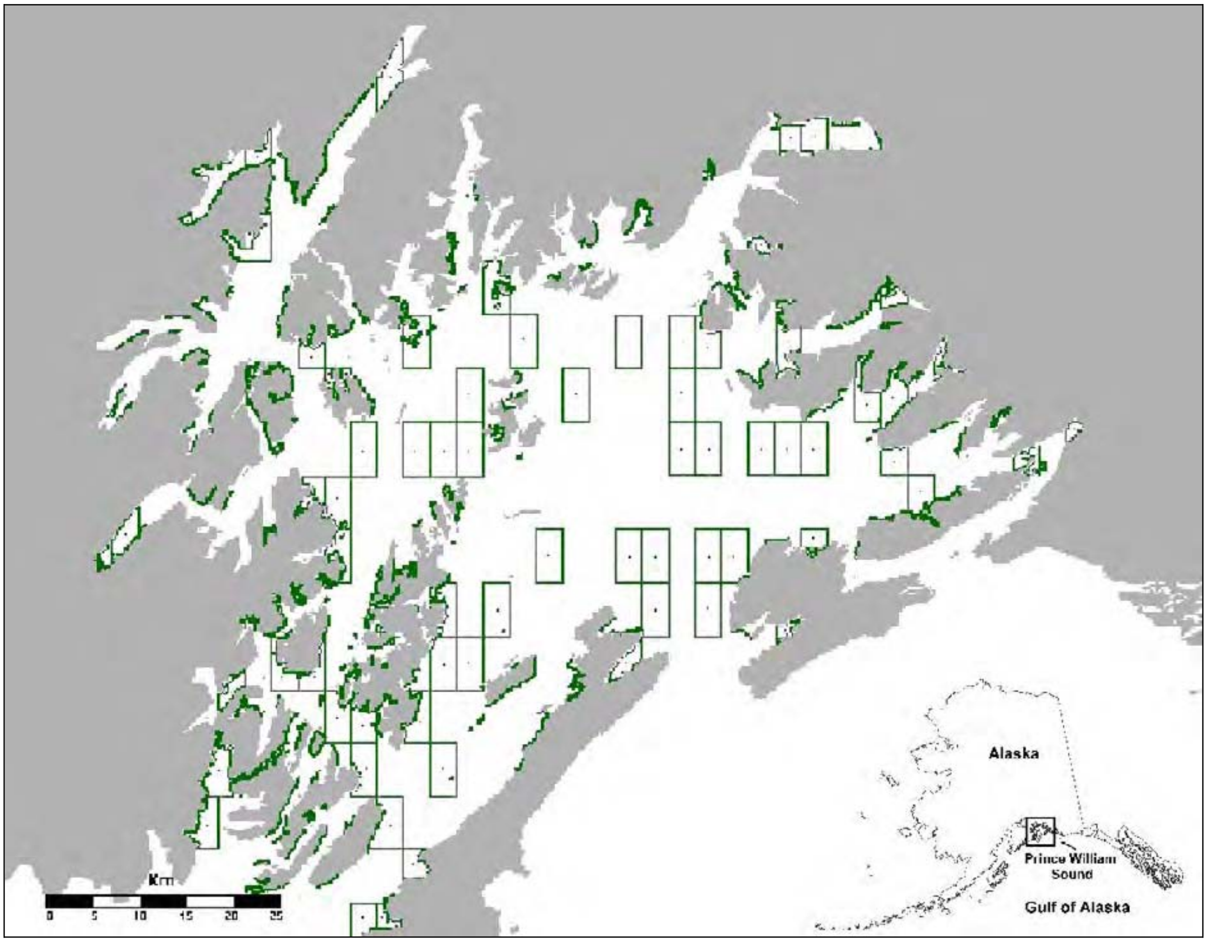


Figure J1. Prince William Sound, Alaska, showing locations of the shoreline transects (in heavy green) and blocks used for pelagic transects for marine surveys from 1989–2004. Two parallel transects running north-south were averaged for every pelagic block to obtain bird density.

others, 2001 for details). The total field estimates were derived from the summed estimates and variances of each stratum. Data used for the analyses reported here were field estimates of population size and their standard errors (table J1). Standard errors (SE) were obtained from the 95-percent confidence intervals (CI) originally calculated from the survey data, using SE = CI/1.96. The rate of change for population estimates of identified birds was calculated with linear regression analyses of log-transformed values. We then compared rates of change over time between the two species with a homogeneity of slopes test (Freud and Littell, 1981) using linear models.

Using the field estimates and variances for Marbled, Kittlitz's, and unidentified *Brachyramphus* murrelets, we developed a population model that accounts for the unidentified birds, and provides 'model

Table J1. Original field population estimates and standard errors (SE) for *Brachyramphus* murrelets in July in Prince William Sound.

Year	Kittlitz's Murrelets		Marbled Murrelets		Unidentified birds	
	Estimate	SE	Estimate	SE	Estimate	SE
1972	63,229	40,879	236,633	26,391	4,570	4,018
1989	6,436	1,608	59,284	6,033	41,634	4,194
1990	5,231	4,315	39,486	5,095	36,624	4,036
1991	1,184	572	42,477	4,669	62,816	7,149
1993	2,710	685	14,177	2,295	142,546	21,365
1996	1,280	696	63,455	8,185	17,429	3,056
1998	279	98	49,879	4,818	3,036	1,089
2000	1,033	683	52,377	7,383	1,077	519
2004	778	516	35,658	7,809	840	370

predictions' of population sizes. The model assumes that the probability of being identified is the same for both species but may differ from year to year. Identifications are assumed implicitly to be correct—e.g., a bird identified as a Kittlitz's Murrelet is not a Marbled Murrelet. The model also assumes that Kittlitz's and Marbled Murrelets have independent but constant trends over time. Let $N_{K,0}$ and $N_{M,0}$ represent the unknown numbers of Kittlitz's and Marbled, respectively, in the starting year, t_0. The symbols K_t, M_t, and U_t are the field estimates of Kittlitz's, Marbled, and unidentified birds, respectively, in year t. Let θ_K and θ_K represent the annual population growth rate for Kittlitz's and Marbled, respectively, let γ_t be the probability that a bird will be identified in year t, and let E_{K_t}, E_{M_t}, and E_{U_t} represent error terms (including discrepancies between predictions of the fitted model and the observations, but also assuming measurement error in the field). The model is then

$$\begin{aligned} K_t &= N_{K,0}\theta_K^{t-t_0}\gamma_t + E_{K_t} \\ M_t &= N_{M,0}\theta_K^{t-t_0}\gamma_t + E_{M_t} \\ &\text{and} \\ U_t &= (N_{K,0}\theta_K^{t-t_0} + N_{M,0}\theta_K^{t-t_0})(1-\gamma_t) + E_{U_t} \end{aligned} \quad , \qquad (1)$$

Note that model predictions for K_t, M_t, and U_t are predicted numbers seen in surveys, not predicted population sizes. To make the distinction clear, we henceforth refer to K_t, M_t, and U_t, whether from field observations or model predictions, using the term survey size. We estimated the unknown parameters (N_K, N_M, θ_K, θ_K, γ_t) in the model above through a weighted least-squares nonlinear regression. Least squares chose the parameter values that minimized the criterion Q,

$$Q = \sum_i \sum_t \frac{\left(Y_{i,t} - \hat{Y}_{i,t}\right)^2}{V_{i,t}} \quad , \qquad (2)$$

where

$Y_{i,t}$ was the observed survey size for the i^{th} group of birds at time (i.e., either K_t, M_t, or U_t),

$\hat{Y}_{i,t}$ was the corresponding predicted value, and

$V_{i,t}$ was the corresponding variance (the standard error squared from table J2.

For the nonlinear minimization, we used "reasonable" initial guesses based on available information. Initial values for N_K and N_M were taken from field estimates in year t_0 (table J2). In all analyses, initial values were $\theta_K = \theta_M = 1$, representing stable populations, and $\gamma_t = (K_t + M_t)/(K_t + M_t + U_t)$, the observed proportions of identified birds.

We obtained variance for our estimators by simulation. We assumed that field observations for all three groups of birds (Kittlitz's, Marbled, and unidentified) were log normally distributed with means and variances determined by the field estimates (table J2). Random survey sizes were generated 5,000 times, based on this assumption in place of the field estimates, and parameters were re-estimated from the simulated data sets using nonlinear regression. Empirical variances were then estimated from the simulated parameter estimates using

$$V\left(\hat{\phi}\right) = \frac{\sum_{i=1}^{n}\left(\hat{\phi}_i - \bar{\hat{\phi}}\right)^2}{n-1} \quad , \qquad (3)$$

where

$n_{i,t}$ was the number of successful optimizations,

$\bar{\hat{\phi}}_i$ was the i^{th} parameter estimate, and

$\bar{\hat{\phi}}$ was the mean of the n estimates.

While each simulation entailed 5,000 iterations, the nonlinear optimization routine failed to converge occasionally (generally <5 percent of the time).

Projections of population size (rather than survey size) were generated using a simple exponential growth model implied by Eq. 1. Projected numbers of Kittlitz's Murrelet, $N_{K,t}$, and Marbled Murrelet, $N_{M,t}$ were calculated as

$$\begin{aligned} N_{K,t} &= \hat{N}_{K,0}\hat{\theta}_K^{t-t_0} \\ &\text{and} \\ N_{M,t} &= \hat{N}_{M,0}\hat{\theta}_M^{t-t_0} \end{aligned} \quad , \qquad (4)$$

where all parameter estimates on the right hand side of the equations were obtained from the fitted nonlinear regression. We also modeled the predicted population size to quasi-extinction (<100 birds) for total *Brachyramphus* murrelets. All analyses were conducted in Matlab 6.5.

Table J2. Model parameter estimates from July survey data.

Parameter	All years[1]		Exclude 1972[2]		Exclude 1972 and 1993[3]	
	Mean	SE	Mean	SE	Mean	SE
$N_{K,0}$	70,119	21,403	9,402	2,294	9,008	2,428
$N_{M,0}$	232,710	9,447	94,981	4,716	93,517	4,779
θ_K	0.8226	0.0098	0.6908	0.0351	0.6825	0.0561
θ_M	0.9487	0.0024	0.9468	0.0074	0.9467	0.0078
γ_{1972}	0.9853	0.0129	–	–	–	–
γ_{1989}	0.5944	0.0361	0.6105	0.0334	0.6091	0.0340
γ_{1990}	0.5415	0.0344	0.5568	0.0345	0.5546	0.0343
γ_{1991}	0.4331	0.0443	0.4171	0.0451	0.4212	0.0462
γ_{1993}	0.1776	0.0303	0.1834	0.0310	–	–
γ_{1996}	0.7673	0.0424	0.7650	0.0443	0.7641	0.0437
γ_{1998}	0.9425	0.0176	0.9430	0.0185	0.9438	0.0178
γ_{2000}	0.9798	0.0098	0.9795	0.0098	0.9792	0.0099
γ_{2004}	0.9803	0.0086	0.9797	0.0089	0.9793	0.0089

[1] Optimization successful in 4,790 of 5,000 iterations (95.8 percent).

[2] Optimization successful in 5,000 of 5,000 iterations (100 percent).

[3] Optimization successful in 4,967 of 5,000 iterations (99.3 percent).

Results

Population Estimates and Trends

Surveys.—Between 1972 and 2004 the field survey population estimates for identified birds (table J2) showed a decline of 19.9 percent per year for Kittlitz's murrelet and 2.3 percent for Marbled Murrelets. The slope for Kittlitz's population estimates was significant ($P = 0.04$) while that for Marbled Murrelets was not ($P = 0.69$), with the latter influenced by large numbers of unidentified birds in some years (table J2). The decline of all *Brachyramphus* murrelets, however, was highly significant ($r^2 = 0.85$, $F = 40.7$, $p < 0.001$) with long-term rate of -6.3 percent per year (and slightly higher rate of -6.9 percent per year when the 1972 data are excluded). The rate of decline between species was significantly different (Homogeneity of slopes test; F1,8 = 6.2, $P = 0.03$). In July, Kittlitz's Murrelets were primarily found in the upper fjords, and in 2004, their distribution was much more restricted than in 1989, with most birds found in the northwest area of Prince William Sound (fig. J2*A*). Marbled Murrelets were found throughout nearshore areas in all years (fig. J2*B*). Although the trend for *Brachyramphus* murrelets largely reflects that of Marbled Murrelet, owing to their much greater abundance, we developed models to assign unidentified birds to species and develop better assessments of trends for Kittlitz's.

