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Growth of Selected Fishes in Navigation Pool 8 of the Upper Mississippi River:
A Test of the Flood-Pulse Concept

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Growth of Selected Fishes in Navigation Pool 8 of the Upper Mississippi River: A Test of the Flood-Pulse Concept

by

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Reprinted by

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January 1997

Preface

This master of science thesis was submitted to the faculty of the graduate school of the University of Wisconsin-La Crosse and is being provided in this format as a service to Long Term Resource Monitoring Program (LTRMP) partners.

LTRMP interests in the subject matter of this report are embodied in the LTRMP Operating Plan[1] in Strategy 1.3.2, *Select new problems for research*, Task 1.3.2.4, *Conduct research*, Substrategy 4, *Flood responses*, Work Unit M, *Testing fish growth predictions of the flood-pulse concept*. This report was developed with funding provided by the Long Term Resource Monitoring Program.

The LTRMP is being implemented by the Environmental Management Technical Center, a U.S. Geological Survey science center, in cooperation with the five Upper Mississippi River System (UMRS) States of Illinois, Iowa, Minnesota, Missouri, and Wisconsin. The U.S. Army Corps of Engineers provides guidance and has overall Program responsibility. The mode of operation and respective roles of the agencies are outlined in a 1988 Memorandum of Agreement.

The UMRS encompasses the commercially navigable reaches of the Upper Mississippi River, as well as the Illinois River and navigable portions of the Kaskaskia, Black, St. Croix, and Minnesota Rivers. Congress has declared the UMRS to be both a nationally significant ecosystem and a nationally significant commercial navigation system. The mission of the LTRMP is to provide decision makers with information for maintaining the UMRS as a sustainable large river ecosystem given its multiple-use character. The long-term goals of the Program are to understand the system, determine resource trends and effects, develop management alternatives, manage information, and develop useful products.

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[1] U.S. Fish and Wildlife Service. 1993. Operating Plan for the Upper Mississippi River System Long Term Resource Monitoring Program. Environmental Management Technical Center, Onalaska, Wisconsin, Revised September 1993. EMTC 91-P002R. 179 pp. (NTIS #PB94-160199)

Growth of Selected Fishes in Navigation Pool 8 of the Upper Mississippi River: A Test of the Flood-Pulse Concept

A Thesis
Submitted to the Faculty
of
University of Wisconsin - La Crosse
La Crosse, Wisconsin

By
Andrew D. Bartels

In Partial Fulfillment
of the Requirements for the Degree of
Master of Science in Biology

December 1995

ABSTRACT

Size-specific growth of bluegill, black crappie, and freshwater drum was significantly different over four years in Navigation Pool 8 of the upper Mississippi River. Differences in growth were positively related to annual hydrographs for bluegill but less related to hydrographs for black crappie and freshwater drum. These results are consistent with predictions of the Flood Pulse Concept. Extensions of analysis of covariance (ANCOVA) models were used to account for differences in growth due to the size of fish and tested for annual differences in growth rates. Planned comparisons examined differences in growth among years with a large flood event, two years of normal hydrology, and a drought. Some sizes of bluegill and freshwater drum, but not black crappie, grew significantly faster during the flood year than during years of normal flow. Some sizes of bluegill and black crappie grew slower during the drought year when freshwater drum were not sampled. Growth curves for bluegill and black crappie indicate that the magnitude of the effects on growth rate was greater for the drought year than for the flood year. Differences in growth rate among years were most apparent for bluegill from 50 - 100 mm, black crappie greater than 200 mm, and drum longer than 100 mm. These data suggest that (1) patterns in growth for some riverine fishes are consistent with the Flood Pulse Concept, (2) droughts may be of greater consequence than floods to riverine communities, and (3) growth responses related to hydrology are size- and species-specific.

Acknowledgements

Financial, technical, and administrative support of this study was provided by the Long Term Resource Monitoring Program of the upper Mississippi River system through the Wisconsin Department of Natural Resources and the National Biological Service Environmental Management Technical Center, and by the Biology Department of the University of Wisconsin-La Crosse. I thank my graduate committee for insight and guidance. I thank my colleagues at the Onalaska DNR station for help with field work and camaraderie. I thank Shaun Hyde, Kristi Jackson, Jeremy Winch, and Steve Lounsbury for laboratory assistance. Finally, I thank my family for giving me motivation and support and my Lord for giving me the talent to complete this project.

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INTRODUCTION

Several theories have been proposed to explain the energy and nutrient dynamics of large rivers and the adaptation of biota to lotic conditions. Few specific hypotheses, however, have been isolated from these broad theories and tested. The River Continuum Concept (RCC), using a stream order framework, predicts types of communities that process organic matter, production and respiration ratios, and the extent of nutrient spiraling to be expected in streams of various sizes (Vannote et al. 1980). Sedell et al. (1989) examined the applicability of the RCC to large rivers and asserted that lateral interactions may be of greater importance than downstream transport of carbon and nutrients in determining productivity. Cummins (1977) previously proposed the general concepts comprising the RCC but also acknowledged the contribution of floods to the ecology of large streams and rivers.

The Flood Pulse concept (FPC), which is primarily based on observations from tropical rivers (Junk et al. 1989), differs from the RCC by stating (1) that periodic flood events are the main determinants of productivity and community structure for large floodplain rivers and (2) that biota within these systems are uniquely adapted to take advantage of the opportunities provided by a predictable flood pulse. According to the FPC, the aquatic/terrestrial transition zone (ATTZ) is the primary location of biological productivity during flood pulses and contains a "moving littoral zone" (Junk et al. 1989). Plant species that exploit flood resources at different water levels exist in a gradient along the floodplain topography (Junk et al. 1989). Phytoplankton, zooplankton, invertebrates, and fish move with the flood waters to exploit nutrients provided by decomposition and dissolution (Bayley 1995). Natural fluctuations in the timing and duration of floods and human alterations, such as dams and floodplain levees, may influence the degree to which flood pulses affect the floodplain and enhance productivity of the system (Junk et al. 1989, Sparks 1995). The FPC is attractive because of its breadth and consistency with gross observations of the structure and function of some tropical floodplain rivers; however, it cannot be tested as a single hypothesis.

The FPC has recently undergone some of the same scrutiny as the RCC and is subject to some of the same criticisms (Johnson et al. 1995)--i.e., it applies to rare, pristine systems. Field tests are necessary to examine the applicability of the FPC to regulated rivers. One testable hypothesis derived from the FPC is that some fishes are able to capture additional increments of energy from flooded terrestrial sources during flood pulses and that these increments are measurable as temporary increases in size-specific growth rates. The flood of 1993 in the upper Mississippi River provided an excellent opportunity to study specific effects of a flood pulse on fish growth in this temperate river. The flood occurred in summer, when high temperatures allowed considerable biological activity to occur, and was of sufficient duration for most organisms to migrate and use flooded areas.

Although body size has traditionally been considered as an important factor influencing growth of fish (Ricker 1979, Larkin et al. 1957), studies often report estimates of cumulative growth only in terms of length-at-age. However, traditional models of length-at-age, such as the von Bertalanffy, Logistic, and Gompertz functions, are derived from difference, or differential, equations expressing growth rates as functions of body size (Ricker 1979). Larkin et al. (1957) showed that the use of absolute age as a reference point for comparisons of growth was unsatisfactory because fish of the same age were often of different sizes and had different growth rates. Gutreuter (1987) assessed differences among methods used for modeling fish growth and found that estimates based on size explained about 8% more of the variation in growth than estimates based on age. There are two main reasons differences occur in growth of fish of the same age. First, most fish exhibit indeterminate growth. Increases in body size only occur when fish find conditions that meet their basic growth requirements (Sebens 1987). Second, predator-prey relationships (Larkin et al. 1957), ontogenic niche shifts (Osenberg et al. 1988), and other ecological factors may change growth rates during the life of a fish. Thus, fish that encounter different conditions, even in the same body of water, may have different growth patterns and reach different sizes over a defined period of time. Comparisons of growth among fish of the same size are justified because of the innate phenomenon of indeterminate growth, and the influence of ecological interactions of fish with their environment.

To detect an increase in growth rates due to a flood pulse, it is necessary to compare growth from a single season to that from other seasons. Length-at-age analyses measure cumulative historic growth and confound prior growth with current growth, which renders impossible any attempt at isolation of growth differences for a particular season. However, the differential, or difference, form of traditional size-based growth functions allows for analysis of individual annual growth increments.

Theoretically, any increase in growth rates due to a flood pulse would be most evident in fishes that are highly adapted for life in the shallow, inundated floodplains that comprise the ATTZ. Because gross changes in the productivity of their preferred habitat would not occur during a flood, an increase in growth would be lesser or undetectable for fishes specialized for life in flowing channel areas. Species selected for this study encompassed both of these characteristics. Two centrarchid fishes, bluegill (*Lepomis macrochirus*) and black crappie (*Pomoxis nigromaculatus*), were selected as representative of fish that would exploit floodplain margins. Both species are primarily found in lacustrine habitats. In large rivers they inhabit shallow areas with low velocity currents and aquatic or flooded terrestrial vegetation (Becker 1983). Because they are associated with shallow areas and vegetation, both species should be ideally suited to exhibit FPC responses. I hypothesized that these fish would most likely grow faster during a flood pulse than during years of low flow because of the sudden availability of large areas of new backwater habitat. Freshwater drum (*Aplodinotus grunniens*) was selected as being representative of species highly specialized for life in flowing channel habitats (Becker 1983), and I therefore hypothesized that it would respond minimally to a flood pulse.

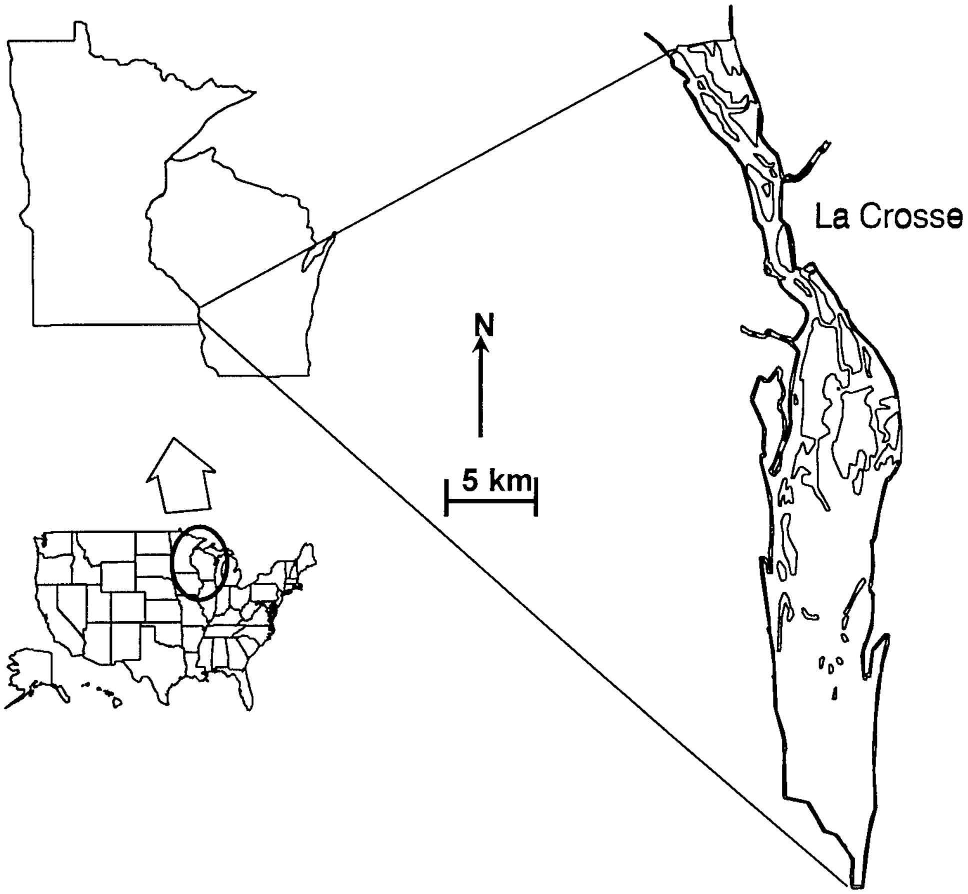
This study assessed the somatic growth of these species under several hydrologic regimes in Navigation Pool 8 of the upper Mississippi River (UMR). The objectives of this study were to: (1) estimate, from analysis of scales and otoliths, annual growth increments for populations of bluegill, black crappie, and freshwater drum in Navigation Pool 8 of the UMR during four years with different hydrologic regimes, (2) test for differences in size-specific growth rates among years, including 1993--a major flood-event year, and (3) identify potential causal mechanisms that might explain flood-related differences in growth by relating differences in growth rates to differences in habitat-associated variables.