Model estimates.—The parameter estimates show that both Marbled and Kittlitz's Murrelets are declining ($\theta < 1.0$; table J2). The estimated rate of decline is greater for Kittlitz's than for Marbled Murrelets, and θ_M is larger than θ_K in all scenarios (with 1972 or 1993, or without) even considering the estimated variances in those parameters (table J1). Using all July data from Prince William Sound (table J2), the estimate of θ_K is 0.8226 (a decline of 17.74 percent per year). Excluding data from 1972 or both 1972 and 1993 results in even lower estimates of θ_K, 0.6908 and 0.6825, respectively (declines of 30.82 and 31.75 percent per year). The estimates of θ_M and γ_t (for those years in common) are strikingly similar in all three cases (θ_M is approximately 0.94 in each case). The model estimates indicate a rate of decline of about 5 percent per annum, with a total 85 percent decline since 1972 or 63 percent decline since 1989. The parameter estimates for both Kittlitz's ($N_{K,0}$) and Marbled Murrelets ($N_{M,0}$) differ substantially, depending on the starting year (note that 1972 had much higher field estimates than 1989; table J2).

Comparison of model and field estimates.—In most cases, the models appear to fit the field estimates reasonably well, although Kittlitz's tended to show more divergence between model and field estimates than did Marbled or unidentified murrelets (figs. J3, J4). Model predictions show a pronounced decline in numbers of Kittlitz's Murrelets irrespective of whether data from 1972 are included (fig. J3*A*) or not (fig. J4*A*). Pattern in predicted numbers of Marbled Murrelets is less clear particularly when data from 1972 are excluded (figs. J3*B*, J4*B*). The sharp decline in unidentified murrelets after 1993 (figs. J3*C*, J4*C*) reflects both greater success in species identification and decline in total *Brachyramphus* murrelets (fig. J5). Model predictions of survey sizes for Kittlitz's change when data from problematic years (either 1972 alone, or both 1972 and 1993) are excluded (figs. J3*A*, J4*A*). Omitting the problematic years, in both scenarios, led to smaller residuals (differences between field estimates and model predictions) in 1989 and 1990, but larger residuals in 2000 and 2004. However, whether only 1972 or both 1972 and 1993 (figure not shown) are excluded makes little difference in predicted survey size for the years in common. In contrast to the situation with Kittlitz's, results for Marbled Murrelets and unidentified birds (most of which would have been Marbled Murrelets) are little affected by exclusion of the 1972 data.

Projected trends.—Parameter estimates from the fitted model were used to project population sizes (table J3) and trends of Kittlitz's and Marbled Murrelets (fig. J6). Assuming Kittlitz's had an initial (1972) population of $N_{K,0} = 70{,}119$ (table J2, including all years), the model estimate of θ_K leads to a predicted population of 294 in 2000, and less than 100 (treated as a quasi-extinction threshold) by 2006. Starting with the 1989 model estimate of 9,008 and $\theta_K = 0.6825$ (table J2, excluding 1972 and 1993) yields a predicted population of only 149 in 2000. Within one year, i.e., by 2001, the predicted population is less than 100, thus, the latter set of estimates leads to a much more rapid decline (fig. J6).

The projections for Marbled Murrelets are very similar whether or not model estimates include 1972 and 1993 July data. Using data from all years, where the initial population is 232,710 and $\theta_M = 0.9487$ (table J2), the projected population in 2000 is 53,105. Because of the modest reduction and larger initial population, the predicted population does not decline below 100 until the year 2120.

Table J3. Population projections for murrelets in Prince William Sound in July, with estimates based on data from all years (table 1), excluding 1972, and excluding 1972 and 1993. The projections incorporated unidentified *Brachyramphus* murrelets (see section, "Methods").

Year	Kittlitz's Murrelets			Marbled Murrelets		
	All years	Omit 1972	Omit 1972 and 1993	All years	Omit 1973	Omit 1972 and 1993
1972	63,209			236,598		
1989	2,425	9,269	8,843	95,510	95,210	93,669
1990	2,002	6,420	6,100	90,547	90,112	88,667
1991	1,653	4,446	4,209	85,842	85,288	83,932
1993	1,126	2,133	2,003	77,153	76,400	75,207
1996	633	709	658	65,740	64,774	63,791
1998	432	340	313	59,086	58,024	57,159
2000	294	163	149	53,105	51,977	51,218
2004	137	38	34	42,898	41,709	41,123

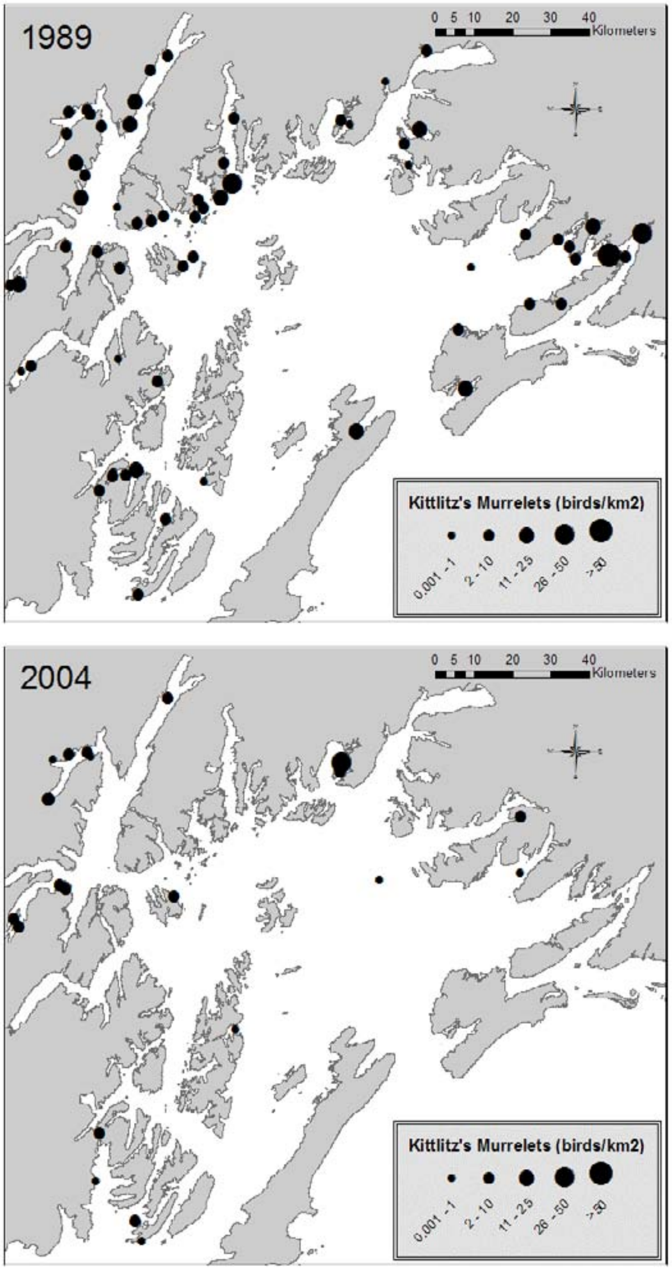


Figure J2A. Distribution of Kittlitz's Murrelets in Prince William Sound, Alaska, in July 1989 (top) and 2004 (bottom).

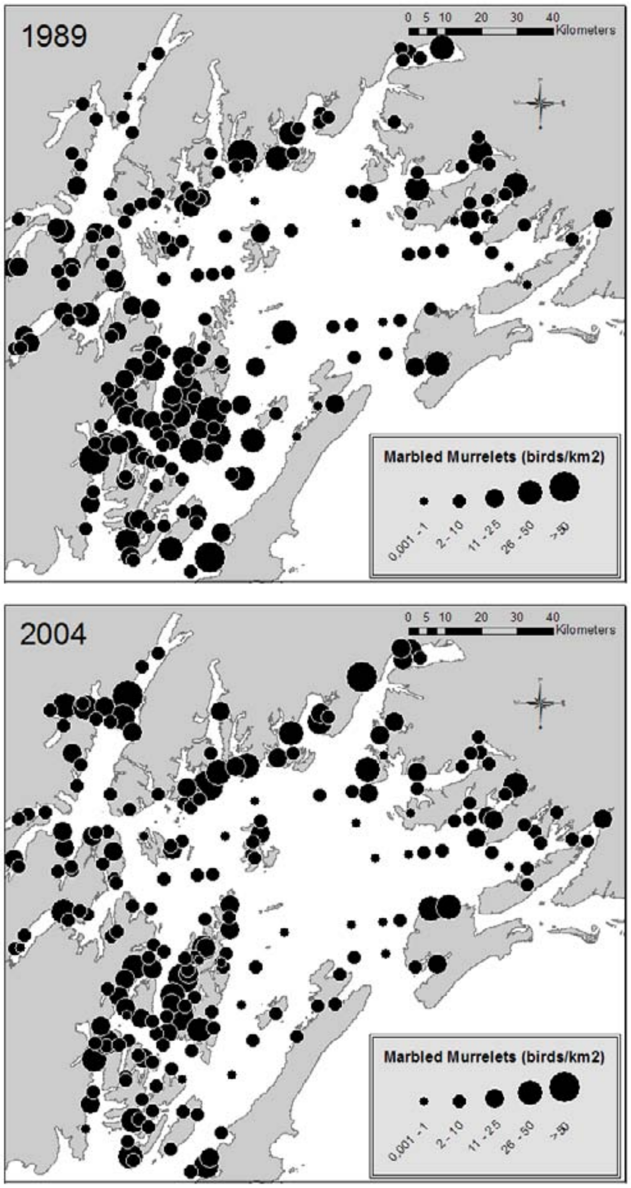


Figure J2B. Distribution of Marbled Murrelets in Prince William Sound, Alaska, in July 1989 (top) and 2004 (bottom).

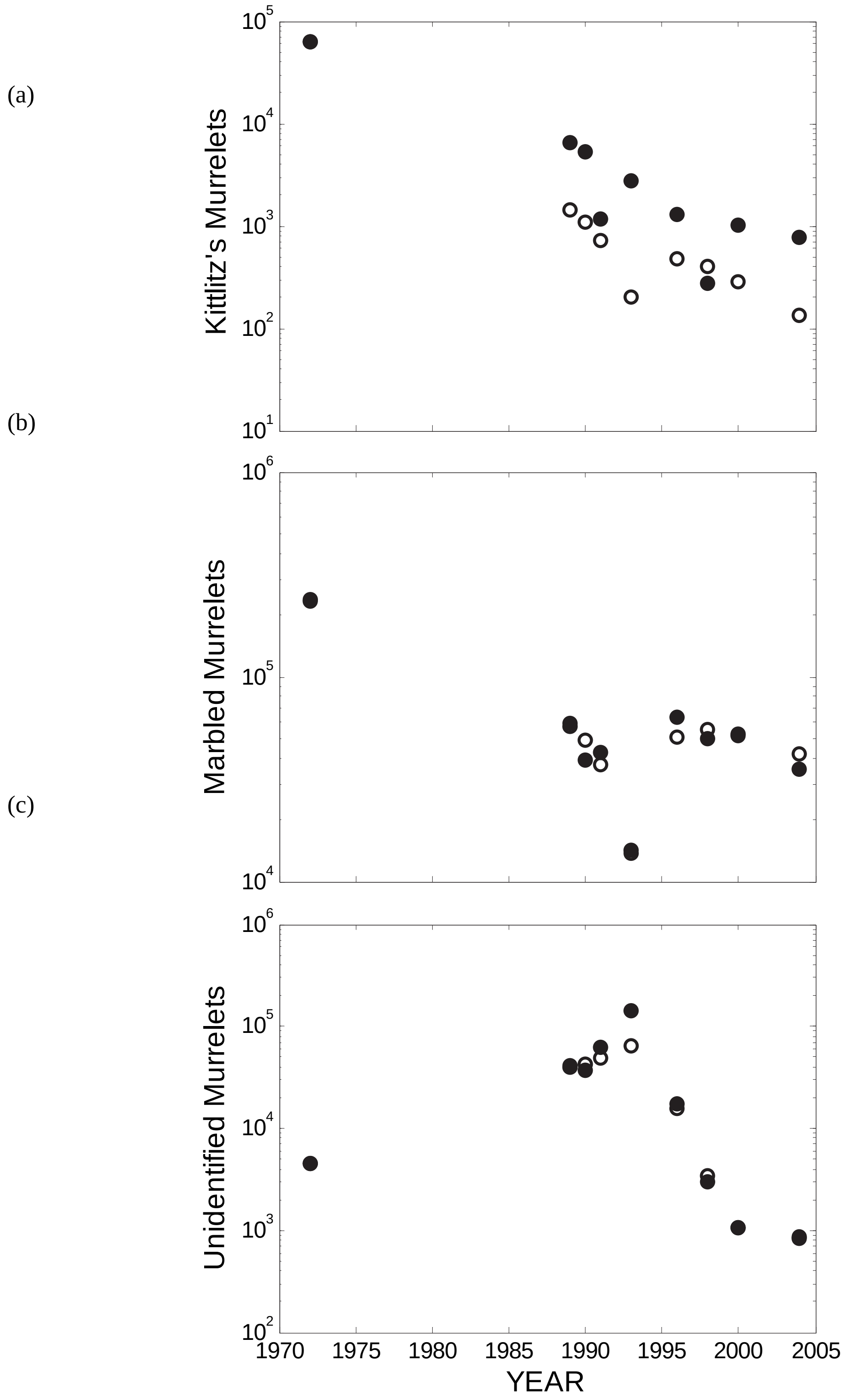


Figure J3. Estimated and predicted July survey sizes, including all years.