METHODS

Study Area

Fish were collected in Navigation Pool 8 (hereafter called Pool 8) of the UMR near La Crosse, Wisconsin (Figure 1). This 8,094-ha pool extends 37.8 km from Lock and Dam 7 at Dresbach, Minnesota to Lock and Dam 8 at Genoa, Wisconsin. Pool 8 is considered typical of northern reaches of the river and contains large complexes of backwater lakes and braided channels. The cities of La Crosse, Wisconsin, and La Crescent, Minnesota, occupy much of the historic floodplain in the northern third of the pool and are near the confluences of the Black, La Crosse, Root, and Mississippi Rivers. In the middle third and in portions of the upstream third of the pool, the floodplain is undeveloped and is naturally inundated during flood events. The floodplain in the downstream third of the pool has remained permanently flooded from impoundment by Lock and Dam 8, which raised water levels about 2 m. In addition to the lock and dam system, human alterations to Pool 8 include nearly 100 wingdams, which direct the flow of water within the main navigation channel, and more than 28 km of revetted shoreline along the main navigation channel. Emergent and submergent vegetation are commonly found in backwaters and

Figure 1. Map of Navigation Pool 8, upper Mississippi River, near La Crosse, Wisconsin.


La Crosse
N
5 km

slow-flowing channels, usually in water less than 1 m deep.

Data Collection

I collected scales from bluegill and black crappie in Pool 8 during September and October of 1990 and 1992-1994. Scales from freshwater drum were also collected at the same time of year in 1992-1994. All scales were taken from just below the lateral line and underneath the tip of the flattened pectoral fin (Carlander 1982). All fish were measured to the nearest 1-mm total length (TL) in the field. The goal was to procure scale samples from 5 fish per 10-mm group.

A heated hydraulic scale press and 2 mm-thick acetate sheets were used to make imprints of scales from each fish. About 5 scales per fish were pressed, and interpreters selected the impression with the clearest detail and most symmetrical appearance for interpretation. Regenerated scales were not used.

Saggittal otoliths were also collected from bluegill and black crappie in 1994 and from freshwater drum in 1992-1994. The goal was to collect otoliths from 3 fish per 10-mm group. Large otoliths were sectioned with a fine cutting disk and mounted on microscope slides. Small whole otoliths were mounted on microscope slides. Scale imprints and otoliths were viewed on a stereomicroscope, and measurements were recorded with an optical imaging system. The scale or otolith radii and distances (mm) from the focus to all annuli were recorded. Scale radii were measured along a straight line extending from the focus to one of the anterior corners. Distances for scale annuli were measured from the focus to the point on the radius line where a line perpendicular from the radius line intercepted the corner of the annulus. For otoliths, interpreters 1 and 2 measured radii and annuli along a line from the focus to the ventral outer edge of the sulcus. Interpreter 3 measured otolith distances along a line from the focus to the ventral margin. All otolith measurements, whether from sections or from whole otoliths, were made along the same plane of orientation.

From these measurements, the penultimate annual growth increment and initial radius for the penultimate increment were obtained. The penultimate growth increment was assumed to be the growth accrued during the calendar year previous to the data collection year (e.g., data on growth for 1993 were obtained from fish collected in 1994). This increment was measured from annulus to annulus, with the next-to-last annulus inside the margin considered as the starting point. The initial scale radius was the distance from the focus to the next-to-last annulus inside the margin. Thus, the growth increment was complete, as opposed to the increment from the year in which the fish was collected. The possibility of bias from length-dependent mortality (Gutreuter 1987) or contraction of aging structures with age (Duncan 1980) was also minimized with this procedure, as only data from the most recent complete growth year was used. The result of this conservative approach was that only the most reliable growth increment was recorded from each fish.

Hydrologic patterns and related water quality data for Pool 8 were examined for relationships with observed annual differences in growth. The data were provided by staff from the Long Term Resource Monitoring Program at the Environmental Management Technical Center in Onalaska, Wisconsin. Annual hydrographs for 1989 and 1991-1993 were constructed by plotting mean monthly water elevations at Lock and Dam 8 (outflow of Pool 8). These were compared to the 25th and 75th percentile mean monthly exceedence values for the period of record from 1934 to 1994. Mean monthly water temperature and specific conductivity were calculated from bi-weekly samples collected during the study period at three backwater locations in Pool 8. Water temperatures were compared among years because prolonged differences in temperature affect metabolic processes and growth rates of fish. Specific conductivity is an indirect estimate of dissloved solids, which may affect primary and secondary productivity.

Comparisons of Methods Used to Estimate Ages of Fish

All scale and otolith samples were viewed independently by three interpreters, and estimates of age were compared among interpreters. The percentage agreement among interpreters in the age estimates was used as an estimate of precision. For each species, the percentage of age estimates that were identical for individual fish was calculated as a percentage of the total sample where either none (no agreement), two (majority), or all three (unanimous) interpreters agreed.

To detect systematic biases among interpreters, age bias plots (Campana et al. 1995) were developed by plotting the mean age of the fish and 95% confidence interval estimated by one interpreter against the ages assigned by another interpreter. Systematic biases were present when one interpreter consistently under- or over-estimated fish of a certain age when compared to ages from another interpreter. Deviations from a slope of 1.0 indicated interpretation biases between interpreters. The 95% confidence limits are for visual comparison of the ranges of age interpretations to the mean but do not have statistical worth for determination of relationships between values.

The coefficients of determination (r^2) derived from simple linear regressions were computed for each species to compare among interpreters the percentage of variability in scale radius explained by fish length. A good relationship between fish length and measured scale radius indicated precise measuring technique.

Regressions of scale age against otolith age from the same fish provided evidence of agreement between scale and otolith age estimates by each interpreter. Age estimate comparisons of scale and otolith interpretations from individual fish revealed probable error in the age estimation technique. Scales were chosen for analysis of growth rate of bluegill and black crappie because they were collected in all years and did not require sacrificing the fish to obtain a large sample. Scales from freshwater drum did not clearly show annuli beyond age 4 or 5, thus otoliths were selected for analyses of growth rates.

Analysis of Growth Rates

Direct scale measurements were used in the statistical models to eliminate the possibility of estimation error caused by back-calculation fish length-at-age (Weisberg and Frie 1987). Therefore, any differences in growth among years are directly attributable to measured differences in growth. Back-calculated estimates of length-at-age and accrued growth increments were then used to translate the actual scale measurements to the more practical scale of body size.

Annual increments of growth for each species were compared among years with an extended heterogeneity of slopes analysis of covariance (ANCOVA) model which was used as a categorical predictor of annual growth and initial scale radii as the covariate. Based on the curvilinear shape of preliminary plots of growth increments versus initial scale radii, a Gompertz growth function (Ricker 1979) was selected as the general form of the model. The statistical model used differs from a traditional Gompertz model due to the addition of an intercept term, which prevents the corresponding differential equation from being solved in closed form and requires numerical computations to obtain length-at-age estimates. The statistical model corresponding to the difference form of the Gompertz model, which tested for differences in growth rate among years and incorporated fish length as a covariate was:

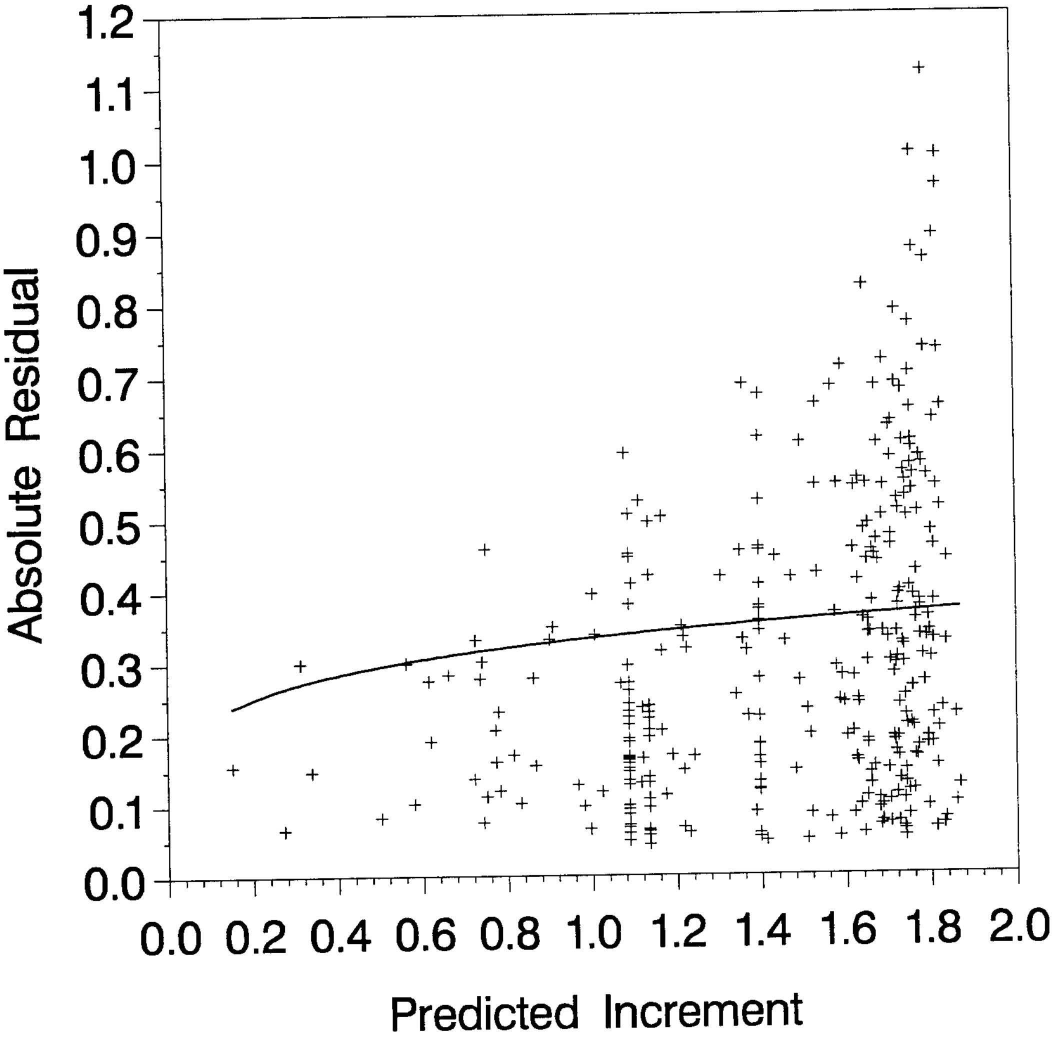
$$\Delta R_{ij} = \beta_0 + \beta_{0j} + \beta_1 R_{ij} + \beta_{1j} R_{ij} + \beta_2 R_{ij}\log(R_{ij}) + \beta_{2j} R_{ij}\log(R_{ij}) + \epsilon_{ij}, \qquad (1)$$

where ΔR_{ij} denotes the penultimate scale increment width from the i'th fish (i=1 ... $\sum_{j=1}^{k} n_j$) captured during the j'th growth year (j=1 ... k) and R_{ij} denotes the scale radius at the start of the j'th growth year. The model contains an overall intercept value (β_0), an intercept value for each individual year (β_{0j}), an overall slope value for fish length effects ($\beta_1 R_{ij}$), a slope value for each year's fish length effects ($\beta_{1j} R_{ij}$), an overall log term slope value [$\beta_2 R_{ij}$log(R_{ij})], and a log term slope value for each year [$\beta_{2j} R_{ij}$log(R_{ij})]. The scale terms in the model represent fish growth along the continuum of scale radii (or fish lengths). The logarithm terms represent the curvilinearity of the growth increment vs. initial scale radius plots, again along a continuum of scale radii. Both of these terms identify differences in growth based on scale radius size alone, i.e., independent of years. The year terms (β_{0j}) in the model test for differences in growth from year to year, assuming homogeneous slopes for the scale radius and scale radius x log(scale radius) terms. To test for differences in growth, influenced by both fish size and year effects, interaction terms, $\beta_{1j}\mathrm{R}_{ij}$ and $\beta_{2j}\mathrm{R}_{ij}\log\mathrm{R}_{ij}$, must be examined. These interaction values indicate the presence or absence of size-specific differences among years in growth rates of fish.