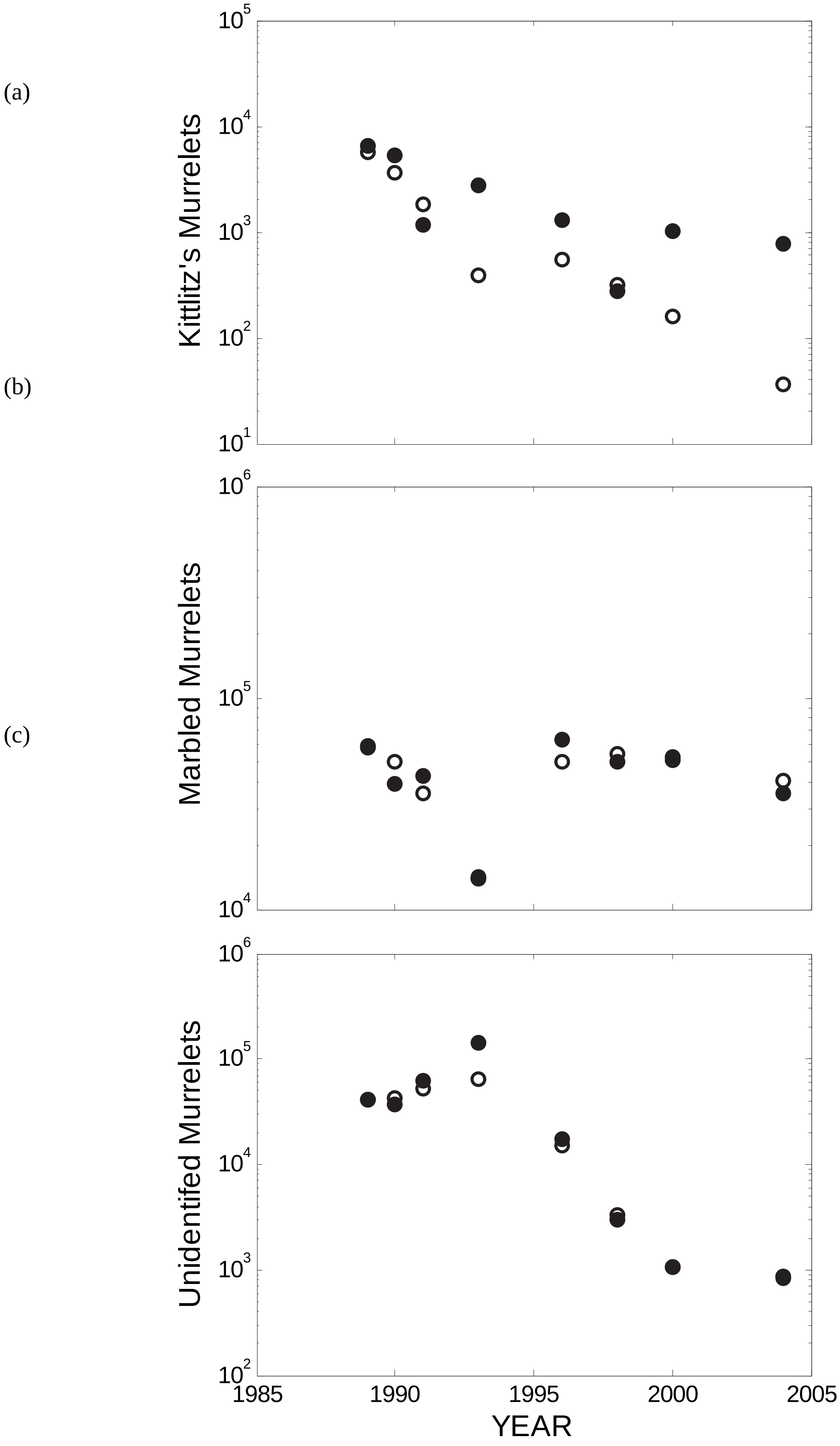


Figure J4. Estimated and predicted July survey sizes, excluding 1972.

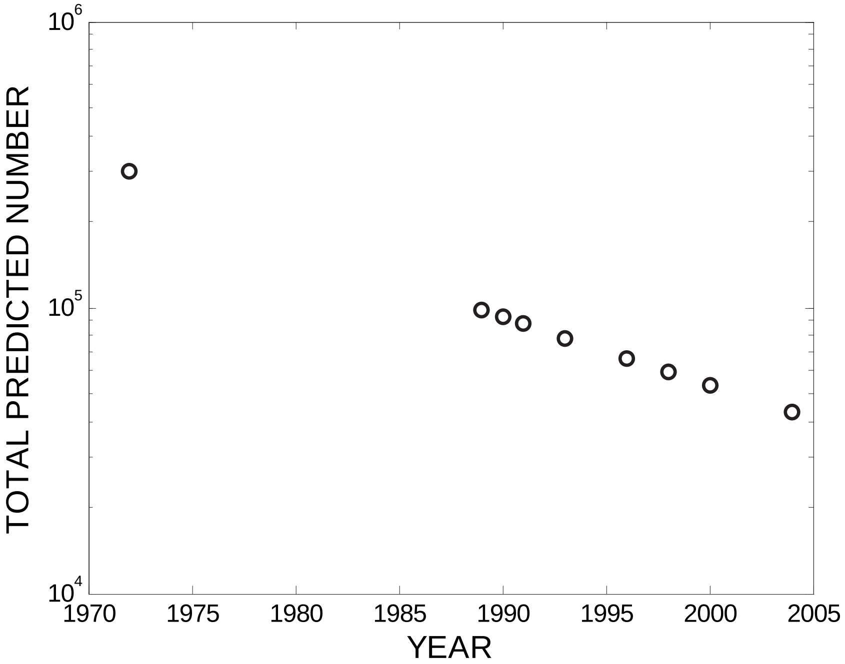


Figure J5. Total predicted survey size for July survey, including all years.

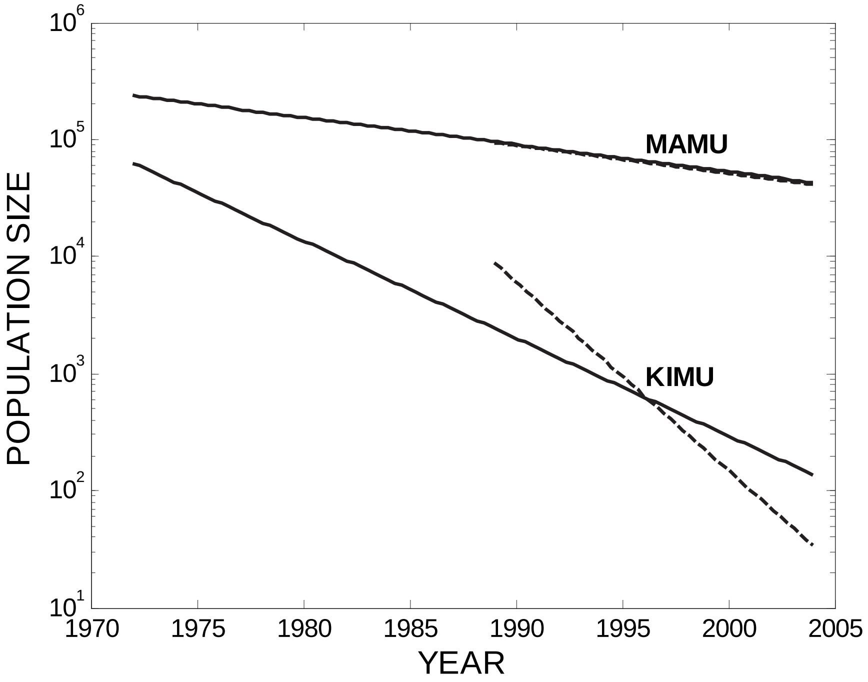


Figure J6. Population projections (eq. 4) based on model estimates of initial numbers and growth rates.

Discussion

Both the original population field estimates and the model estimates indicate declining populations of total *Brachyramphus* murrelets in Prince William Sound, and a more drastic decline in the Kittlitz's Murrelet than the Marbled Murrelet. Of course, any prediction of extirpation or quasi-extinction must be qualified by the possibly unrealistic assumption of a constant rate of change in population size, and by the uncertainty in the model estimates of population growth rate. This is evident in the model estimates for Kittlitz's, which predicted less than 100 birds by 2001 (based on estimated growth rate from data since 1989) or by 2006 (using estimated growth rate from data since 1972), whereas the actual field estimates were about 1,000 birds in 2000 and about 700 birds in 2004 (table J1). Nonetheless, the rate of decline for field estimates of identified birds indicates that the general conclusions of the model are consistent with trends observed for identified birds. The model estimates were much closer to field estimates for Marbled Murrelets (e.g., the model predicted about 53,000 birds in 2000, and the field estimate for that year was about 52,000), which at the current rate of decline indicate extirpation of Marbled Murrelets in about 100 years. The inclusion of the 1972 data did not affect the predicted trends of Marbled Murrelets, and actually reduced the estimated decline of Kittlitz's Murrelets when included. Although the 1972 field estimates were obtained with a different set of transects, we included them because they were a valid sampling method. They suggest that declines in both species began at least between 1972 and 1989, although for Kittlitz's, the rate of decline may have accelerated in the last 15 years.

The decline of two closely related species suggests a regional and long-term alteration in their environment may be responsible. For Marbled Murrelets, loss of old-growth forests where they nest has been implicated in murrelet declines farther south (Burger, 2002; McShane and others 2004). In Prince William Sound, roughly 10,000 acres of forest have been harvested since the 1940s, which is approximately 5 percent of the total forested acreage today, or between 5–10 percent of 'harvestable' timber (of commercial quality in harvestable areas) (U.S. Forest Service, Chugach National Forest, unpub. data, 2005). Thus, although timber harvests could have impacted Marbled Murrelets in Prince William Sound, the loss of potential nesting habitat there has been low, relative to the 80 percent loss of nesting habitat from British Columbia to California (Burger, 2002; McShane and others, 2004). Kittlitz's Murrelets nest in remote alpine areas (Day and others, 1999) with little human impact, and alteration of nesting habitat is not documented. The Prince William Sound declines in *Brachyramphus* murrelets likely are primarily related to changes in the marine environment, either in their breeding or wintering grounds.

Both murrelet species face similar documented threats at sea. First, they are susceptible to mortality in gillnet fisheries (Carter and others, 1995; Day and others, 1999), and a 1990–91 study in Prince William Sound estimated that between 450 and 1,470 murrelets were killed in drift gillnets per year (extracted from data in Wynne and others, 1991, 1992). The proportion of Kittlitz's killed in nets was higher than for Marbled Murrelets, relative to their abundance in Prince William Sound, suggesting greater susceptibility to or overlap with Prince William Sound gillnet fisheries (Day and others, 1999). Second, oil spills were and continue to be a threat in Prince William Sound. In 1989, the largest spill in North America, the *Exxon Valdez* oil spill, caused direct mortality of an estimated minimum of 8,400 *Brachyramphus* murrelets (Kuletz, 1996). Although most were likely Marbled Murrelets (Carter and Kuletz, 1995), Kittlitz's lost a greater proportion of its population in the spill zone (Day and others, 1999). Small spills occur from tour and fishing vessel accidents (Kuletz, 2001; U.S. Fish and Wildlife Service, 2004), primarily during the summer, when murrelets occupy inshore waters. Third, since the 1980s tourism has increased in Prince William Sound (Murphy and others, 2004), and related vessel traffic is heaviest in the fjords with tidewater glaciers, where Kittlitz's forage (Day and others, 2003, Kuletz and others, 2003). Finally, in the Gulf of Alaska, prey species composition and abundance has changed since the 1970s (Piatt and Anderson, 1996; Anderson and Piatt, 1999), and in Prince William Sound these changes appear to correspond to population declines in piscivorous birds in particular (Agler and others, 1999). All these factors could have impacted the survival or productivity of murrelets in Prince William Sound. In addition, two large scale anthropogenic factors of unknown impact include fishery impacts to the ecosystem (Pearson and others, 1999) and possible long-term damage from the *Exxon Valdez* Oil Spill (Peterson and others, 2003).

Differences Between Species

Population declines of the magnitude we show for murrelets in Prince William Sound would be a concern for any long-lived species. *Brachyramphus* murrelets exhibit life-history traits that make them sensitive to loss of adults and adversity (Stearns, 1992; Croxall and Rothery, 1995). As with many seabirds, they are long-lived, with an estimated lifespan of 10–11 years (Burger, 2002; McShane and others, 2004). They have delayed breeding, with age at first breeding estimated to be 2–3 years (Burger, 2002; Cam and others, 2003) and low fecundity (1 egg/year). The declines were not equal for these two species, however, and the proportion of Kittlitz's Murrelet in the field counts of *Brachyramphus* murrelets went from 21 percent in 1972 to less than 2 percent since 1996. The faster trajectory of Kittlitz's toward extirpation suggests greater sensitivity to the same, or additional, environmental pressures. The different rates of decline for these two species could be a result of different dietary and habitat needs, and warrant further investigation.

Changes in food availability have often been linked to changes in seabird populations (review in Croxall and Rothery, 1995). Both murrelet species are generalist feeders, consuming small, planktivorous fish in addition to invertebrates, but Kittlitz's Murrelets appear to take a larger portion of macro-zooplankton (Nelson, 1997; Day and others, 1999). There is evidence that warming trends in northern waters affects birds that feed on macro-zooplankton more than primarily piscivorous birds, because these plankton often require cooler water (Kitaysky and Golubova, 2000; Crick, 2004). Since the 1970s, Prince William Sound sea surface temperatures (SST) generally have increased (National Center for Atmospheric Research, data from http://www.ncar.ucar.edu).

Kittlitz's Murrelets also are more specialized than Marbled Murrelets in their selection of foraging habitat (Day and others, 2003). In Prince William Sound, Kittlitz's are closely associated with glacially influenced, turbid waters in the upper fjords (Day and others, 2003, Kuletz and others, 2003), as was evident in our surveys (fig. J2). Kittlitz's also may be impacted by changes in these habitats arising from glacial recession, as suggested by their present day concentration in the few remaining fjords with stable or advancing glaciers (Kuletz and others, 2003). Across all taxa, species with more northerly distribution, and those more specialized, are experiencing greater declines in response to climate changes (Root and others, 2003, Julliard and others, 2004). Our results are consistent with this scenario, since Kittlitz's are both more northerly in distribution and more specialized in foraging habitat than Marbled Murrelets.

The causes of declines in Marbled Murrelets in Prince William Sound could include several factors already mentioned (timber harvest, oil spills, gillnet mortality) or extended periods of low recruitment to the population due to reproductive failure. However, unlike populations in California (Peery and others, 2004), there was no evidence of the latter. In Prince William Sound, juvenile Marbled Murrelet densities have been relatively high compared to populations farther south (Kuletz and Kendall, 1998), and although juvenile densities declined from 1995 to 1999, the juvenile:adult ratios did not decline significantly (Chapter 4). This suggests that loss or emigration of adults is the main factor in the decline of the Prince William Sound population.

Notably, in Prince William Sound, the decline in the murrelet population parallels the 88 percent decline in stocks of Pacific herring (*Clupea pallasi*) between 1989 and 2000 (Thomas and Thorne, 2003). The Prince William Sound herring crash could have been a consequence of the 1989 oil spill, disease, over-harvest in the early 1990s, environmental conditions, or a combination of those factors (Pearson and others, 1999; Brown and others, 1996; Petersen and others, 2003; Thomas and Thorne, 2003), but the net effect on murrelets was drastic reduction of an important prey base. Juvenile herring are a key prey for Marbled Murrelets in Prince William Sound, both for adults (which eat age classes 0 and 1+ herring; Ostrand and others, 2004; Chapter 2) and as chick food (which require age class 1+; Chapter 2). Although 'forage fish' are protected from commercial fisheries in Alaska (Witherell and others, 2000), abundance of juveniles of commercial species, such as herring, could be indirectly impacted (Pikitch and others, 2004).

The trends in *Brachyramphus* murrelets was complicated by the unusual spike in their numbers in 1993. Although our surveys covered a large geographic area, the extent of movement between Prince William Sound and the Gulf of Alaska by murrelets is unknown, and it is possible that large-scale movements result in fluctuations in the size of the population within Prince William Sound. The unusually high numbers of murrelets present in July 1993 coincided with a year of anomalously warm waters in the Gulf of Alaska that year, while Prince William Sound remained relatively cool (Piatt and Van Pelt, 1997, Pearson and others, 1999). Marbled Murrelets appear to alter their distribution at sea and their inland breeding activity in response to oceanographic conditions (Becker and Beissinger, 2003; Burger, 2000). In California, Marbled Murrelets foraged farther from nesting areas in a year with warmer SST, and they selected areas with cooler SST in a year when prey abundance was low (Becker and Beissinger, 2003). Together with our results, these studies highlight the necessity of maintaining long-term monitoring programs. Managers must also acknowledge the potential for large-scale movements when tracking murrelet population trends.

Management Implications

Marbled Murrelets.—The size of the Alaska population of Marbled Murrelets relative to populations farther south (McShane and others, 2004) might lead to the conclusion that the meta-population is healthy. However, the published Alaska population estimates were based on surveys conducted from 1993 to 1996 (Agler and others, 1998), and given the rapid changes evident in Prince William Sound, those estimates may not represent current populations in Alaska. In addition to Prince William Sound, recent declines in *Brachyramphus* murrelets have been documented at Glacier Bay in Southeast Alaska (Robards and others, 2003), the Malaspina Forelands near Yakutat (Kissling and others, U.S. Fish and Wildlife Service, unpub. data, 2002–04), and Kachemak Bay in Cook Inlet (Speckman and others, 2005). An exception was the Kenai Fjords, where a relatively small population (about 9,500 birds) of Marbled Murrelets declined between 1976 and 1986 and then increased between 1986 and 2003 (Van Pelt and Piatt, 2003). Because four of five Alaska sites with trend data show evidence of declines, we suggest that the status of Marbled Murrelet populations warrant closer examination. In particular, current data are lacking for Southeast Alaska, which was last surveyed entirely in 1994 (Agler and others, 1998) and may support more than 70 percent of the world population of Marbled Murrelets (McShane and others, 2004).

Kittlitz's Murrelet.—The rate of decline we found for the Prince William Sound population of Kittlitz's Murrelet is rare for any long-lived species, and to our knowledge has not been documented in another seabird species, with the exception of intense hunting or bycatch mortality of some albatrosses. Because Kittlitz's were a small portion of *Brachyramphus* murrelets, their population trend could have been increasing or decreasing without necessarily affecting the trend for the genus. Similar situations have been found in fisheries, where the aggregate (lumped species) trend was stable, but some species within the group declined or went extinct before managers could act (Ludwig and others, 1993; Dulvy and others, 2000, 2003; Harwood and Stokes, 2003). The problem of masked trends and crypto-extinctions, while documented and discussed for invertebrates and fishes, has not been widely recognized for marine birds. Yet, marine birds, especially if they are not conspicuous when nesting, have many of the same attributes that contribute to crypto-extinctions in fish; they are widely dispersed in uninhabited areas most of the year, difficult to encounter and enumerate, and may change distribution in response to a dynamic and structurally complex habitat (Croxall and Rothery, 1995).

Monitoring.—While multi-species monitoring programs such as the one in Prince William Sound are not always ideal, when protocols are consistent and continue over long time frames, they can be useful even for rare, patchily distributed species such as the Kittlitz's Murrelet. The model presented here demonstrates a way to make optimum use of population estimates for rare species that coexist with abundant ones, or when species identification is a source of error. The problem of variable proportions of unidentified *Brachyramphus* murrelets occurs in other regions of Alaska, and this model could be used to re-examine murrelet trends wherever these two species co-exist. Similar modeling could benefit trends analysis for other species groups as well. For example, during marine surveys in Alaska, cormorants (4 spp), murres (2 spp), mergansers (3 spp), and loons (5 spp) were not always identified to species (North Pacific Pelagic Seabird Database, USFWS, Anchorage, Alaska).

Compared to many species listed under the Endangered Species Act, Marbled, and even Kittlitz's Murrelets, still have relatively high numbers of individuals. Nonetheless, as population size is reduced, fluctuations in population size increase the probability of extinction, particularly for vertebrate populations numbering in the low thousands (Reed and Hobbs, 2004). Furthermore, rapid population decline is recognized as a cause for listing species and triggering recovery actions regardless of population size (World Conservation Union, 2001; U.S. Fish and Wildlife Service, 2004). The trends observed in Prince William Sound for Marbled and Kittlitz's Murrelets over the last 30 years, and especially in the past decade, suggest that both *Brachyramphus* species should be conservation priorities.

Acknowledgments

The field surveys were conducted by dozens of people over the years, and we can not thank them all by name, but special recognition goes to project and field crew leaders Beverly Agler, Steve Kendall, Steve Klosiewski, Karen Laing, Brian Lance, and Kelsy Sullivan. The 1972 surveys were conducted in part by Pete Isleib and Mimi Hogan. The U.S. Forest Service, Chugach National Forest, gave us permission to camp on Forest lands. Ally McKnight and Elizabeth Labunski provided some of the figures. Drafts were greatly improved by review and comments from Alan Burger and Tom Reimchen. This research was supported by, but does not necessarily reflect the views of, the *Exxon Valdez* Oil Spill Trustee Council.

References Cited

Agler, B.A., Kendall, S.J., Irons, D.B., and Klosiewski, S.P., 1999, Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift: Waterbirds, v. 22, no. 1, p. 98-103.

Agler, B.A., Kendall, S.J., Seiser, P.E., and Irons, D.B., 1998, Abundance and distribution of Marbled and Kittlitz's murrelets in south central and southeast Alaska: Condor, v. 100, no. 2, p. 254-265.

Anderson, P.J., and Piatt, J.F., 1999, Trophic reorganisation in the Gulf of Alaska following ocean climate regime shift: Marine Ecology Progress Series, v. 189, p. 117-123.

Becker, B.H., and Beissinger, S.R., 2003, Scale-dependent habitat selection by a nearshore seabird, the Marbled Murrelet, in a highly dynamic upwelling system: Marine Ecology Progress Series, v. 256, p. 243-255.

Brown, E.D., Norcross, B.L., and Short, J.W., 1996, Introduction to studies on the effects of the *Exxon Valdez* oil spill on early life history stages of Pacific herring, *Clupea pallasi*, in Prince William Sound, Alaska: Canadian Journal of Fisheries and Aquatic Sciences, v. 53, p. 2337-2342.

Burger, A.E., 2000, Bird in hot water: Responses by Marbled Murrelets to variable ocean temperatures off southwestern Vancouver Island, *in* Darling, L.M., ed., Biology and Management of Species and Habitats at Risk Conference, Kamloops, British Columbia, 1999, v. 2, p. 723-732.

Burger, A.E., 2002, Conservation assessment of Marbled Murrelets in British Columbia. Part A: Review of the biology, populations, habitat associations, and conservation: Delta, British Columbia, CWS, Pacific and Yukon Region, Technical Report 387, 194 p.

Cam, E., Lougheed, L.W., Bradley, R.W., and Cooke, F., 2003, Demographic assessment of a Marbled Murrelet population from capture-mark-recapture and radio telemetry data: Conservation Biology, v. 17, no. 4, p. 1118-1126.

Carter, H.R., and Kuletz, K.J., 1995, Mortality of Marbled Murrelets due to oil pollution in North America, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 261-269.

Carter, H.R., McAllister, M.L.C., and Isleib, M.E.P., 1995, Mortality of Marbled Murrelets in gill nets in North America, *in* Ralph, C.J., Hunt, G.L. Jr., Raphael, M.G., and Piatt, J.F., eds., Ecology and conservation of the Marbled Murrelet: Albany, California, U.S. Forest Service, Pacific Southwest Research Station, General Technical Report 152, p. 271-283.

Cochran, W.G., 1977, Sampling techniques: New York, John Wiley and Sons, 428 p.

Crick, H.Q.P., 2004, Impact of climate change on birds: Ibis, v. 146, p. 48-56.

Croxall, J.P., and Rothery, P., 1995, Population regulation of seabirds: Implications of their demography for conservation, *in* Perrins, C.M., LeBreton, J.D., and Hirons, G.M., eds., Bird population studies: Relevance to conservation and management: United Kingdom, Oxford University Press, p. 272-296.

Day, R.H., Kuletz, K.J., and Nigro, D.A., 1999, Kittlitz's Murrelet (*Brachyramphus brevirostris*), *in* Poole, A., and Gill, F., eds., Birds of North America: Washington, D.C., Academy of Natural Science and American Ornithologists' Union, p. 28.

Day, R.H., Prichard, A.K., and Nigro, D.A., 2003, Ecological specialization and overlap of *Brachyramphus* murrelets in Prince William Sound, Alaska: Auk, v. 120, no. 3, p. 680-699.

Dulvy, N.K., Metcalfe, J.D., Glanville, J., Pawson, M.G., and Reynolds, J.D., 2000, Fishery stability, local extinctions, and shifts in community structure in skates: Conservation Biology, v. 14, p. 283-293.

Dulvy, N.K., Sadovy, Y., and Reynolds, J.D., 2003, Extinction vulnerability in marine populations: Fish and Fisheries, v. 4, p. 25.

Freud, R.J., and Littell, R.C., 1981, SAS for linear models: Guide to the ANOVA and GLM procedures: Cary, North Carolina, SAS Institute, Inc.

Harwood, J., and Stokes, K., 2003, Coping with uncertainty in ecological advice: Lessons from fisheries: Trends in Ecology and Evolution, v. 18, p. 617-622.

Hey, J., Waples, R.S., Arnold, M.L., Butlin, R.K., and Harrison, R.G., 2003, Understanding and confronting species uncertainty in biology and conservation: Trends in Ecology and Evolution, v. 18, p. 597-603.