This model assumes errors (ϵ_{ij}) are independent and normally distributed, with mean zero and variance $\sigma^2 {\mu_{\Delta R}}^{2\theta}$, where $\mu_{\Delta R}$ denotes the conditional mean of ΔR_{ij} (growth increment) given R_{ij} (the *i*th fish from year *j*). Because variances of growth increments are typically greatest for the largest growth increments (fish exhibit widest fluctuations in growth when they are growing most quickly; Gutreuter 1987; Gutreuter and Childress 1990), it was necessary to weight the ΔR_{ij} by the reciprocal of the estimated variance of ΔR_{ij}. By modeling the exponent term (θ) of the variance function, I accounted for non-constant variance (heteroscedasticity) of growth increments of fish of different sizes. The modeling process used the following generalized least squares (GLS) estimation procedure (Davidian and Carroll 1987; Carroll et al. 1988): (1) pass size-specific growth increment data through the ANCOVA model, (2) perform non-linear least-squares fitting of the variance function with absolute residuals as the response variable and predicted growth from the first step as the predictor, and (3) accept the estimates of β_0, β_{0j}, β_1, β_{1j}, β_2, β_{2j}, σ^2, and θ when the error sums of squares from successive iterations of this process converged to within 5% of each other. Figure 2 shows an example of the fitted variance function from this process.

A priori planned comparisons of growth among years consisted of: (1) comparing growth of fish in 1993 to that in all other years to determine if FPC effects occurred, (2) comparing growth of fish in 1991-1992 to that in 1993 to

Figure 2. Plot of absolute values of residuals from equation (1) and the fitted variance function from Generalized Least Squares (GLS) regression analysis, demonstrating increases in error term variance with increasing growth increments. The absolute residuals are equal to the absolute values of the departure of the raw data points from the regression line produced by the extended ANCOVA model. Units are mm.



1.2
1.1
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.0
Absolute Residual
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
Predicted Increment

determine if the growth of fish during a flood year was different from that during years of normal flow, and (3) comparing growth of fish in 1989 to that in 1991-1992 to examine growth of fish during a drought with that of fish from years with normal flow.

Back-calculation of Body Size

Estimates of initial length of the fish each year and increment of growth in length during the year were constructed by back-calculating fish lengths from scale or otolith measurements. These estimates show the magnitude of somatic growth rates and the range of body sizes at which they occurred. Back-calculated estimates were initially made by two methods (Francis 1990). The body-proportional hypothesis (BPH) and the scale-proportional hypothesis (SPH) were used. Different regressions were used for each model (SPH: scale radius is regressed on fish length; BPH: fish length is regressed on scale radius). In both models, the proportional deviation of an individual measurement from the average of the sample is taken into account. Annual growth increments estimated by the SPH and BPH were regressed against measured growth increments from the scales to determine which method explained a greater percentage of the variability in growth rate. Estimates from the two methods varied less than 4%, but the BPH explained more variability in growth and was selected for back-calculations.

Back calculations were also used to demonstrate the potential consequences of the observed growth patterns projected out through the life of a fish. The statistical models were refitted with back-calculated fish lengths and growth increments instead of scale radii and scale growth increments. This procedure yielded new Gompertz growth curve equations for each year in terms of fish length. Estimates of length-at-age that might be obtained under different water elevation regimes (different years) over the life of hypothetical fish were then calculated with the Gompertz curve equations obtained for each year and assigning an initial length at hatch of 5 mm. Predicted growth increments from the Gompertz curves were added to the initial fish length for successive ages. The procedure was terminated when predicted initial body length reached the initial length of the largest fish in the sample. Estimates of length-at-age were plotted to produce comparative graphs that demonstrate cumulative growth effects that might accrue from sustaining the different water elevations. These plots project the growth effects from a particular year additively over the life of a fish and illustrate how the differing growth rates could eventually affect size structure of the population.

RESULTS

Hydrology and Water Quality

Hydrographs differed among years (Figure 3). As indicated by the 25th and 75th percentiles for the period of record, water elevations are usually similar from September to February, and fluctuate widely from April to July. The hydrographs for 1989 and 1991-1993 followed this trend, but the magnitudes of fluctuation for 1989 and 1993 were unusual. The 1989 hydrograph was consistently low, never departing more than one foot (0.31 m) from the 25th percentile line. The 1993 hydrograph encompassed the other extreme, and was equal to, or in excess of, the 75th percentile for 10 months of the year.

Water temperatures among the same four years did not follow the same trend as water elevations. Mean monthly water temperatures were similar in most months and differed less than 5^0C for any one month (Figure 4). Water temperatures were highest in 1991 during April, May, June, and July.

Specific conductivities (Figure 5) followed the same overall trend as water elevation. With few exceptions, the highest mean monthly conductivities were recorded in 1993, the lowest in 1989.

Figure 3. Annual hydrograph for Navigation Pool 8, upper Mississippi River, as depicted by mean monthly water surface elevations (feet above mean sea level) at Lock and Dam 8. The 25th and 75th percentile exceedence values were calculated from the period of record, 1934-1994.

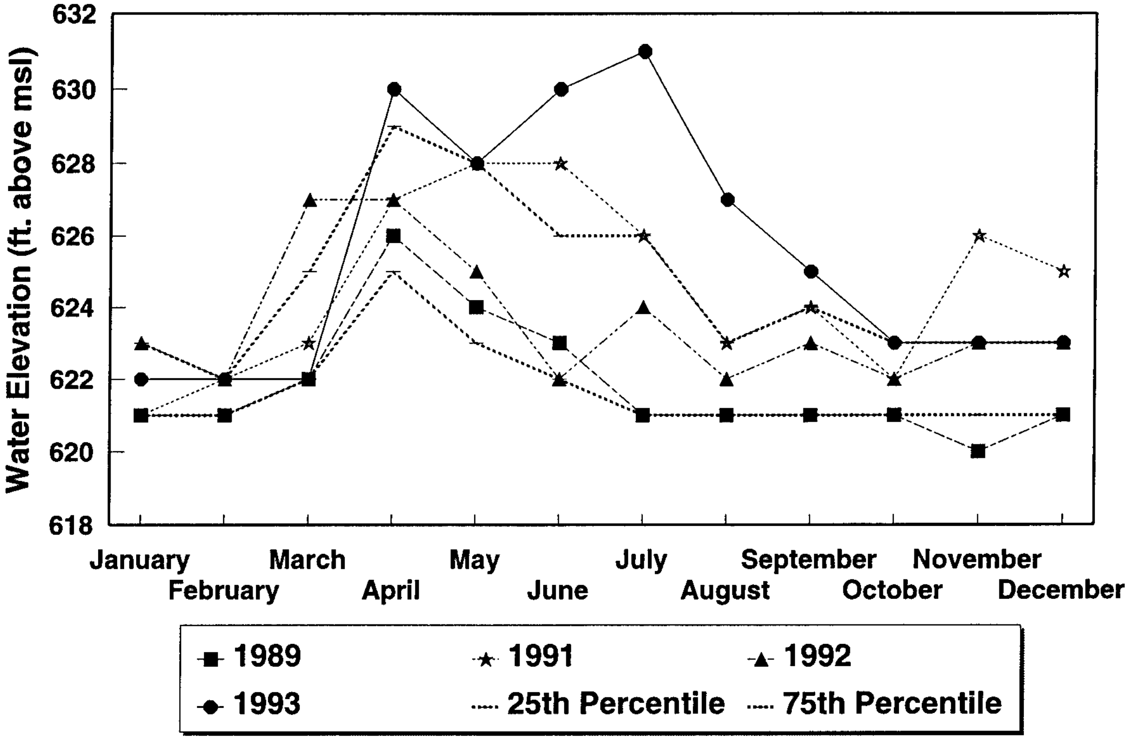

632
630
628
626
624
622
620
618
Water Elevation (ft. above msl)
January
February
March
April
May
June
July
August
September
October
November
December
1989
1991
1992
1993
25th Percentile
75th Percentile

Figure 4. Mean monthly water temperatures from three backwater sites in Navigation Pool 8, upper Mississippi River.

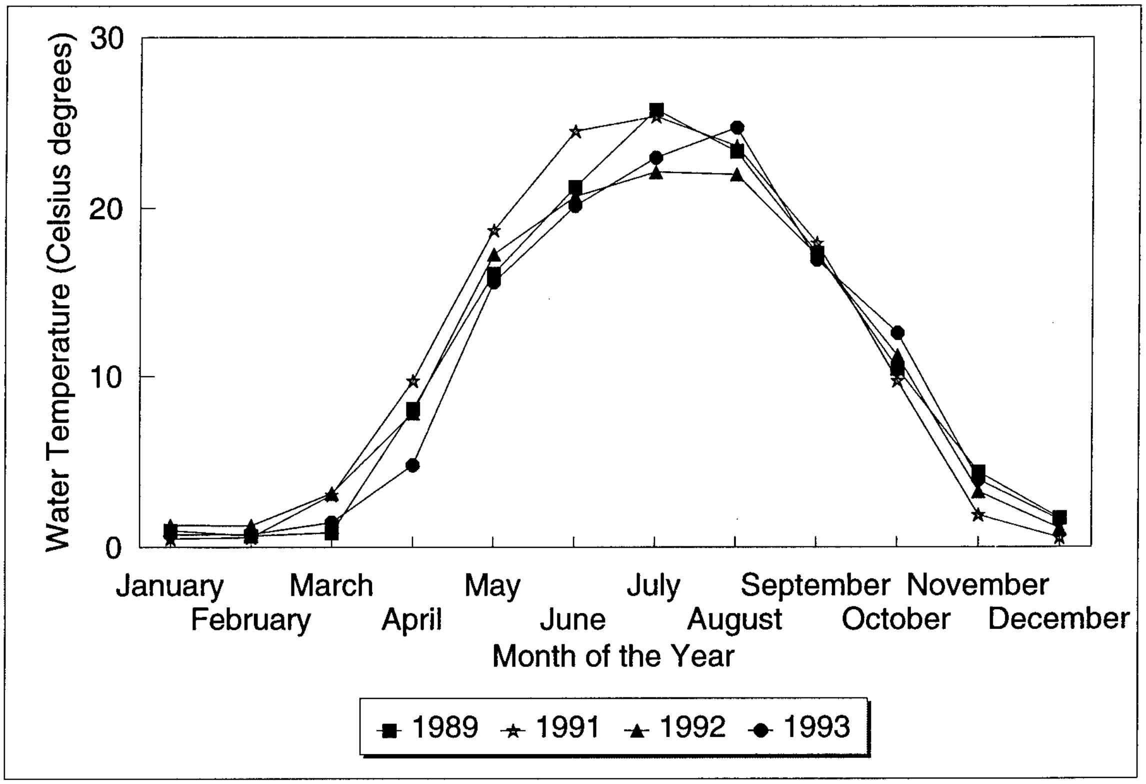
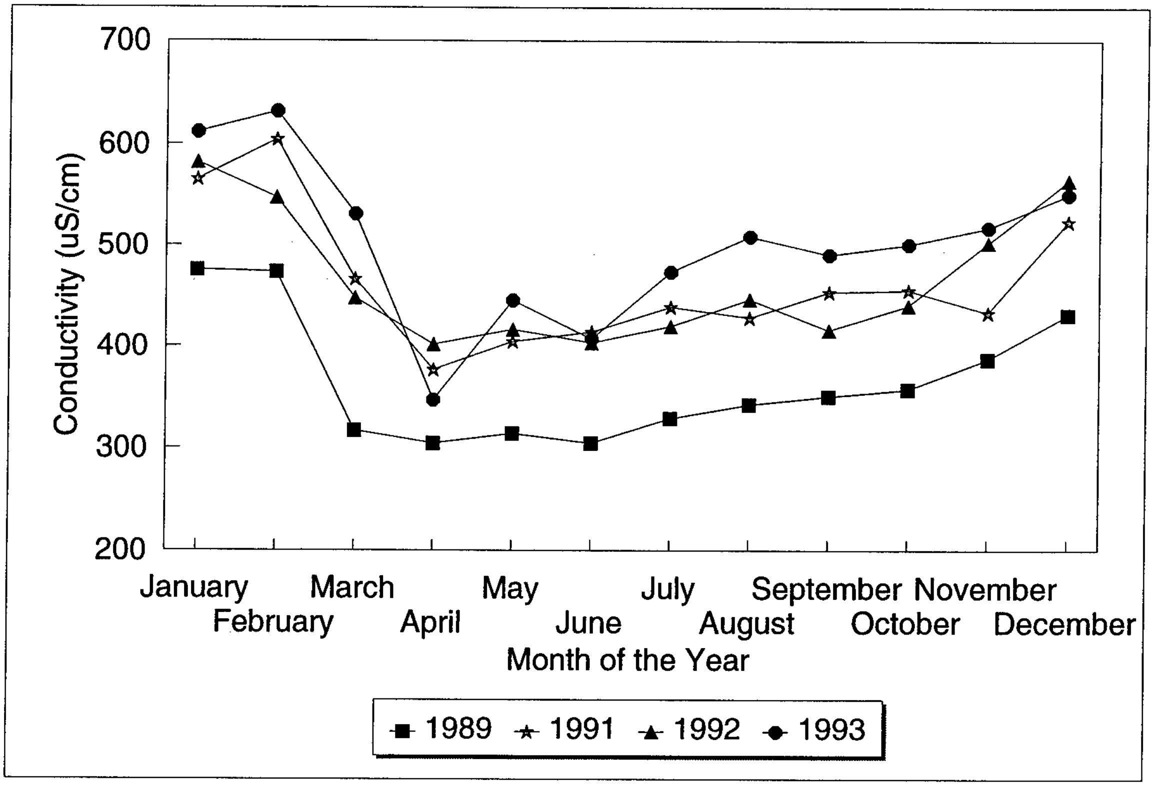

Water Temperature (Celsius degrees)
30
20
10
0
January
February
March
April
May
June
July
August
September
October
November
December
Month of the Year
1989
1991
1992
1993

Figure 5. Mean monthly specific conductivity from three backwater sites in Navigation Pool 8, upper Mississippi River. Units are μSiemens/cm (1 μSiemen = 1 μmho).


700
600
500
400
300
200
Conductivity (uS/cm)
January
February
March
April
May
June
July
August
September
October
November
December
Month of the Year
1989
1991
1992
1993

Comparisons of Methods Used to Estimate Ages of Fish

Comparisons of age estimates and scale measurements revealed mild biases among interpreters. Unanimous agreement among interpreters on the estimated age of the fish ranged from 35% for bluegill to 62% for freshwater drum; majority agreement was consistently high for all three species (Table 1). Age bias plots for bluegill indicated that systematic differences occurred among all three interpreters; the best relationship occurred between interpreters 2 and 3 (Figure 6). Similarly, estimates of the ages of black crappie exhibited systematic biases among interpreters (Figure 6), with interpreters 1 and 3 agreeing most closely. For freshwater drum, there was good linearity among all interpreters (Figure 6).

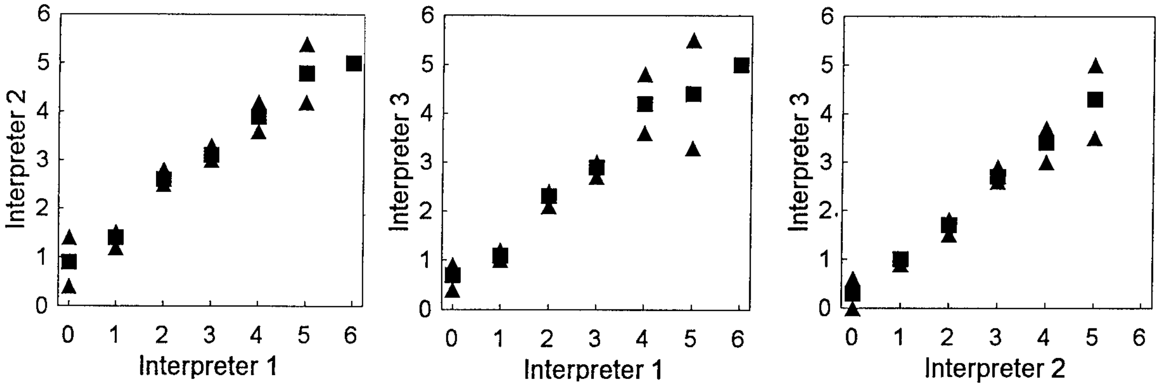
Simple linear regressions modelling the relationship between scale or otolith radius and fish length (Table 2) yielded patterns of similarity that reflected those from age bias plots for bluegill and freshwater drum. For black crappie, the coefficient of determination was similar for all three interpreters, suggesting all three interpreters practiced good measuring technique. Radius measurements from interpreter 3 explained the greatest amount of variability in fish length for each species. When age interpretations for scales and otoliths from the same fish were compared, interpreter 3 had the most consistent

Table 1. Percentage agreement among three individuals on the age of fish estimated from scales and otoliths. All fish were collected from Navigation Pool 8, upper Mississippi River

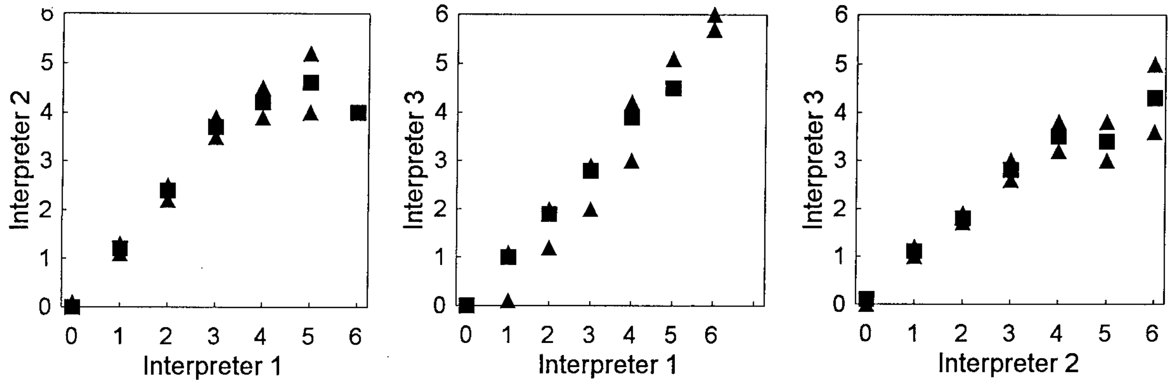
	Otoliths		Scales	
Comparison	Number analyzed	Percent agreement	Number analyzed	Percent agreement
	bluegill			
All 3 interpreters	5	25	111	35
2 of 3 interpreters	19	95	293	93
No agreement	1	5	21	7
	black crappie			
All 3 interpreters	8	24	192	47
2 of 3 interpreters	26	79	375	91
No agreement	7	21	36	9
	freshwater drum			
All 3 interpreters	65	62	45	35
2 of 3 interpreters	92	88	107	84
No agreement	12	12	21	16
	all species			
All 3 interpreters	78	50	348	41
2 of 3 interpreters	137	87	775	91
No agreement	20	13	78	9

Figure 6. Age bias plots for detecting systematic biases among interpreters for estimation of the age of bluegill (A), black crappie (B), and freshwater drum (C). Squares are mean values for y-axis interpreter compared to values from x-axis interpreter. Triangles are 95% confidence intervals about the mean.

(A) Bluegill



(B) Black crappie



(C) Freshwater drum

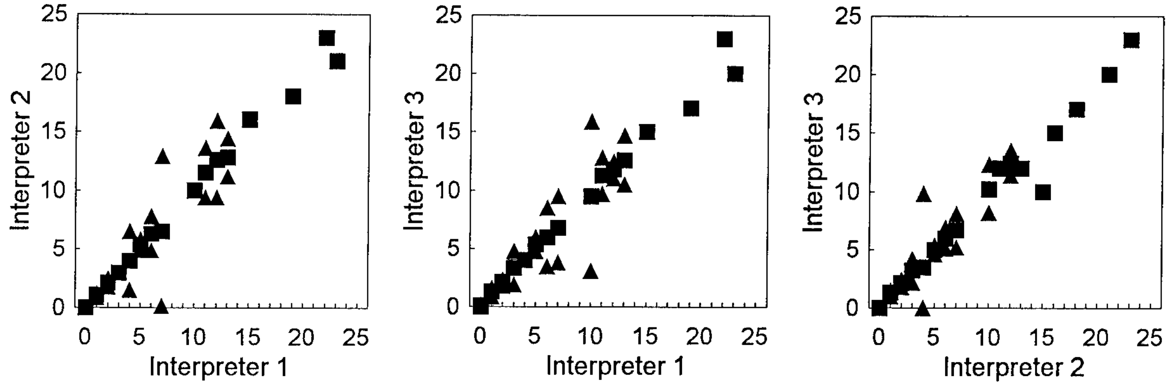


Table 2. Simple linear regression analyses of scale and otolith radius (mm) with fish length as measured by three different interpreters. All fish were collected from Navigation Pool 8, upper Mississippi River

	Coefficient of determination (r^2)					
	Bluegill		Black crappie		Freshwater drum	
Interpreter	Scale	Otolith	Scale	Otolith	Scale	Otolith
1	0.91	0.65	0.95	0.25	0.77	0.89
2	0.85	0.72	0.93	0.13	0.84	0.91
3	0.92	0.63	0.95	0.92	0.85	0.94

estimates. Estimates of age made by interpreter 3 explained approximately 84%, 82%, and 65% of the variability in age estimated from otoliths for black crappie, bluegill, and freshwater drum, respectively (Table 3). These values were much greater than values for the other interpreters. In summary: (1) systematic biases were present in age estimates for black crappie and bluegill, and estimates from one or more interpreters were suspect, (2) the data from interpreter 3 produced the best relationship between structure radius and fish length, and (3) estimates of fish age made from scales agreed better with estimates of age made from otoliths for interpreter 3 than for the other two interpreters. Thus, only data from interpreter 3 were included in subsequent analyses of growth rates.

Analysis of Growth Rates

Bluegills. All planned contrasts examining differences in growth among years were significantly different (Table 4). These contrasts demonstrated that the Gompertz curves differed among all combinations of the flood year, the normal flow years, and the drought year. The interaction effects for scale radius (R) and (R)log(R) were both significant and indicated size-specific growth differences among years. There was no overall significant linear trend for all years combined, but the curvilinear (R)log(R) term

Table 3. Agreement between ages of fish estimated with two methods (scale and otolith) by each interpreter for each of three species. Data are presented as coefficients of determination from simple linear regressions of age determined from scales (x-axis) and age determined from otoliths (y-axis) collected from the same fish. All fish were collected from Navigation Pool 8, upper Mississippi River

	Coefficient of determination (r^2)		
Interpreter	Bluegill	Black crappie	Freshwater drum
1	0.54	0.21	0.54
2	0.28	0.44	0.55
3	0.82	0.84	0.65

Table 4. Results of the extended ANCOVA model testing for size-specific differences in growth increments of bluegill, black crappie, and freshwater drum from Navigation Pool 8, upper Mississippi River, among the years 1989-1993

Source of Variation	df	F value	p > F
	bluegill		
Model	11	25.49	0.0001
Scale Radius (R)	1	0.05	0.8280
(R)log(R)	1	226.56	0.0001
Year	3	11.71	0.0001
(R)xYear	3	2.86	0.0372
(R)log(R)xYear	3	3.34	0.0197
Error	293		
Total	304		
Contrasts:			
1989-1992 vs 1993	3	5.36	0.0013
1991-1992 vs 1993	3	4.43	0.0046
1989 vs 1991-1992	3	7.92	0.0001
	black crappie		
Model	11	46.05	0.0001
Scale Radius (R)	1	126.69	0.0001
(R)log(R)	1	333.20	0.0001
Year	3	8.85	0.0001
(R)xYear	3	2.87	0.0364
(R)log(R)xYear	3	3.84	0.0100
Error	348		
total	359		
Contrasts:			
1989-1992 vs 1993	3	3.90	0.0092
1991-1992 vs 1993	3	2.17	0.0917
1989 vs 1991-1992	3	4.20	0.0061
	freshwater drum		
Model	8	52.15	0.0001
Otolith Radius (R)	1	247.50	0.0001
(R)log(R)	1	141.30	0.0001
Year	2	5.09	0.0089
(R)xYear	2	4.35	0.0170
(R)log(R)xYear	2	4.78	0.0116
Error	64		
Total	72		
Contrasts:			
1991-1992 vs 1993	2	6.82	0.0005
1991 vs 1993	2	5.20	0.0028
1992 vs 1993	2	6.74	0.0005

showed that β_2 was significantly different from zero.