Irons, D.B., Kendall, S.J., Erickson, W.P., and McDonald, L.L., 2000, Nine years after the *Exxon Valdez* oil spill: Effects on marine bird populations in Prince William Sound, Alaska: Condor, v. 102, no. 4, p. 723-737.

Julliard, R., Jiguet, F., and Couvet, D., 2004, Common birds facing global changes: What makes a species at risk?: Global Change Biology, v. 10, p. 148.

Kendall, S.J., and Agler, B.A., 1998, Distribution and abundance of Kittlitz's Murrelets in southcentral and southeastern Alaska: Colonial Waterbirds, v. 21, no. 1, p. 53-60.

Kitaysky, A.S., and Golubova, E.G., 2000, Climate change causes contrasting trends in reproductive performance of planktivorous and piscivorous alcids: Journal of Animal Ecology, v. 69, p. 248-262.

Klosiewski, S.P., and Laing, K.K., 1994, Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, State / Federal Natural Resource Damage Assessment Final Report, Bird Study 2, 88 p.

Kuletz, K.J., 1996, Marbled Murrelet abundance and breeding activity at Naked Island, Prince William Sound, and Kachemak Bay, Alaska, before and after the *Exxon Valdez* oil spill, *in* Rice, S.D., Spies, R.B., Wolfe, D.A., and Wright, B.A., eds., *Exxon Valdez* Oil Spill Symposium, Anchorage, Alaska, 1996, American Fisheries Society Symposium 18, p. 770-784.

Kuletz, K.J., 2001, Marine bird and mammal surveys pre- and post-spill for areas affected by the Windy Bay oil spill in Prince William Sound, Summer 2001: Anchorage, Alaska, USFWS.

Kuletz, K.J., and Kendall, S.J., 1998, Productivity index for Marbled Murrelets in Alaska based on surveys at sea: Journal of Wildlife Management, v. 62, no. 2, p. 446-460.

Kuletz, K.J., Stephensen, S.W., Irons, D.B., Labunski, E.A., and Brenneman, K.M., 2003b, Changes in distribution and abundance of Kittlitz's Murrelets *Brachyramphus brevirostris* relative to glacial recession in Prince William Sound, Alaska: Marine Ornithology, v. 31, no. 2, p. 133-140.

Lance, B.K., Irons, D.B., Kendall, S.J., and McDonald, L.L., 2001, Evaluation of marine bird population trends following the *Exxon Valdez* oil spill, Prince William Sound, Alaska: Marine Pollution Bulletin, v. 42, no. 4, p. 298-309.

Ludwig, D., Hilborn, R., and Walters, C., 1993, Uncertainty, resource exploitation, and conservation: Lessons from history: Science, v. 260, no. 5104, p. 17, 36.

McShane, C., Hamer, T.E., Carter, H.R., Swartzman, G., Friesen, V.L., Ainley, D.G., Tressler, R., Nelson, S.K., Burger, A.E., Spear, L.B., Mohagen, T., Martin, R., Henkel, L.A., Prindle, K., Strong, C., and Keany, J., 2004, Evaluation report for the 5-year status review of the Marbled Murrelet in Washington, Oregon,and California: Seattle, Washington, EDAW, Inc., 356 p.

Molnia, B., 2001, Glaciers of Alaska: Alaska Geographic, v. 28, no. 2.

Murphy, K.A., Suring, L.H., and Iliff, A., 2004, Western Prince William Sound human use and wildlife disturbance model: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, Restoration Project 99339 Final Report, 271 p.

Nelson, S.K., 1997, Marbled Murrelet (*Brachyramphus marmoratus*), *in* Poole, A., and Gill, F., eds., Birds of North America: Philadelphia, Pennsylvania, Academy of Natural Sciences and American Ornithologists' Union, p. 276.

Niebauer, H.J., Royer, T.C., and Weingartner, T.J., 1994, Circulation of Prince William Sound, Alaska: Journal of Geophysical Research, v. 99, no. C7, p. 14.113-14.126.

Ostrand, W.D., Howlin, S., and Gotthardt, T.A., 2004, Fish school selection by Marbled Murrelets *Brachyramphus marmoratus* in Prince William Sound, Alaska: Reponses to changes in availability: Marine Ornithology, v. 32, no. 1, p. 69-76.

Pearson, W.H., Elston, R.A., Bienert, R.W., Drum, A.S., and Antrim, L.D., 1999, Why did the Prince William Sound, Alaska, Pacific herring (*Clupea pallasi*) fisheries collapse in 1993 and 1994? Review of hypotheses: Canadian Journal of Fisheries and Aquatic Sciences, v. 56, p. 711-737.

Peery, M.Z., Beissinger, S.R., Newman, S.H., Becker, B.H., Burkett, E., and Williams, T.D., 2004a, Individual and temporal variations in inland flight behavior of Marbled Murrelets: Implications for population monitoring: Condor, v. 106, p. 344-353.

Peery, M.Z., Beissinger, S.R., Newman, S.H., Burkett, E.B., and Williams, T.D., 2004b, Applying the declining population paradigm: Diagnosing causes of poor reproduction in the Marbled Murrelet: Conservation Biology, v. 18, no. 4, p. 1088-1098.

Peterson, C.H., Rice, S.D., Short, J.W., Esler, D., Bodkin, J.L., Ballachey, B.E., and Irons, D.B., 2003, Long-term ecosystem response to the *Exxon Valdez* oil spill: Science, v. 302, no. 5653, p. 2082-2086.

Piatt, J.F., and Anderson, P., 1996, Response of Common Murres to the *Exxon Valdez* oil spill and long-term changes in the Gulf of Alaska marine ecosystem, *in* Rice, S.D., Spies, R.B., Wolfe, D.A., and Wright, B.A., eds., *Exxon Valdez* Oil Spill Symposium, Anchorage, Alaska, 1993, American Fisheries Society Symposium 18, p. 720-737.

Piatt, J.F., and Van Pelt, T.I., 1997, Mass-mortality of Guillemots (*Uria aalge*) in the Gulf of Alaska in 1993: Marine Pollution Bulletin, v. 34, p. 656-662.

Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R., Conover, D.O., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., and Sainsbury, K.J., 2004, Ecosystem-based fishery management: Science, v. 305, p. 346-347.

Ralls, K., and Taylor, B.L., 2000, Better policy and management decisions through explicit analysis of uncertainty: New approaches for marine conservation: Conservation Biology, v. 14, p. 1240-1242.

Reed, J.M., and Blaustein, A.R., 1997, Biologically significant population declines and statistical power: Conservation Biology, v. 11, p. 281-282.

Reed, D.H., and Hobbs, G.R., 2004, Relationship between population size and temporal variability in population size: Animal Conservation, v. 7, p. 1-8.

Robards, M., Drew, G.S., Piatt, J.F., Anson, J.M., Abookire, A., Bodkin, J.L., Hooge, P., and Speckman, S.G., 2003, Ecology of selected marine communities in Glacier Bay: Zooplankton, forage fish, seabirds and marine mammals: Anchorage, USGS Alaska Science Center, Final Report to USNPS, GBNPP, 156 p.

Roberts, C.M., and Hawkins, J.P., 1999, Extinction risk in the sea: Trends in Ecology and Evolution, v. 14, p. 241-246.

Root, T.L., Price, J.T., Hall, K.R., Schneider, S.H., Rosenzweig, C., and Pounds, J.A., 2003, Fingerprints of global warming on wild animals and plants: Nature, v. 421, p. 57-60.

Speckman, S.G., Piatt, J.F., and Kuletz, K.J., 2005, Population status and trends of *Brachyramphus* murrelets in Lower Cook Inlet, Alaska: Anchorage, USGS Alaska Science Center, Final Report to USFWS, Science Support Program / Species at Risk.

Stephensen, S.W., and Andres, B.A., 2001, Marine bird and mammal survey of Yakutat Bay, Disenchantment Bay, Russell Fiord, and Nunatak Fiord, Alaska: Anchorage, Alaska, U.S. Fish and Wildlife Service, 24 p.

Stearns, S., 1992, Evolution of life histories: United Kingdom, Oxford University Press.

Taylor, B.L., and Gerrodette, T., 1993, Uses of statistical power in conservation biology: Vaquita and Northern Spotted Owl: Conservation Biology, v. 7, p. 489-500.

Thomas, G.L., and Thorne, R.E., 2003, Acoustical-optical assessment of Pacific herring and their predator assemblage in Prince William Sound, Alaska: Aquatic Living Resources, v. 16, p. 247-253.

U.S. Fish and Wildlife Service, 2004, Endangered and threatened wildlife and plants: Review of species that are candidates or proposed for listing as endangered or threatened: Washington, D.C., Federal Register 69(86): 24875-24904, 50 CFR Part 17.

Van Pelt, T.I., and Piatt, J.F., 2003, Population status of Kittlitz's and Marbled murrelets and surveys for other marine bird and mammal species in the Kenai Fjords area, Alaska: Anchorage, USGS Alaska Science Center, Science Support Program Annual Report to USFWS.

Witherell, D., Pautzke, C., and Fluharty, D., 2000, Ecosystem-based approach for Alaska groundfish fisheries: Journal of Marine Sciences, v. 57, p. 771-777.

World Conservation Union, 2001, Categories and criteria for critically endangered, endangered, and vulnerable species: Gland, Switzerland.

Wynne, K.M., Hicks, D.L., and Munro, N.R., 1991, 1990 Salmon gillnet fisheries observer programs in Prince William Sound and south Unimak Alaska: Anchorage, Alaska, Saltwater, Inc, Final Report to NOAA NMFS, 65 p.

Wynne, K.M., Hicks, D.L., and Munro, N.R., 1992, 1991 Marine mammal observer program for the salmon driftnet fishery of Prince William Sound: Anchorage, Alaska, Saltwater, Inc, Final Report to NOAA NMFS, 33 p.

Appendix K. Population Changes of Marbled Murrelet at Adak Island, Alaska

By John Piatt[1], Marc Romano[1], James Bodkin[1], Kathy Kuletz[2], and Jeff Williams[2]

Most populations of Marbled Murrelet and Kittlitz's Murrelet (*B. brevirostris*) outside the Southcentral and Southeast Alaska core area have not previously been surveyed. The Alaskan distribution of both murrelet species extends along the Alaska Peninsula and Aleutian Islands (Day and others, 1999; Nelson, 1997). Murrelets are known to occur on larger islands of the Aleutians including Unalaska Island, Atka Island, Adak Island and Attu Island (Gibson and Byrd, in press). Breeding has been confirmed at Atka Island (Day and others, 1983) and birds in breeding condition have been collected at Adak Island (Byrd and others, 1974). Due to an increased concern for murrelets (e.g., Kittlitz's Murrelet is a candidate species for listing under the Endangered Species Act), we systematically surveyed murrelets at Attu, Agattu, Alaid-Nizki, Shemya, Atka and Unalaska islands in recent years to determine population size and lay the foundation for assessing population trends in the future (Piatt and others, 2005; Romano and others, 2005a, 2005b). We surveyed Adak Island in 2006 for murrelets, and here we compare results of our survey with one conducted in 1995 (Meehan, 1996). This constitutes the only dataset in the Aleutian Islands, (and indeed west of Cook Inlet) for which historical data allow for a measure of population change.

Survey Methods

Adak is the only Aleutian Island for which there exists quantitative, replicated survey data on murrelets. Both species are reasonably common at Adak, where they nest on the ground and feed in nearshore waters. As part of the Department of Defense Legacy Resource Management Program, the U.S. Fish and Wildlife Service (USFWS) conducted a study of distribution, relative abundance, seasonal trends and breeding chronology of Marbled and Kittlitz's murrelets at Adak, Alaska, from 1993 to 1995 (Meehan, 1996). In addition to land-based observations of murrelets flying inland to nest sites, biologists conducted a series of shoreline transects (fig. K1) using the same protocols developed elsewhere for small-boat surveys (Klosiewski and Laing, 1994). Strip transects were conducted from a 25' Boston Whaler or inflatable skiff using a 200-m transect width. All birds on the water and flying were counted, and identified to species when possible. Surveys covered more than half the coast, from the Northeast to Southwest corners of Adak (fig. K1). Shagak Bay on the west coast was surveyed in an inflatable using a series of parallel transects spaced 200 m apart. Incomplete sets of shoreline surveys were conducted in 1993, and at Shagak in 1993–95, but only in June 1995, was a complete set of transects surveyed in all areas.