The Gompertz curves developed from bluegill scale increments (Figure 7) revealed that growth rate differences were greatest for scales with medium-sized radii and that fastest scale growth occurred for these fish during the 1993 flood year. The greatest differences in growth rates of fish between the flood and normal flow years were observed mainly in fish with medium-sized scales; however, differences in fish growth between the drought year and the normal flow years occurred in scales of all sizes. Figure 8 shows the raw data points and the fitted Gompertz curves developed with the model ($r^2 = 0.49$).

Estimates of bluegill annual length increments (Figure 9) were back-calculated from the scale measurements and were similar to the Gompertz curves. The greatest differences between years occurred for medium-sized fish (50-100 mm TL). The largest growth increment (70 mm) occurred in fish initially about 60 mm TL in 1993. In contrast, fish of the same initial size grew only about 50 mm in 1989 (low flow) and about 60 cm in 1991 and 1992 (intermediate flow).

I projected the additive effects of each growth curve over the life of a fish to demonstrate potential size impacts on the fish if each of the annual hydrologic regimes could be repeated over time. Assuming constant growth, differences in total length would become apparent for age 2+

Figure 7. Gompertz growth curves depicting differences in size-specific growth rates of bluegill from scale data. All fish were collected from Navigation Pool 8, upper Mississippi River.

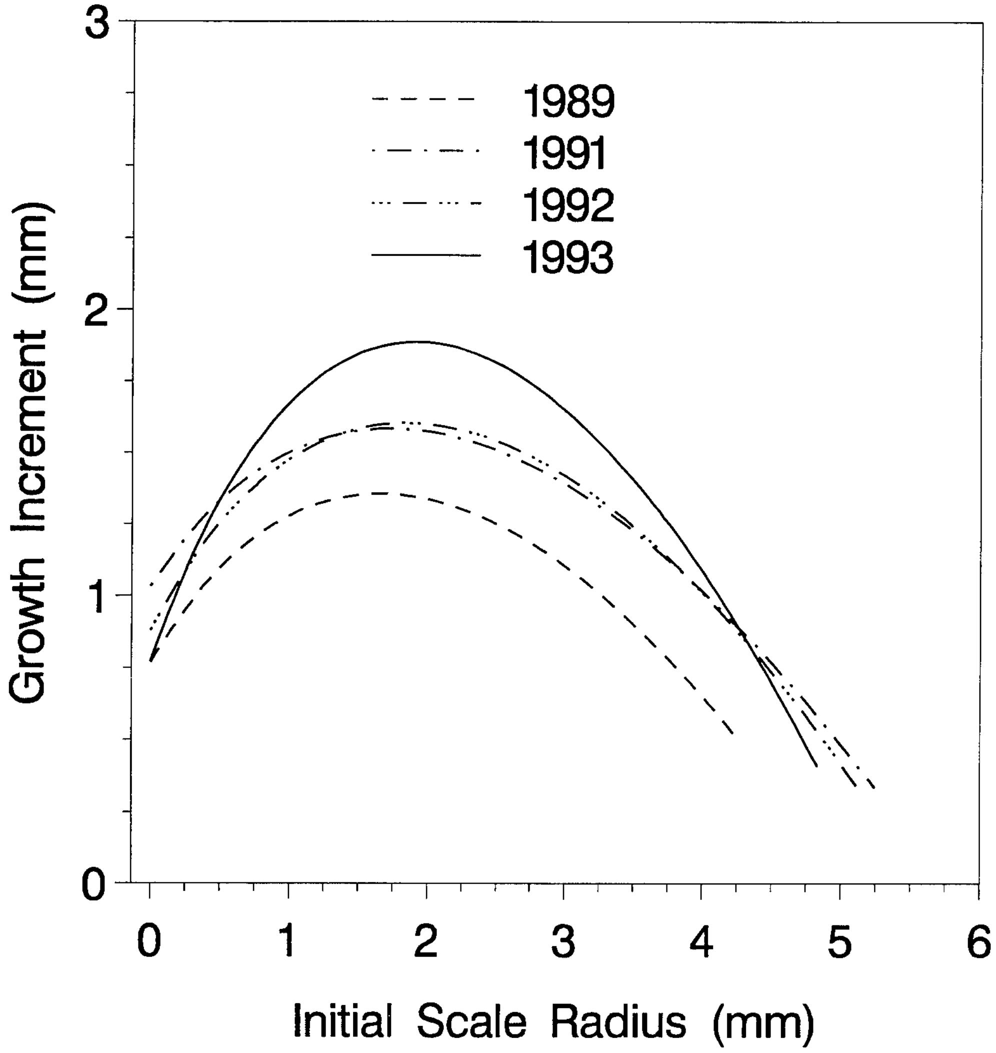

3
2
1
0
0
1
2
3
4
5
6
Growth Increment (mm)
Initial Scale Radius (mm)
1989
1991
1992
1993

Figure 8. Plots of growth increment on initial scale radius for bluegill collected in Navigation Pool 8, upper Mississippi River in 1989 (A), 1991 (B), 1992 (C), and 1993 (D). The solid line indicates the Gompertz curve, which models the data.

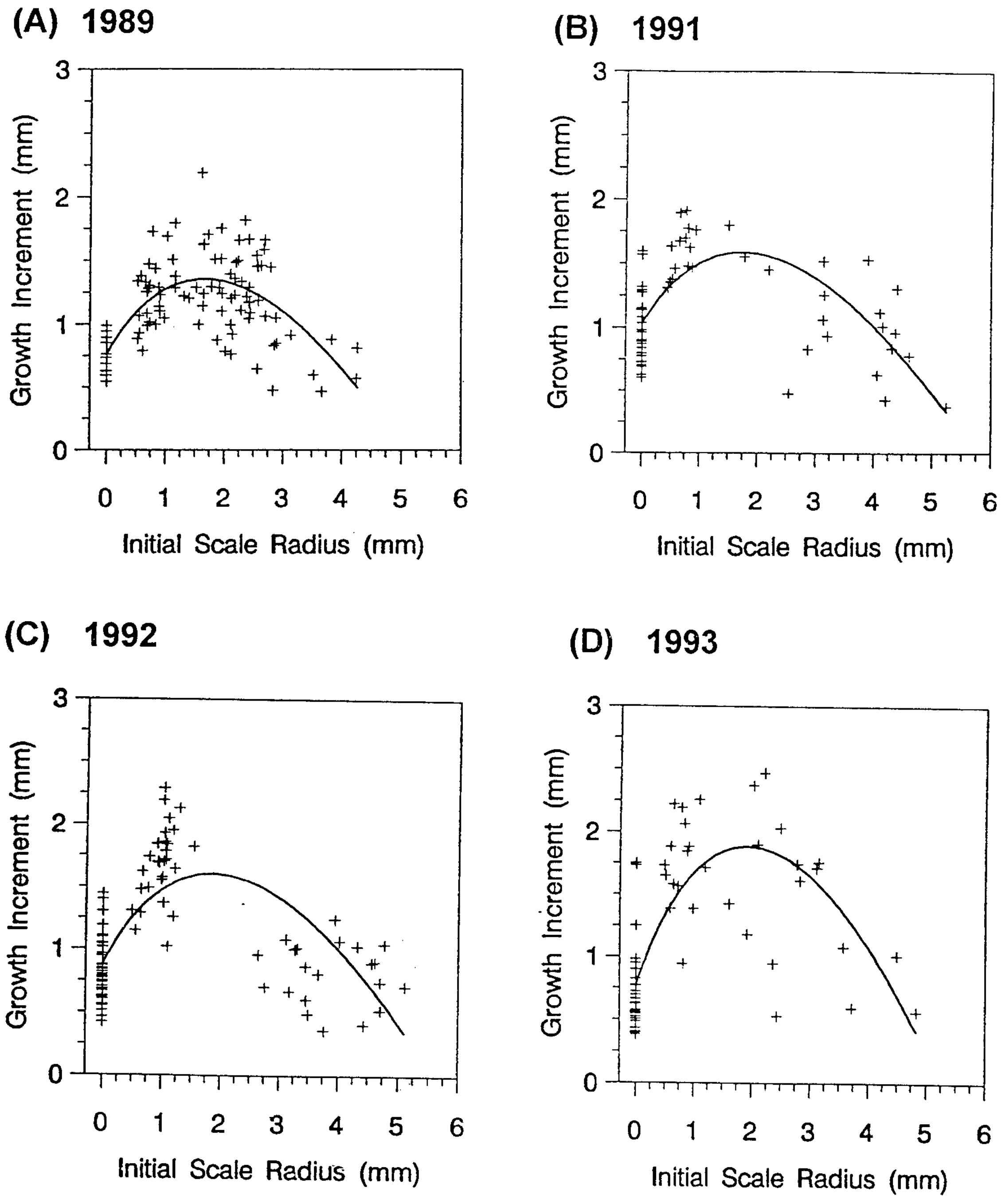
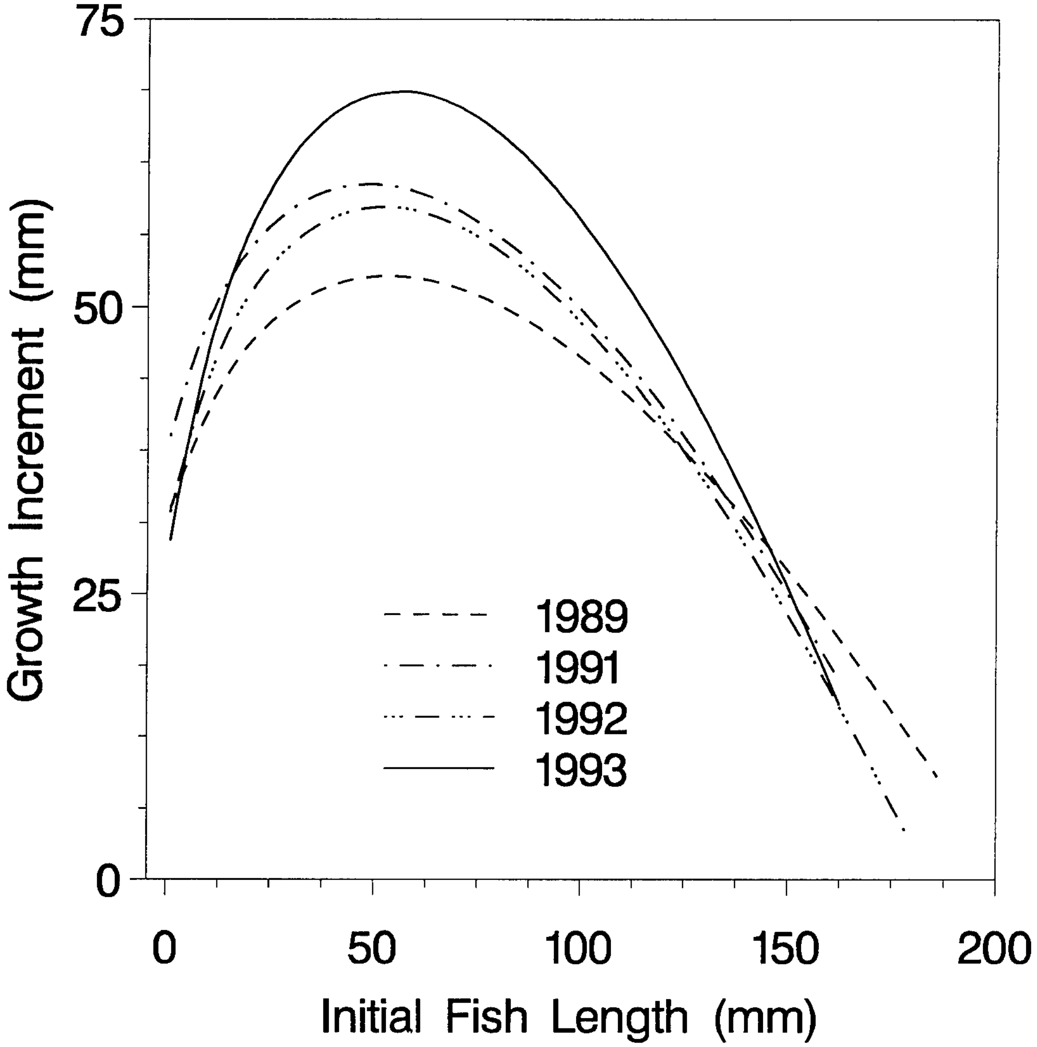
(A) 1989
(B) 1991
(C) 1992
(D) 1993
Growth Increment (mm)
Initial Scale Radius (mm)
0
1
2
3
4
5
6

Figure 9. Estimated growth increments and initial length of bluegill, back-calculated from scale data. All fish were collected from Navigation Pool 8, upper Mississippi River.



75
50
25
0
Growth Increment (mm)
0
50
100
150
200
Initial Fish Length (mm)
1989
1991
1992
1993

and 3+ bluegill (Figure 10). These length-at-age estimates illustrate the possibilities for future growth by the fish if the observed pattern for a particular year was repeated through time. For a bluegill in its third growing season there would be as much as 22 mm difference in total length under the flood growth pattern compared to the other years. Assuming 150 mm as a minimum "quality" size for bluegills (Anderson 1978), the 1993 flood growth curve would have produced quality size fish most quickly (Fig. 10). In contrast, the drought conditions would have required nearly another year to produce fish of quality size.

Black crappie. The planned contrasts for black crappie indicated that significantly different growth rates occurred between the flood year and all other years combined, between the drought year and the normal flow years, but not between the normal flow years and the flood year (Table 4). The interaction terms showed that there were size-specific growth differences among years, as both interaction terms were highly significant. Overall slope effects were highly significant for both terms [(R) and (R)log(R)], indicating that the linear and the curvilinear slope terms were both different from zero.

The Gompertz curves developed from black crappie scale increments (Figure 11) showed that growth rate differences were evident only for fish with very large scales. Fastest

Figure 10. Estimated length-at-age of bluegill collected under different hydrologic regimes from Navigation Pool 8, upper Mississippi River.

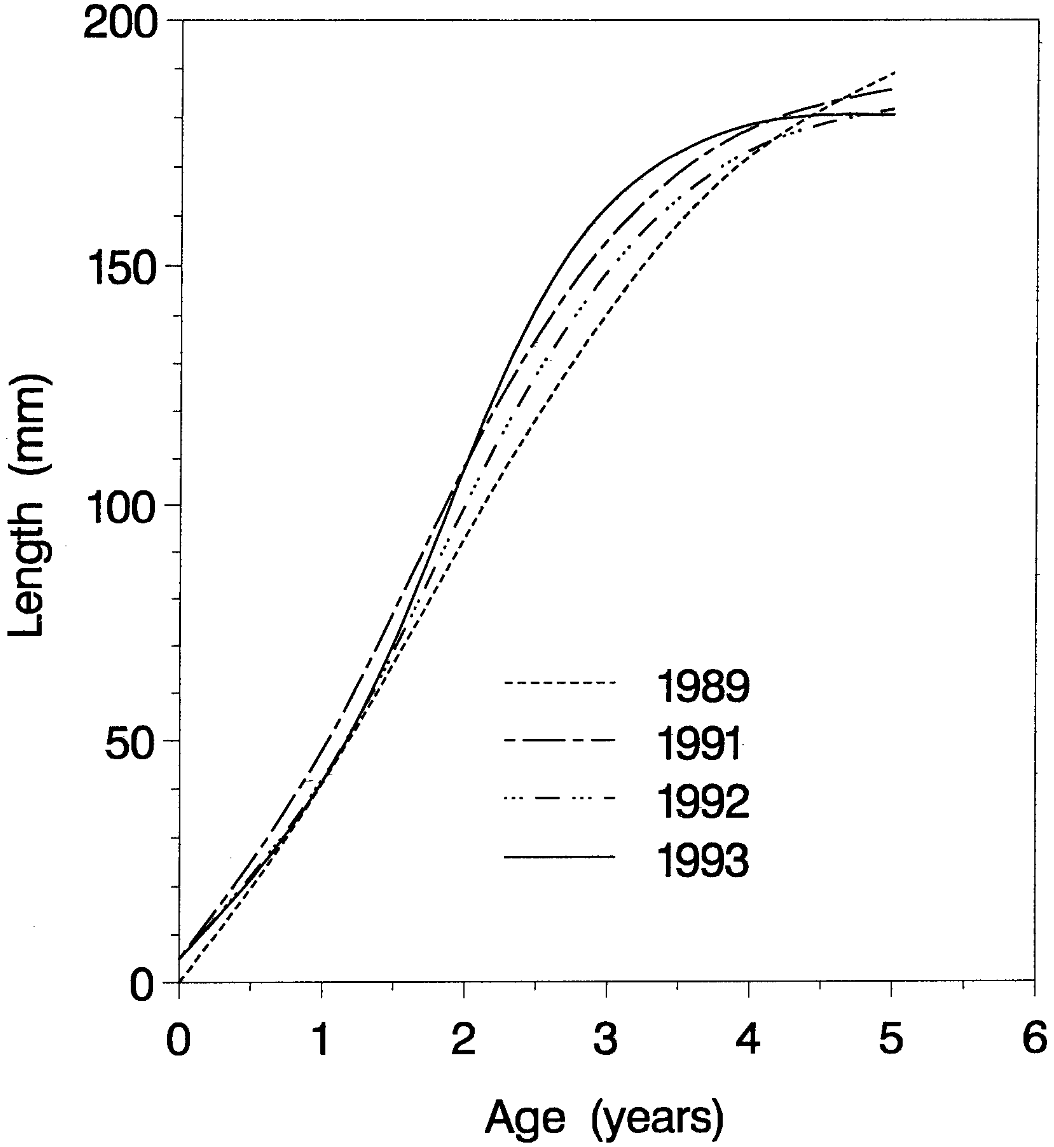
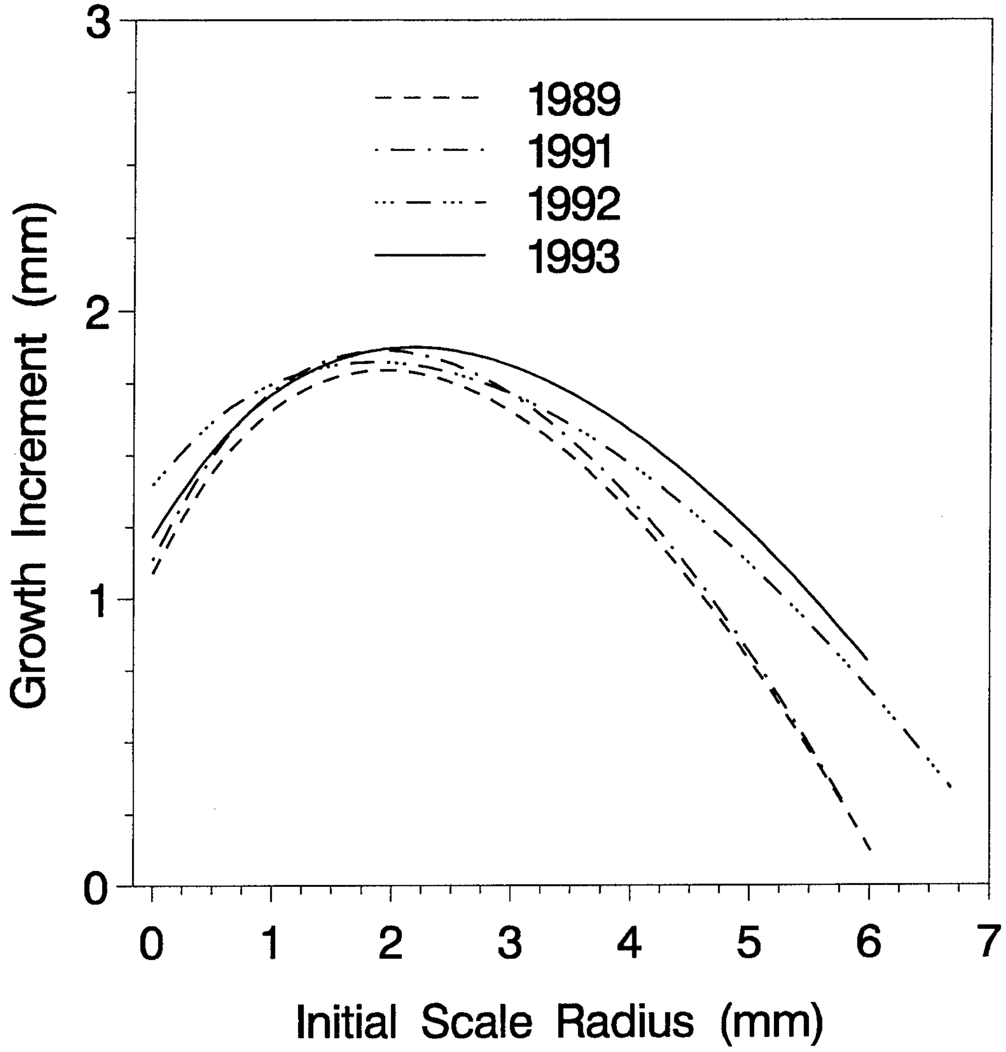

200
150
100
50
0
Length (mm)
0
1
2
3
4
5
6
Age (years)
1989
1991
1992
1993

Figure 11. Gompertz growth curves depicting differences in size-specific growth rates of black crappie from scale data. All fish were collected from Navigation Pool 8, upper Mississippi River.



1989
1991
1992
1993
Growth Increment (mm)
0
1
2
3
Initial Scale Radius (mm)
0
1
2
3
4
5
6
7

scale growth occurred for these fish during the 1993 flood year, and the slowest growth occurred during the drought year. Growth patterns during the normal flow years differed from each other. Growth in 1991 was more similar to that in 1989, whereas growth in 1992 was more similar to that in 1993. Figure 12 shows the raw data points and the fitted Gompertz curves developed by the model ($r^2 = 0.59$).

Estimates of annual length increments of black crappie (Figure 13) were back-calculated from the scale measurements. Differences in growth rate among years were observed when fish surpassed 150 mm TL. The greatest difference among years in growth increments was about 25 mm for fish that were 250 mm TL at the start of the year.

The additive effects of each growth curve demonstrate potential effects on black crappie if each annual growth pattern could be maintained over time. The growth equations for the flow regime from each year (Figure 14) produced similar additive effects until fish reached age 3+. Maximum differences in total length occurred at age 5+ and amounted to 35 mm. For small black crappie, the projected growth curves indicated similar growth among flow regimes.

Freshwater Drum. The ANCOVA model for freshwater drum revealed significant differences in growth between the flood year and all other years combined and between each year of normal flow and the flood (Table 4). The interaction terms

Figure 12. Plots of growth increment on initial scale radius for black crappie collected in Navigation Pool 8, upper Mississippi River in 1989 (A), 1991 (B), 1992 (C), and 1993 (D). The solid line indicates the Gompertz curve, which models the data.