We used these data for comparison with a repeated survey of this coast in June 2006, which we conducted in the nearshore and offshore waters of Adak Island during June 13–17, 2006 (fig. K1). We not only wanted to replicate the shoreline surveys conducted earlier by Meehan (1996), but we wanted to substantially increase survey effort so that we could obtain an estimate of population size for the entire island, and add to the foundation for future studies of population trend. Surveys were conducted, with some modification, according to strip survey protocols established by the U.S. Fish and Wildlife Service for surveying marine birds (Gould and Forsell, 1989, using modifications in Agler and others, 1998). Surveys were made from the 40-m *M/V Tiglax*, and a 4.5 m Achilles inflatable skiff. Surveyors from the skiff identified swimming birds (and mammals), and flying birds, within 100 m of either side or 100 m forward of the vessel, resulting in a 200-m wide survey strip. Only the skiff was used for coastal transects. The survey strip width was increased to 300 m wide aboard the *Tiglax* with surveyors identifying birds (and mammals) within 150 m on either side and 150 m forward of the vessel. Only offshore surveys were conducted from the ship. The greater height above the water surface from the observation area of the *Tiglax* allowed for a greater viewing distance. For surveyors aboard either vessel, only birds and mammals sighted forward of mid-ship were counted. Ground speed of the vessels while conducting surveys was held between 7–12 knots.

Sightings were recorded by entering them directly into a real-time computer data-entry system (DLogCE; Glenn Ford, ECI) that logs sightings continuously along with their Global Positioning System (GPS) coordinates. A waterproof, shock-proof, hand-held computer (TDS Recon) was used for data entry. GPS locations were obtained from a Garmin GPS unit. All flying birds that crossed within transect were counted, regardless of their elevation. Observers actively scanned ahead of and alongside the survey vessel, and species identifications were confirmed with 8–10 power binoculars. Standard guides were used for identification of birds and mammals. Weather conditions and sea state were constantly monitored. If observation conditions became unsuitable for sighting and identifying birds and mammals at the extreme range of the survey window then the survey was discontinued until conditions improved. Surveys were not conducted if wave height exceeded 0.5 m in height.

---

[1] U.S. Geological Survey

[2] U.S. Fish and Wildlife Service

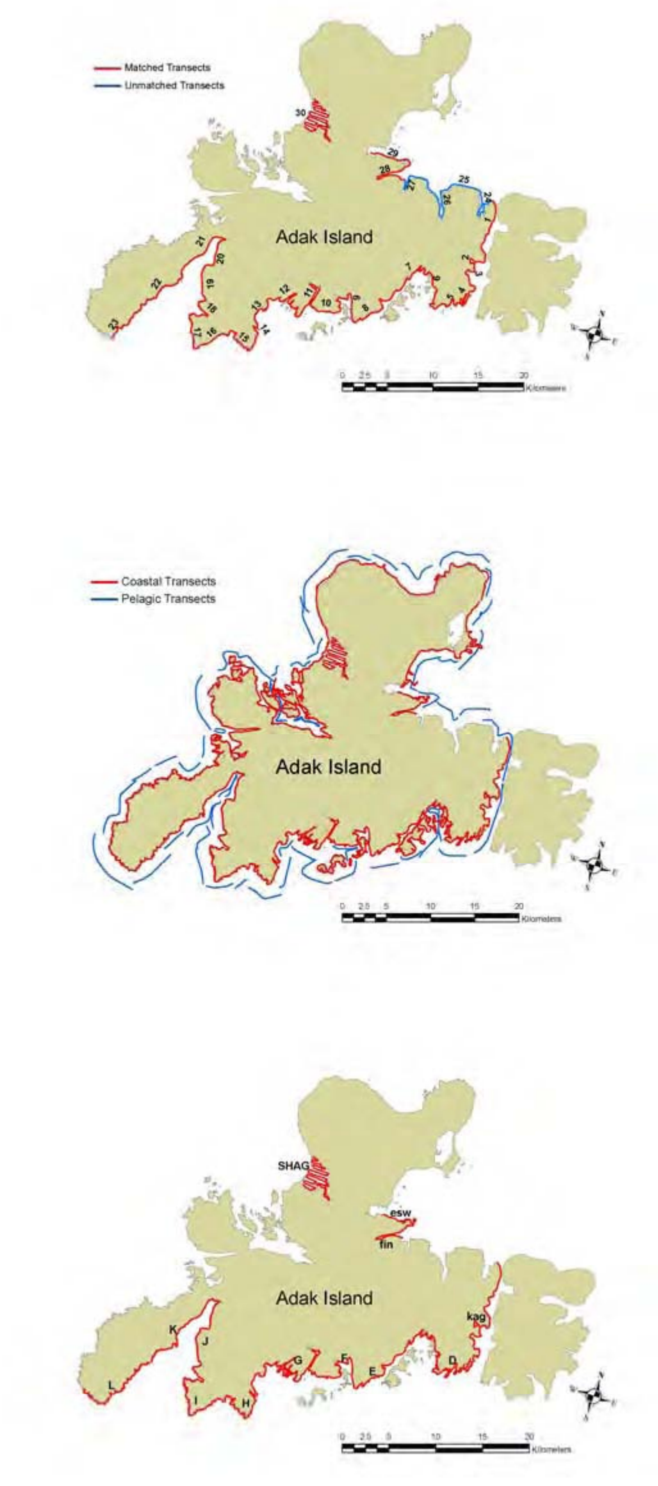


Figure K1. Seabird surveys conducted around Adak Island in 1993 and 2006. Top map shows coastal transects completed in 1995, and red lines indicate which of these were compared to 2006 data. Middle map shows all transects conducted in 2006, including coastal (red) and offshore (blue) transects. Bottom map shows coastal transects from 2006 used for comparison with 1995 data.

Data Analysis

Because we were also conducting shoreline surveys for sea otters (*Enhydra lutris*) for comparison with historical surveys (Jim Estes and Jim Bodkin, U.S. Geological Survey, unpub. data, 2006), we gathered data into transects developed for that study (fig. K1). However, for comparison with murrelet surveys of 1995, we are using only that part of sea otter survey transects that overlap completely with the 1995 surveys. Owing to a computer error, data from several shoreline transects on the Northeast side of Adak were lost from the 2006 dataset. We also surveyed the entire coast in 2006, as well as offshore, to obtain a total population estimate. Population density of murrelets in 2006 was calculated as the ratio (number per square kilometer) of total murrelets observed to total area surveyed (Cochran, 1977) of coastal (0–500 m) and offshore (500–3,000 m) strata. The total population size of was estimated by extrapolation from the ratio estimator of density to the total area of each stratum, and combining results of both strata.

Because of uncertainty about identification of murrelets to species in 1995, we simply lumped all *Brachyramphus* species for this analysis of trend. The whole island survey in 2006 indicated that 83 percent of all *Brachyramphus* identified were Marbled Murrelets. We estimated the density of birds on transects and variances using the ratio of total count to area surveyed (Cochran, 1977). We added the numbers of murrelets observed on all transects surveyed and divided by the sum of the areas of all transects surveyed. We then calculated the 95-percent confidence intervals for these estimates from the estimated variance of the ratio of total count to area surveyed (Cochran, 1977). Shoreline transects in both 1995 and 2006 were larger than 3 km in length, a scale below which spatial autocorrelation among adjacent segments may be significant for a variety of seabirds (Yen and others, 2004; Huettman and Diamond, 2006). Thus, we assumed that counts of adjacent transects were independent. Density estimates were compared among years using a *t*-test, with Welch's approximate *t* accounting for differences in variance among samples (Zar 1999, p. 129) and assuming that counts among the transects are independent.

Results and Conclusions

On those surveys which could be compared among years, we estimated a density in 1995 of 11.5 birds per square kilometer (± 8.08 SE, n=26) and in 2006 of 3.97 birds/km2 (± 1.52 SE,n=14). Despite the large difference in density among years, it was not statistically significant ($t = 1.04$, $p>0.05$, df = 36.8 using Welch's correction for unequal variance). This lack of power to detect statistical significance in a change of this magnitude is due in part to the small number of transects and in part to the patchiness of murrelet distribution around Adak. The problem should be rectified in future years by the large increase in sample size in 2006 (increased coverage with smaller transects of 2–6 km length). Considered simply as a complete census of the same stretch of shoreline, murrelet numbers declined by about 60 percent between 1995 (389 birds) and 2006 (167). Noting that two points are obviously minimal for assessing a trend, it represents an average decrease of 7.4 percent per annum. A change of this magnitude, with appropriate statistical rigor, would be of great biological significance.

This represents the only data on change for murrelets in the Aleutians. This is an important sub-population to monitor because genetic studies suggest that populations in the Aleutians are different enough from populations elsewhere in Alaska and British Columbia to warrant status as a distinct management unit (Friesen and others, 2005). From water and land-based surveys conducted in 1995, Meehan (1996) estimated that about 800–1,000 murrelets (predominantly Marbled) resided at Adak during summer. This was certainly an underestimate since he did not survey the entire shoreline of Adak, or sample much of the offshore. Our survey in 2006 suggests a population of 1,674 birds (95-percent confidence limits: 1,015–2,333) within a 3-km zone around the coast of the entire island.

References Cited

Agler, B.A., Kendall, S.J., Seiser, P.E., and Irons, D.B., 1998, Abundance and distribution of Marbled and Kittlitz's murrelets in south central and southeast Alaska: Condor, v. 100, no. 2, p. 254-265.

Byrd, G.V., Gibson, D.D., and Johnson, D.L., 1974, Birds of Adak Island, Alaska: Condor, v. 76, no. 3, p. 288-300.

Cochran, W.G., 1977, Sampling techniques: New York, John Wiley and Sons, 428 p.

Day, R.H., Oakley, K.L., and Barnard, D.R., 1983, Nest sites and eggs of Kittlitz's and Marbled Murrelets: Condor, v. 85, no. 3, p. 265-273.

Day, R.H., Kuletz, K.J., and Nigro, D.A., 1999, Kittlitz's Murrelet (*Brachyramphus brevirostris*), *in* Poole, A., and Gill, F., eds., Birds of North America: Washington, D.C., Academy of Natural Science and American Ornithologists' Union, p. 28.

Friesen, V.L., Birt, T.P., Piatt, J.F., Golightly, R.T., Newman, S.H., Hébert, P.N., Congdon, B.C., and Gissing, G., 2005, Population genetic structure and conservation of Marbled Murrelets (*Brachyramphus marmoratus*): Conservation Genetics, v. 6, no. 4, p. 607-614.

Gibson, D.D., and Byrd, G.V., in Press, Birds of the Aleutian Islands, Alaska: Ornithological Monographs.Gould, P.J., and Forsell, D.J., 1989, Techniques for shipboard surveys of marine birds: Washington, D.C., U.S. Fish and Wildlife Service Technical Report 25, 22 p.

Huettmann, F., and Diamond, A.W., 2006, Large-scale effects on the spatial distribution of seabirds in the Northwest Atlantic: Landscape Ecology, v. 21, p. 1089-1108.

Klosiewski, S.P., and Laing, K.K., 1994, Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill: Anchorage, Alaska, *Exxon Valdez* Oil Spill Trustee Council, State / Federal Natural Resource Damage Assessment Final Report, Bird Study 2, 88 p.

Meehan, J.P., 1996, Status of Marbled and Kittlitz's murrelets at the Adak Naval Reservation, Alaska: Adak, Alaska, U.S. Fish and Wildlife Service, AMNWRR 08, Department of Defense Legacy Projects 400 and 1658, 48 p.

Nelson, S.K., 1997, Marbled Murrelet (*Brachyramphus marmoratus*), *in* Poole, A., and Gill, F., eds., Birds of North America: Philadelphia, Pennsylvania, Academy of Natural Sciences and American Ornithologists' Union, p. 276.

Piatt, J.F., Romano, M.D., Gill, V., and DeGange, A.R., 2005, Density and abundance of Kittlitz's Murrelets (*Brachyramphus breviro*stris) in the Near Islands, Aleutian Islands, Alaska, July 2003: Anchorage, USGS Alaska Science Center, Final Report to USFWS, 24 p.

Romano, M.D., Piatt, J.F., and DeGange, A.R., 2005a, At-sea density and abundance of Kittlitz's and Marbled murrelets around Unalaska Island, Alaska, June 2005: Anchorage, USGS Alaska Science Center, Final Report to the U.S. Fish and Wildlife Service, 29 p.

Romano, M.D., Piatt, J.F., Williams, J., and DeGange, A.R., 2005b, At-sea density and abundance of Kittlitz's Murrelets (*Brachyramphus brevirostris*) and Marbled Murrelets (*Brachyramphus marmoratus*) at Atka Island, Alaska, June 2004: Anchorage, USGS Alaska Science Center, Final Report to the U.S. Fish and Wildlife Service, 26 p.

Yen, O.P.W., Sydeman, W.J., and Hyrenbach, K.D., 2004, Marine bird and cetacean associations with bathymetric habitats and shallow-water topographies: Implications for trophic transfer and conservation: Journal of Marine Systems, v. 50, p. 79-99.

Zar, J.H., 1996, Biostatistical analysis: Upper Saddle River, New Jersey, Prentice Hall, ed. 3.

This page left intentionally blank.