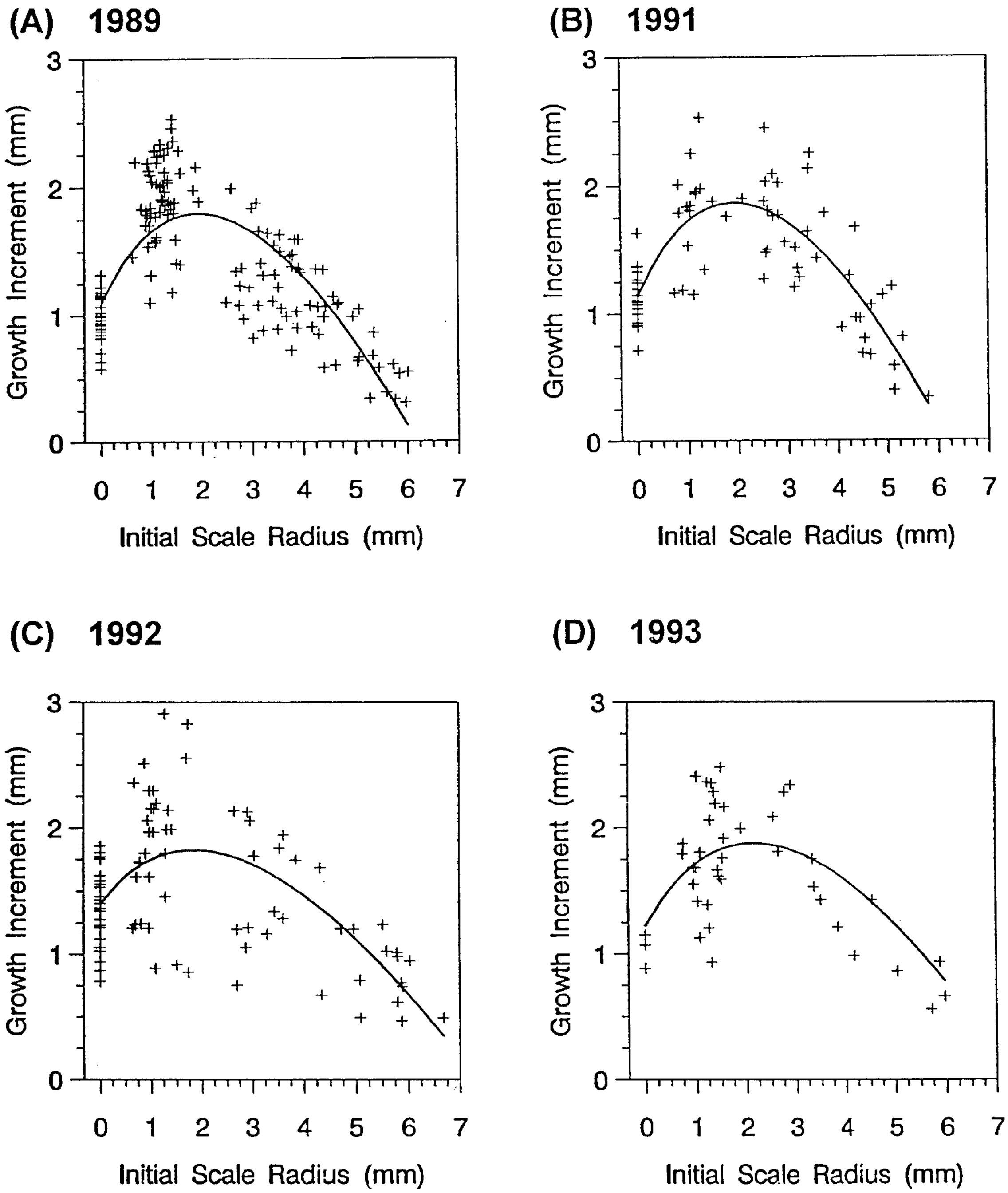

(A) 1989
(B) 1991
(C) 1992
(D) 1993
Growth Increment (mm)
0
1
2
3
Initial Scale Radius (mm)
0
1
2
3
4
5
6
7

Figure 13. Estimated growth increments and initial length of black crappie, back-calculated from scale data. All fish were collected from Navigation Pool 8, upper Mississippi River.

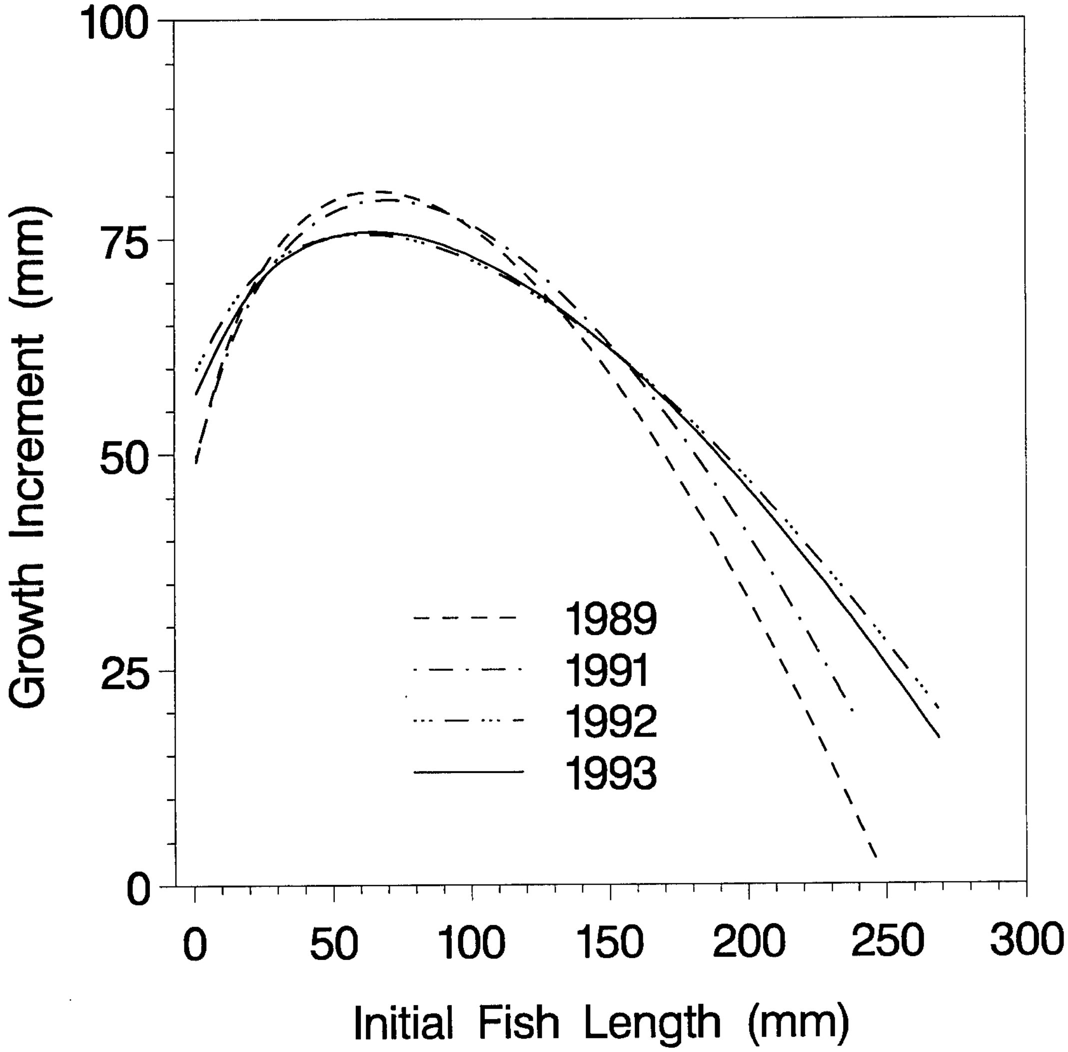
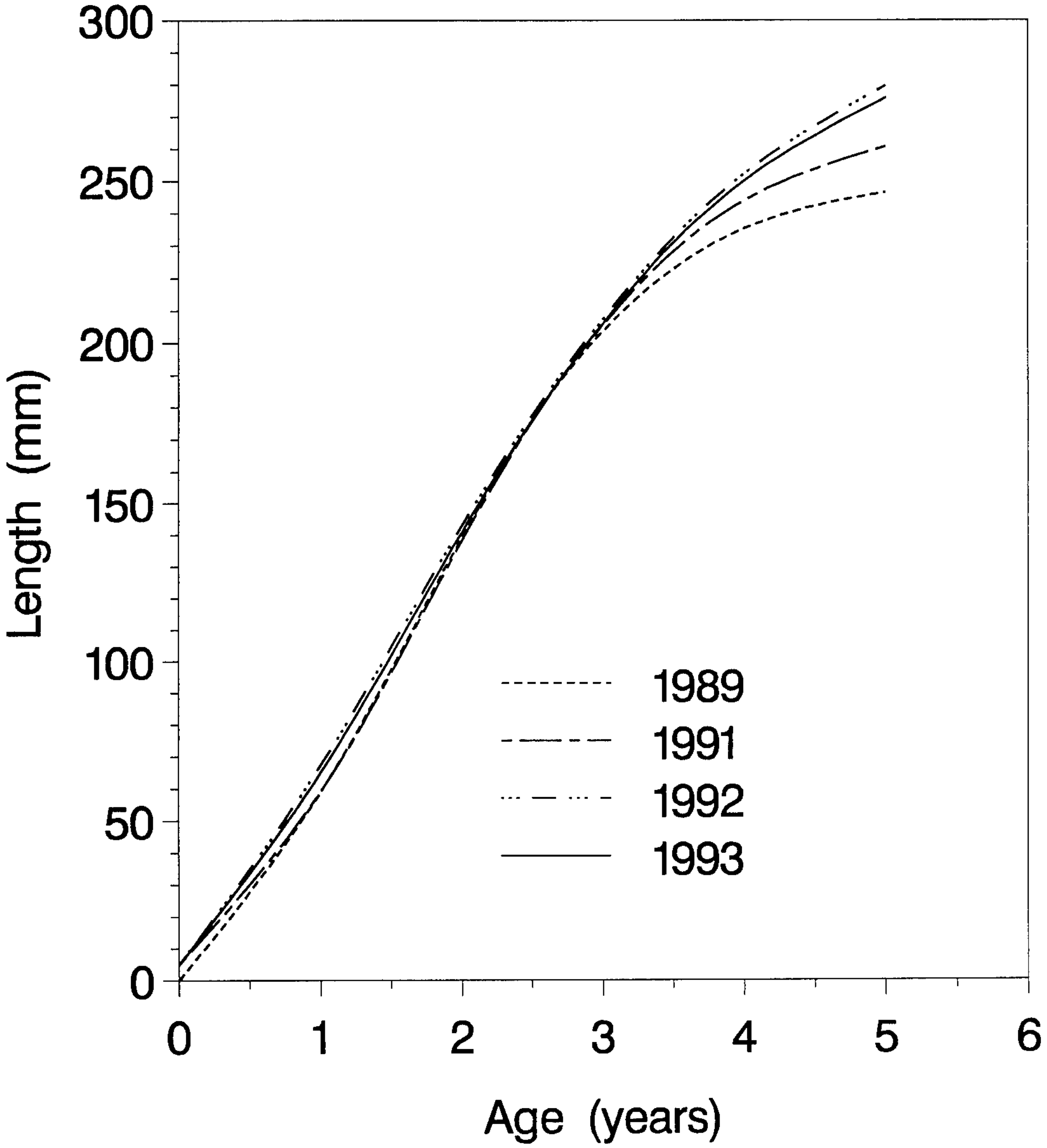

100
75
50
25
0
0
50
100
150
200
250
300
Growth Increment (mm)
Initial Fish Length (mm)
1989
1991
1992
1993

Figure 14. Estimated length-at-age of black crappie collected under different hydrologic regimes from Navigation Pool 8, upper Mississippi River.