Appendix L. Probability of Assignment of Individual Marbled Murrelets to Each of Four Genetic Populations

[See figure 4 for population codes]

Specimen	Sampling site	Probability of assignment to genetic population			
		1	2	3	4
3695	Near	1.000	0.000	0.000	0.000
3696	Near	1.000	0.000	0.000	0.000
3697	Near	0.998	0.001	0.000	0.000
3698	Near	0.531	0.186	0.275	0.008
3705	Near	0.999	0.001	0.000	0.000
95-183	Near	1.000	0.000	0.000	0.000
95-184	Near	0.998	0.001	0.000	0.001
95-185	Near	1.000	0.000	0.000	0.000
95-186	Near	1.000	0.000	0.000	0.000
Attu3	Near	1.000	0.000	0.000	0.000
Attu4	Near	0.999	0.001	0.000	0.000
96-168	Andr	1.000	0.000	0.000	0.000
96-169	Andr	1.000	0.000	0.000	0.000
96-170	Andr	1.000	0.000	0.000	0.000
96-171	Andr	1.000	0.000	0.000	0.000
96-172	Andr	1.000	0.000	0.000	0.000
UAMX660	Andr	1.000	0.000	0.000	0.000
UAMX662	Andr	0.997	0.001	0.001	0.000
UAMX663	Andr	0.946	0.023	0.031	0.000
UAMX673	Andr	0.997	0.000	0.000	0.002
UAMX701	Andr	1.000	0.000	0.000	0.000
UAMX710	Andr	0.898	0.034	0.007	0.061
UAMX712	Andr	1.000	0.000	0.000	0.000
UAMX688	Unal	0.213	0.533	0.254	0.000
1679	Unal	0.645	0.156	0.116	0.083
1680	Unal	0.072	0.239	0.689	0.000
1681	Unal	0.032	0.373	0.594	0.001
1682	Unal	0.338	0.210	0.157	0.294
1704	Unal	0.716	0.093	0.190	0.001
1705	Unal	0.030	0.815	0.154	0.002
1706	Unal	0.889	0.051	0.060	0.000
1707	Unal	0.021	0.676	0.300	0.002
1708	Unal	0.982	0.008	0.009	0.001
1710	Unal	0.008	0.351	0.625	0.016
9304a	Unal	0.751	0.102	0.147	0.000
9304b	Unal	0.109	0.778	0.113	0.000
1645	Shum	0.001	0.643	0.346	0.010
1646	Shum	0.003	0.936	0.060	0.000
1647	Shum	0.002	0.424	0.573	0.001
1662	Shum	0.001	0.142	0.855	0.001
2360	Shum	0.001	0.979	0.020	0.000
2361	Shum	0.000	0.268	0.732	0.000
2362	Shum	0.001	0.710	0.271	0.018
2431	Shum	0.357	0.070	0.571	0.002
2466	Shum	0.000	0.154	0.846	0.000
2623	Shum	0.060	0.229	0.709	0.002
2663	Shum	0.001	0.886	0.113	0.000
2664	Shum	0.000	0.110	0.849	0.041
95-108	Shum	0.000	0.979	0.021	0.000
95-109	Shum	0.035	0.570	0.300	0.095
95-110	Shum	0.005	0.321	0.673	0.000
95-111	Shum	0.002	0.896	0.102	0.000
95-112	Shum	0.000	0.553	0.447	0.000
95-113	Shum	0.000	0.369	0.629	0.001
3870	Shum	0.000	0.163	0.836	0.000
3871	Shum	0.000	0.923	0.077	0.000
3872	Shum	0.002	0.213	0.778	0.007
3873	Shum	0.000	0.479	0.486	0.035
3874	Shum	0.004	0.699	0.297	0.000
3875	Shum	0.005	0.343	0.652	0.000
3876	Shum	0.000	0.036	0.964	0.000
3877	Shum	0.001	0.577	0.252	0.170
3878	Shum	0.315	0.482	0.198	0.005
3879	Shum	0.000	0.072	0.928	0.000
5mamu	Cook	0.000	0.854	0.145	0.000
6mamu	Cook	0.000	0.062	0.183	0.755
8504	Cook	0.000	0.114	0.867	0.018
96-87	Cook	0.000	0.976	0.023	0.001
96-88	Cook	0.478	0.384	0.137	0.000
96-90	Cook	0.000	0.035	0.002	0.963
96-91	Cook	0.000	0.035	0.002	0.963
96-92	Cook	0.000	0.476	0.522	0.002
96-93	Cook	0.033	0.562	0.392	0.013
96-94	Cook	0.004	0.705	0.208	0.083
96-95	Cook	0.004	0.781	0.213	0.002
96-96	Cook	0.000	0.164	0.834	0.001
96-97	Cook	0.000	0.260	0.739	0.001
96-98	Cook	0.000	0.144	0.828	0.028
96-99	Cook	0.086	0.615	0.298	0.001
3100	Cook	0.000	0.222	0.756	0.022
3101	Cook	0.490	0.137	0.373	0.000
3102	Cook	0.000	0.014	0.019	0.966
3103	Cook	0.000	0.860	0.140	0.000
3104	Cook	0.000	0.376	0.623	0.001
96-46	Cook	0.000	0.221	0.774	0.005
96-47	Cook	0.936	0.049	0.015	0.000
96-48	Cook	0.005	0.410	0.585	0.000
96-49	Cook	0.000	0.660	0.340	0.000
96-50	Cook	0.000	0.397	0.602	0.000
96-51	Cook	0.018	0.840	0.133	0.009
96-52	Cook	0.000	0.062	0.937	0.000
96-53	Cook	0.007	0.854	0.139	0.000
96-54	Cook	0.000	0.552	0.444	0.004
96-55	Cook	0.004	0.622	0.374	0.001
96-56	Cook	0.001	0.051	0.948	0.000
3311	PWS	0.000	0.169	0.018	0.813

Specimen	Sampling site	Probability of assignment to genetic population			
		1	2	3	4
3312	PWS	0.004	0.355	0.638	0.002
3313	PWS	0.000	0.067	0.933	0.000
3314	PWS	0.001	0.729	0.192	0.078
3315	PWS	0.011	0.734	0.092	0.163
3316	PWS	0.003	0.157	0.838	0.002
3317	PWS	0.000	0.400	0.600	0.000
3318	PWS	0.000	0.466	0.389	0.145
3321	PWS	0.064	0.781	0.155	0.000
3322	PWS	0.000	0.485	0.515	0.000
96-176	Alex	0.000	0.102	0.782	0.116
1mamu	Alex	0.001	0.497	0.485	0.016
BmYa99-1	Alex	0.295	0.240	0.255	0.210
96-175	Alex	0.000	0.143	0.855	0.001
96-177	Alex	0.000	0.055	0.945	0.000
94-001	Alex	0.000	0.232	0.062	0.706
94-002	Alex	0.000	0.522	0.478	0.000
94-003	Alex	0.000	0.010	0.990	0.000
94-004	Alex	0.000	0.544	0.456	0.000
94-005	Alex	0.000	0.061	0.939	0.000
94-006	Alex	0.016	0.429	0.388	0.168
94-007	Alex	0.002	0.554	0.416	0.028
94-008	Alex	0.005	0.522	0.465	0.008
94-009	Alex	0.000	0.625	0.363	0.011
94-010	Alex	0.000	0.177	0.823	0.000
94-011	Alex	0.001	0.053	0.945	0.000
94-012	Alex	0.000	0.012	0.988	0.000
94-013	Alex	0.002	0.745	0.251	0.002
94-015	Alex	0.001	0.309	0.652	0.037
94-016	Alex	0.983	0.015	0.002	0.000
94-017	Alex	0.000	0.326	0.674	0.000
94-018	Alex	0.000	0.928	0.072	0.000
94-019	Alex	0.001	0.326	0.669	0.004
94-020	Alex	0.000	0.298	0.698	0.004
94-021	Alex	0.000	0.074	0.926	0.000
203	BC	0.004	0.360	0.636	0.000
204	BC	0.000	0.142	0.858	0.000
205	BC	0.009	0.756	0.233	0.001
207	BC	0.974	0.016	0.010	0.000
210	BC	0.002	0.766	0.148	0.084
212	BC	0.012	0.736	0.251	0.001
217	BC	0.005	0.307	0.688	0.000
218	BC	0.070	0.839	0.090	0.001
219	BC	0.000	0.932	0.068	0.000
220	BC	0.000	0.822	0.178	0.000
221	BC	0.000	0.252	0.748	0.000
235	BC	0.000	0.912	0.088	0.000
241	BC	0.000	0.497	0.503	0.000
244	BC	0.000	0.615	0.326	0.059
246	BC	0.018	0.488	0.494	0.000
253	BC	0.000	0.110	0.890	0.000
254	BC	0.000	0.269	0.731	0.000
256	BC	0.000	0.835	0.160	0.004
258	BC	0.000	0.283	0.714	0.002
261	BC	0.003	0.211	0.786	0.000
278	BC	0.000	0.805	0.195	0.001
282	BC	0.000	0.773	0.218	0.009
283	BC	0.000	0.641	0.359	0.000
284	BC	0.000	0.892	0.087	0.020
285	BC	0.000	0.580	0.419	0.001
290	BC	0.011	0.602	0.271	0.116
291	BC	0.000	0.093	0.903	0.004
292	BC	0.000	0.827	0.173	0.000
293	BC	0.579	0.311	0.105	0.006
296	BC	0.000	0.305	0.690	0.005
Wa03-01	WA	0.000	0.693	0.260	0.047
Wa03-02	WA	0.000	0.564	0.161	0.274
Wa03-03	WA	0.003	0.288	0.709	0.000
Wa03-04	WA	0.000	0.259	0.052	0.689
Wa04-01	WA	0.000	0.079	0.041	0.879
Wa04-02	WA	0.000	0.503	0.490	0.007
Wa04-03	WA	0.002	0.841	0.157	0.000
Wa04-04	WA	0.000	0.286	0.714	0.000
Wa04-05	WA	0.000	0.657	0.341	0.002
Wa04-06	WA	0.000	0.346	0.021	0.633
Wa04-07	WA	0.015	0.553	0.431	0.000
Wa04-08	WA	0.000	0.856	0.144	0.000
Wa04-10	WA	0.000	0.358	0.282	0.360
Wa04-11	WA	0.000	0.112	0.887	0.000
Wa04-12	WA	0.010	0.851	0.138	0.000
Wa04-13	WA	0.005	0.721	0.201	0.074
Wa04-14	WA	0.000	0.504	0.468	0.028
Wa04-15	WA	0.001	0.543	0.428	0.028
Wa04-16	WA	0.004	0.117	0.871	0.008
Wa04-17	WA	0.599	0.260	0.053	0.088
Wa04-18	WA	0.000	0.747	0.252	0.000
Wa04-19	WA	0.000	0.630	0.335	0.036
Wa04-20	WA	0.000	0.371	0.629	0.000
Wa04-21	WA	0.000	0.100	0.900	0.000
Wa04-22	WA	0.000	0.243	0.756	0.001
Wa04-23	WA	0.000	0.200	0.799	0.002
Wa04-24	WA	0.000	0.234	0.766	0.000
Wa04-25	WA	0.000	0.436	0.563	0.001
Wa04-26	WA	0.000	0.442	0.556	0.002
Wa04-27	WA	0.001	0.476	0.461	0.062

Specimen	Sampling site	Probability of assignment to genetic population			
		1	2	3	4
Wa04-28	WA	0.001	0.868	0.131	0.000
Wa04-29	WA	0.013	0.738	0.247	0.001
Wa04-30	WA	0.000	0.583	0.417	0.000
2mamu	OR	0.107	0.170	0.706	0.017
3mamu	OR	0.026	0.231	0.729	0.015
4mamu	OR	0.696	0.063	0.156	0.085
OR05-1	OR	0.000	0.085	0.914	0.001
OR05-2	OR	0.147	0.770	0.083	0.000
OR05-3	OR	0.008	0.379	0.612	0.001
OR05-4	OR	0.000	0.246	0.752	0.002
OR05-5	OR	0.000	0.065	0.935	0.000
OR05-6	OR	0.012	0.866	0.121	0.000
OR05-7	OR	0.000	0.167	0.828	0.004
Or-99-16	OR	0.000	0.138	0.743	0.119
Or-99-17	OR	0.100	0.645	0.228	0.027
Or-99-18	OR	0.000	0.237	0.762	0.000
Or-99-21	OR	0.921	0.069	0.010	0.001
Or-99-23	OR	0.075	0.763	0.159	0.003
Or-99-24	OR	0.000	0.830	0.163	0.007
Or-99-25	OR	0.000	0.463	0.535	0.002
Or-99-26	OR	0.002	0.250	0.396	0.352
Ca01-01	NCA	0.000	0.226	0.766	0.008
Ca01-02	NCA	0.000	0.348	0.648	0.005
Ca01-03	NCA	0.002	0.746	0.166	0.086
Ca01-04	NCA	0.003	0.041	0.055	0.901
Ca01-06	NCA	0.000	0.609	0.364	0.026
Ca01-07	NCA	0.005	0.588	0.344	0.062
Ca01-10	NCA	0.003	0.061	0.112	0.824
Ca01-11	NCA	0.000	0.540	0.460	0.000
Ca01-12	NCA	0.000	0.103	0.897	0.000
Ca01-13	NCA	0.002	0.772	0.208	0.018
Ca01-14	NCA	0.000	0.399	0.571	0.030
Ca01-15	NCA	0.000	0.011	0.037	0.952
Ca01-16	NCA	0.000	0.002	0.002	0.996
Ca01-17	NCA	0.000	0.162	0.821	0.017
Ca01-18	NCA	0.000	0.227	0.773	0.000
Ca01-19	NCA	0.000	0.155	0.845	0.000
Ca02-01	NCA	0.000	0.265	0.734	0.001
Ca02-04	NCA	0.000	0.106	0.240	0.654
Ca02-05	NCA	0.000	0.350	0.152	0.498
Ca02-06	NCA	0.001	0.113	0.886	0.000
Ca02-07	NCA	0.000	0.173	0.827	0.000
Ca02-08	NCA	0.000	0.455	0.544	0.000
Ca02-09	NCA	0.000	0.413	0.587	0.000
Ca02-10	NCA	0.000	0.587	0.404	0.009
Ca02-11	NCA	0.000	0.244	0.732	0.024
Ca02-12	NCA	0.001	0.798	0.193	0.008
Ca02-13	NCA	0.000	0.084	0.906	0.010
Ca02-14	NCA	0.000	0.294	0.541	0.165
Ca02-15	NCA	0.000	0.164	0.685	0.151
Ca02-17	NCA	0.000	0.068	0.919	0.013
Ca02-18	NCA	0.000	0.483	0.213	0.304
Ca02-19	NCA	0.001	0.084	0.908	0.008
Ca02-20	NCA	0.000	0.908	0.092	0.000
Ca02-21	NCA	0.022	0.461	0.430	0.088
Ca02-22	NCA	0.000	0.001	0.001	0.998
Ca02-23	NCA	0.002	0.444	0.553	0.000
BmCa97-1	CCA	0.000	0.087	0.006	0.906
BmCa97-2	CCA	0.000	0.019	0.005	0.975
BmCa97-3	CCA	0.000	0.000	0.000	1.000
BmCa97-4	CCA	0.000	0.004	0.025	0.971
BmCa97-5	CCA	0.051	0.267	0.025	0.657
BmCa97-6	CCA	0.000	0.000	0.000	1.000
BmCa97-7	CCA	0.000	0.001	0.000	0.999
BmCa97-8	CCA	0.000	0.001	0.000	0.999
BmCa97-9	CCA	0.000	0.006	0.009	0.984
BmCa97-10	CCA	0.005	0.008	0.003	0.985
BmCa97-11	CCA	0.000	0.000	0.000	1.000
BmCa97-12	CCA	0.000	0.000	0.000	1.000
BmCa97-13	CCA	0.001	0.000	0.000	0.998
BmCa97-14	CCA	0.001	0.002	0.000	0.997
BmCa97-15	CCA	0.000	0.000	0.000	1.000
BmCa97-16	CCA	0.001	0.007	0.003	0.989
BmCa97-17	CCA	0.000	0.000	0.000	1.000
BmCa97-18	CCA	0.000	0.000	0.000	1.000
BmCa97-19	CCA	0.000	0.000	0.000	1.000
BmCa97-20	CCA	0.000	0.000	0.000	1.000
BmCa97-21	CCA	0.000	0.000	0.001	0.999
BmCa97-22	CCA	0.001	0.015	0.004	0.980
BmCa97-23	CCA	0.000	0.000	0.000	1.000
BmCa97-24	CCA	0.000	0.004	0.002	0.994
BmCa97-25	CCA	0.000	0.000	0.000	1.000
BmCa97-26	CCA	0.000	0.000	0.000	1.000
BmCa99-1	CCA	0.000	0.001	0.000	0.999
BmCa99-2	CCA	0.000	0.000	0.000	1.000
BmCa99-3	CCA	0.018	0.946	0.035	0.000
BmCa99-4	CCA	0.000	0.063	0.002	0.936
BmCa99-5	CCA	0.000	0.000	0.000	1.000
BmCa99-6	CCA	0.014	0.123	0.709	0.154
BmCa99-7	CCA	0.000	0.000	0.000	1.000
BmCa99-8	CCA	0.000	0.001	0.001	0.998
BmCa99-9	CCA	0.000	0.001	0.000	0.999
BmCa99-10	CCA	0.000	0.002	0.002	0.997

This page left intentionally blank.

Appendix M. U.S. Forest Service Nearshore Surveys, 1991 to 1995: Summary and Recommendations

By Kirsten Bixler and John Piatt

In the first half of the 1990s, the United States Forest Service surveyed nearshore waters in Southeast Alaska in Craig, Thorne Bay, Hoonah, Juneau, Admiralty, Ketchikan-Misty Fjords, Petersburg, Sitka, Wrangell and Yakutat Ranger Districts for Marbled Murrelets, as well as other marine birds and mammals. These surveys more or less followed one protocol, Methods for Surveys in Southeast Alaska of Seabirds and Mammals in Nearshore Waters: A Guide, by C.J. Ralph and S.L. Miller, 1991. Most of the data were archived in 1991, 1992, and to a lesser extent in 1993 and 1995, at the Redwood Sciences Forest Service Laboratory in Arcata, California. Except for survey routes, the data were digitized when archived. We retrieved a copy of these records in May 2006 and edited a subset in October 2006 (table M1).

The Forest Service surveys combine attributes of both strip transects and line transects. The focus of observation was within 100 meters of either side of the vessel forming a 200-m wide strip. This approach adheres to a standard strip transect survey although sightings outside of the strip were recorded as well. And as in line transect surveys, observers recorded the distance of the animal from the vessel. Observers completed two survey types, extensive and intensive. Extensive surveys, composed of variable length transects, were split into 2-kilometer segments parallel to the shoreline and at 100 m and 500 m from shore. Additionally, every two segments (4 km) a segment extended 3,000 m perpendicular to the shore or to the center of the waterway. Intensive surveys, were composed of segments parallel to shore at 100 m, 500 m, 1,000 m, 1,500 m and 2,000 m from the shoreline. In both survey types, all flying *Brachyramphus* murrelets were recorded. Other species were recorded if within the 200-m strip or if foraging in flight. Birds following the vessel were recorded once per segment. Data collected included observer initials, number of observers, date, forest service district, vessel length, vessel type, swell direction, swell time, visibility, wind direction, cloud cover, precipitation, water temperature, tide, ice cover, swell height, water depth, water boundary (obvious boundaries between water masses), transect start time, bird/mammal species, number of animals seen, direction of observation, behavior of animals, plumage if applicable, distance from vessel, notes and a map of the survey route.

Complete extensive survey data (observational data as well as a map of the survey route), was retrieved for 1,132 segments (2,264 km) parallel to shore and 123 segments perpendicular to shore. The intensive survey data obtained was complete for 42 segments (84 km). For use in Marbled Murrelet population estimation and trend analysis, we edited all complete intensive segments as well as 562 segments (1,124 km) parallel to shore and 7 segments (39 km) perpendicular to shore of extensive transects. Edits included a check for typographical errors, data formatting, standardization of units and codes, entering missing data, deletion of observations off transect as well as observations without a number or distance of animals, removal of perpendicular segments with unknown segment length, elimination of extraneous data, and location (latitude/longitude) of starting position of each segment.

These nearshore surveys, in their entirety, would significantly expand the data available for estimation of population size, trends and distribution of Marbled Murrelets in Southeast Alaska as well as provide a similar, extremely valuable dataset on other populations of marine birds and mammals, such as the Kittlitz's murrelet, Steller's sea lion and harbor seal. To maximize usefulness and accessibility, all data must first be archived in one location, all observational data must be entered and edited in a database and each survey route digitized within a mapping program such as ArcGIS. Further, the data must be made available to interested parties.

We recommend that the following be completed:

1. Digitize maps of surveys for which observational data is entered and edited, 611 transects (1,247 km).

2. Fully digitize and edit remaining extensive surveys for which both observational data and survey route have been acquired, 570 segments (1,140 km) parallel to shore and 116 segments perpendicular to shore.

3. Through travel to individual ranger districts, retrieve a copy of data not archived at the Redwood Sciences Forest Service Laboratory. We estimate that the amount of new data (i.e. not in our possession) currently languishing in warehouses in Southeast Alaska is at a minimum the amount of surveys for which we have incomplete data, 170 segments (340 km). However, it is far more likely to be closer to our estimate of the maximum amount of new data, which is double the number of segments that we now possess, about 2,500 segments (5,000 km). At the same time, a copy of all land-based Marbled Murrelet survey data can be retrieved.

4. Digitize and edit this new data.

Table M1. Forest service nearshore survey data from Southeast Alaska for which both observational data and survey route are in-hand.

Location	Years surveyed	Transect type	Ranger District	No. parallel segments in transect	No. perpendicular segments in transect	Length (km) of parallel transect
Bucareli Bay	1991	Extensive	Craig	60	50	120
Idaho Inlet	1991	Extensive	Hoonah	30	9	60
Lemesurier Island	1991	Extensive	Hoonah	20	5	40
Liskianski Inlet East	1991	Extensive	Hoonah	22	6	44
Liskianski Strait	1991	Extensive	Hoonah	20	4	40
Liskianski Inlet West	1991	Extensive	Hoonah	17	6	34
NE Chichagof Isand	1991, 1992	Extensive	Hoonah	115	7	230
Neka Bay	1991	Intensive	Hoonah	42	0	84
Pleasant Island	1991	Extensive	Hoonah	14	4	28
Point Adolphus	1991, 1992	Extensive	Hoonah	42	6	84
Tracy Arm	1992	Extensive	Juneau	56	0	112
Bakewell	1991	Extensive	Ketchikan - Misty Fjords	13	1	26
Channel Island	1991	Extensive	Ketchikan - Misty Fjords	5	0	10
East Behm	1991	Extensive	Ketchikan - Misty Fjords	13	3	26
Klahini	1991	Extensive	Ketchikan - Misty Fjords	4	2	8
Smeaton Bay	1991, 1992	Extensive	Ketchikan - Misty Fjords	20	2	40
Walker Cove to Rudyard Bay	1991	Extensive	Ketchikan - Misty Fjords	48	2	96
Winstanley Island	1991, 1992	Extensive	Ketchikan - Misty Fjords	7	2	14
Rudyerd Bay	1992	Extensive	Ketchikan - Misty Fjords	24	1	48
West Duncan Canal	1992	Extensive	Petersburg	19	0	38
Frederick Sound	1992	Extensive	Petersburg	76	0	152
Wrangell Narrows	1992	Extensive	Petersburg	7	0	14
Sumner Strait	1992	Extensive	Petersburg	14	0	28
Duncan Canal	1992	Extensive	Petersburg	18	0	36
Kruzof Island, Brents Beach	1992	Extensive	Sitka	8	0	16
Chatham Cannery	1992	Extensive	Sitka	12	0	24
Corner Bay, Chichagof Island	1992	Extensive	Sitka	7	0	14
Krestof Sound, Krestof Island	1992	Extensive	Sitka	10	0	20
Katlain Bay	1993	Extensive	Sitka	7	0	14
Lisianki Pt, Nakwasina Pass.	1993	Extensive	Sitka	15	0	30
St. John Baptist Bay	1993	Extensive	Sitka	13	0	26
Shulze Cove and Baby Bear Bay	1993	Extensive	Sitka	8	0	16
Yellow Point to Rodman Bay	1993	Extensive	Sitka	15	0	30
Rodman Bay	1993	Extensive	Sitka	7	0	14
Anita Bay	1991	Extensive	Wrangell	12	0	24
Kadin Island	1991	Extensive	Wrangell	2	0	4
North Etolin	1991	Extensive	Wrangell	7	2	14
Rynda and Greys Island	1991, 1992	Extensive	Wrangell	15	0	30
Rynda Island	1991	Extensive	Wrangell	6	0	12
Vank and Sokalof Island	1991	Extensive	Wrangell	7	3	14
Bradfield Canal	1992	Extensive	Wrangell	14	0	28
Kadin Island	1992	Extensive	Wrangell	3	0	6
Logan Bluffs	1991	Extensive	Yakutat	9	0	18
Olgan Cape to Dangerous River	1991	Extensive	Yakutat	30	5	60
Redfield	1991	Extensive	Yakutat	22	0	44
Yakutat Bay	1991	Intensive	Yakutat	19	0	38
Knight Island, Krutoi Island	1992	Extensive	Yakutat	31	0	62
Southwest Admiraly	1992	Extensive	Yakutat/Admiralty	14	0	28
Pt. Gardener to Whitewater Bay	1992	Extensive	Yakutat/Admiralty	13	0	26
Chaik Bay	1992	Extensive	Yakutat/Admiralty	22	0	44
Hood Bay	1992	Extensive	Yakutat/Admiralty	46	0	92
Northwest Admiralty	1992	Extensive	Yakutat/Admiralty	44	0	88

For more information concerning the research in this report, contact the
Director, Alaska Science Center
U.S. Geological Survey, 4230 University Dr., Suite 201
Anchorage, AK 99508-4650
http://alaska.usgs.gov

Piatt and others

Status Review of the Marbled Murrelet *(Brachyramphus marmoratus)* in Alaska and British Columbia

OFR 2006–1387