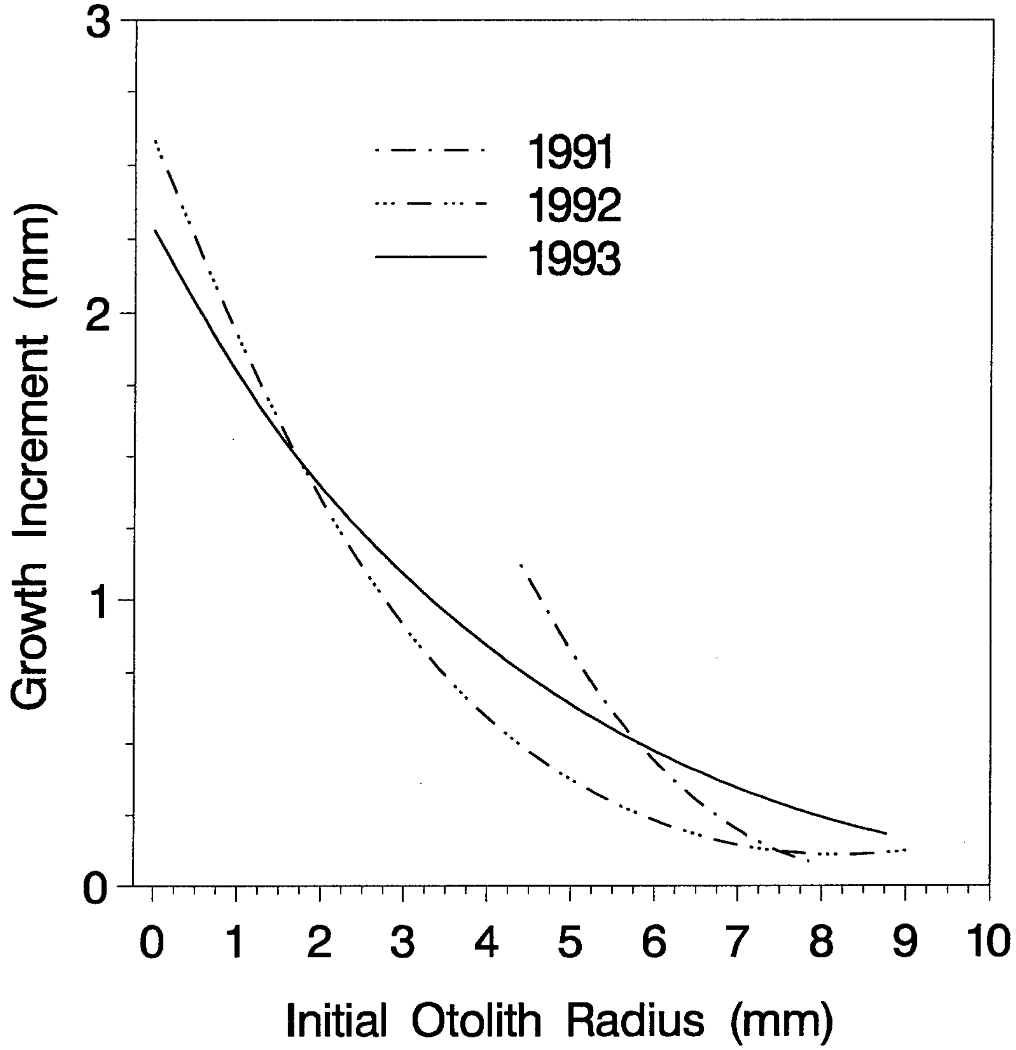
300
250
200
150
100
50
0
Length (mm)
0
1
2
3
4
5
6
Age (years)
1989
1991
1992
1993

showed that size-specific differences in growth were apparent among years; both terms were highly significant. Overall linear and curvilinear effects were evident. Differences were highly significant for both (R) and (R)log(R). These statistical results indicate the coefficient for each of the overall slope terms was different from zero.

The Gompertz curves developed from otolith increments of freshwater drum (Figure 15) showed that differences in growth rate were evident among years for all sizes of otolith. Fish with small otoliths grew fastest in 1992, but fish with intermediate and large otoliths grew fastest in 1993. Although the curve for 1991 was incomplete because small otoliths were unavailable, it indicated that growth of fish with small otoliths during 1991 may have surpassed that of the other two years. Figure 16 shows the raw data points and the fitted Gompertz curves developed by the model (r^2 = 0.87).

Estimates of annual length increments for freshwater drum (Figure 17) were back-calculated from the otolith measurements. Growth was fastest in 1993 for drum greater than 100 mm at the start of the season. The greatest differences in growth between 1991 and 1993 occurred in fish with the largest initial length (about 430 mm). Differences between 1992 and 1993 were greatest in fish with an initial

Figure 15. Gompertz growth curves depicting differences in size-specific growth rates of freshwater drum from otolith data. All fish were collected from Navigation Pool 8, upper Mississippi River.



3
2
1
0
Growth Increment (mm)
1991
1992
1993
0
1
2
3
4
5
6
7
8
9
10
Initial Otolith Radius (mm)

Figure 16. Plots of growth increment on initial otolith radius for freshwater drum collected in Navigation Pool 8, upper Mississippi River in 1991 (A), 1992 (B), and 1993 (C). The solid line indicates the Gompertz curve, which models the data.

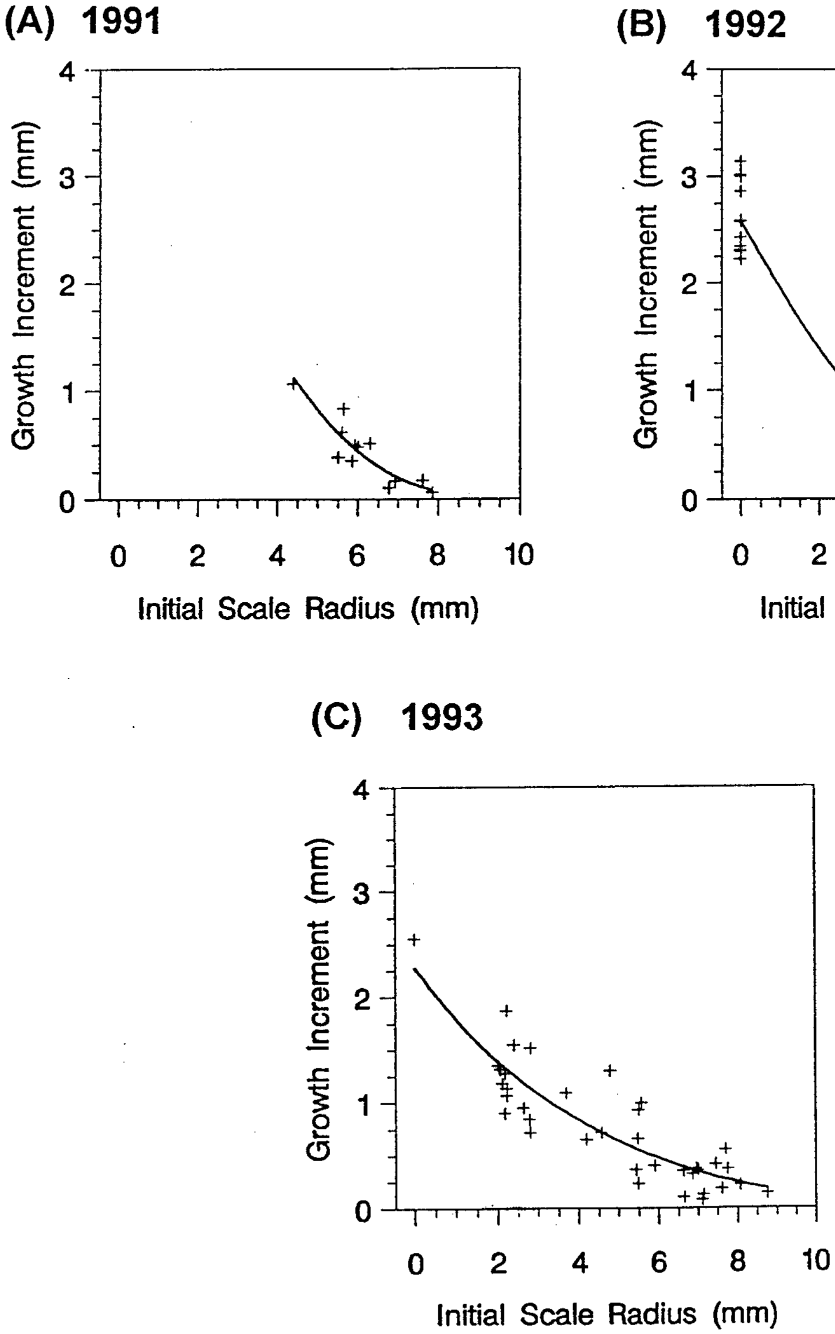
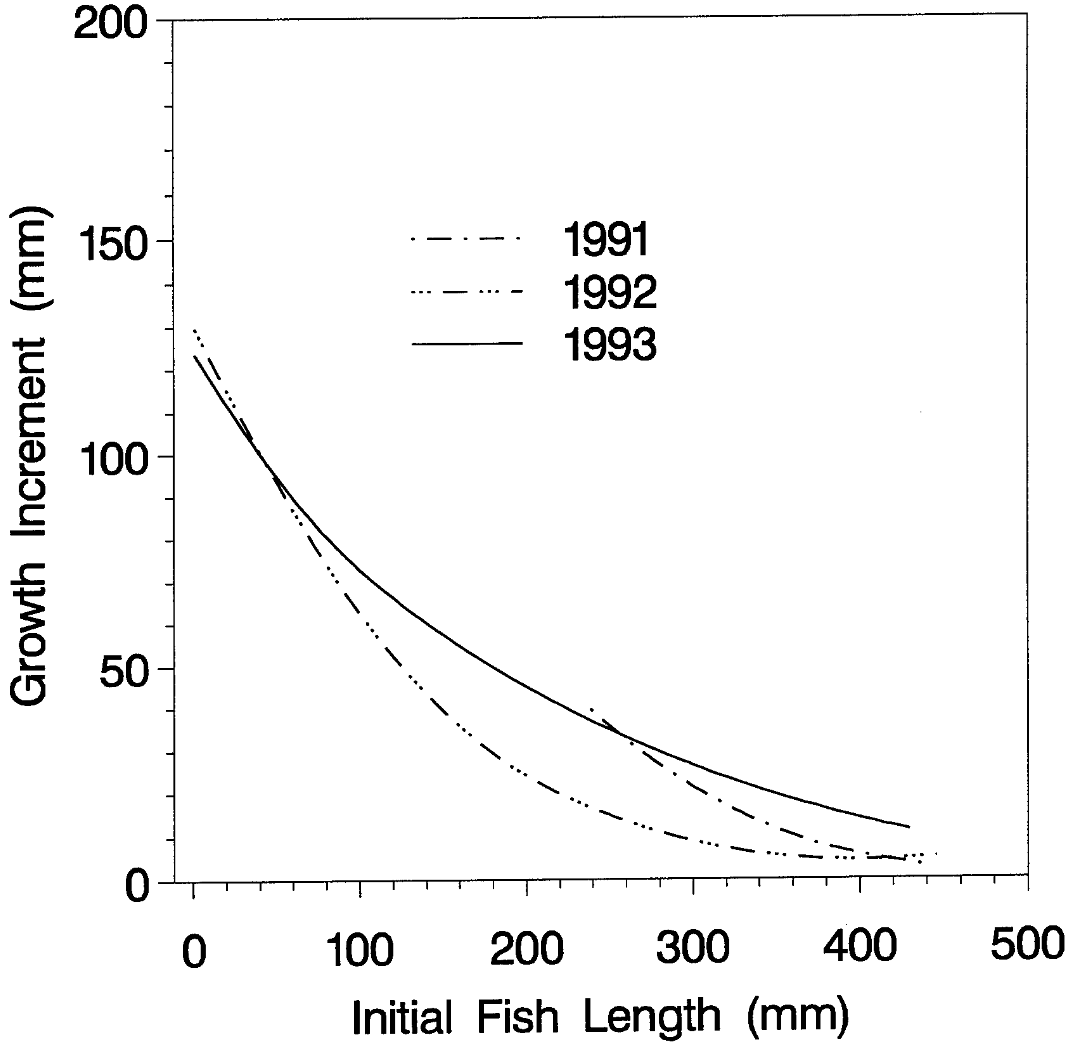

(A) 1991
Growth Increment (mm)
Initial Scale Radius (mm)
0
1
2
3
4
0
2
4
6
8
10
(B) 1992
Growth Increment (mm)
Initial Scale Radius (mm)
0
1
2
3
4
0
2
4
6
8
10
(C) 1993
Growth Increment (mm)
Initial Scale Radius (mm)
0
1
2
3
4
0
2
4
6
8
10

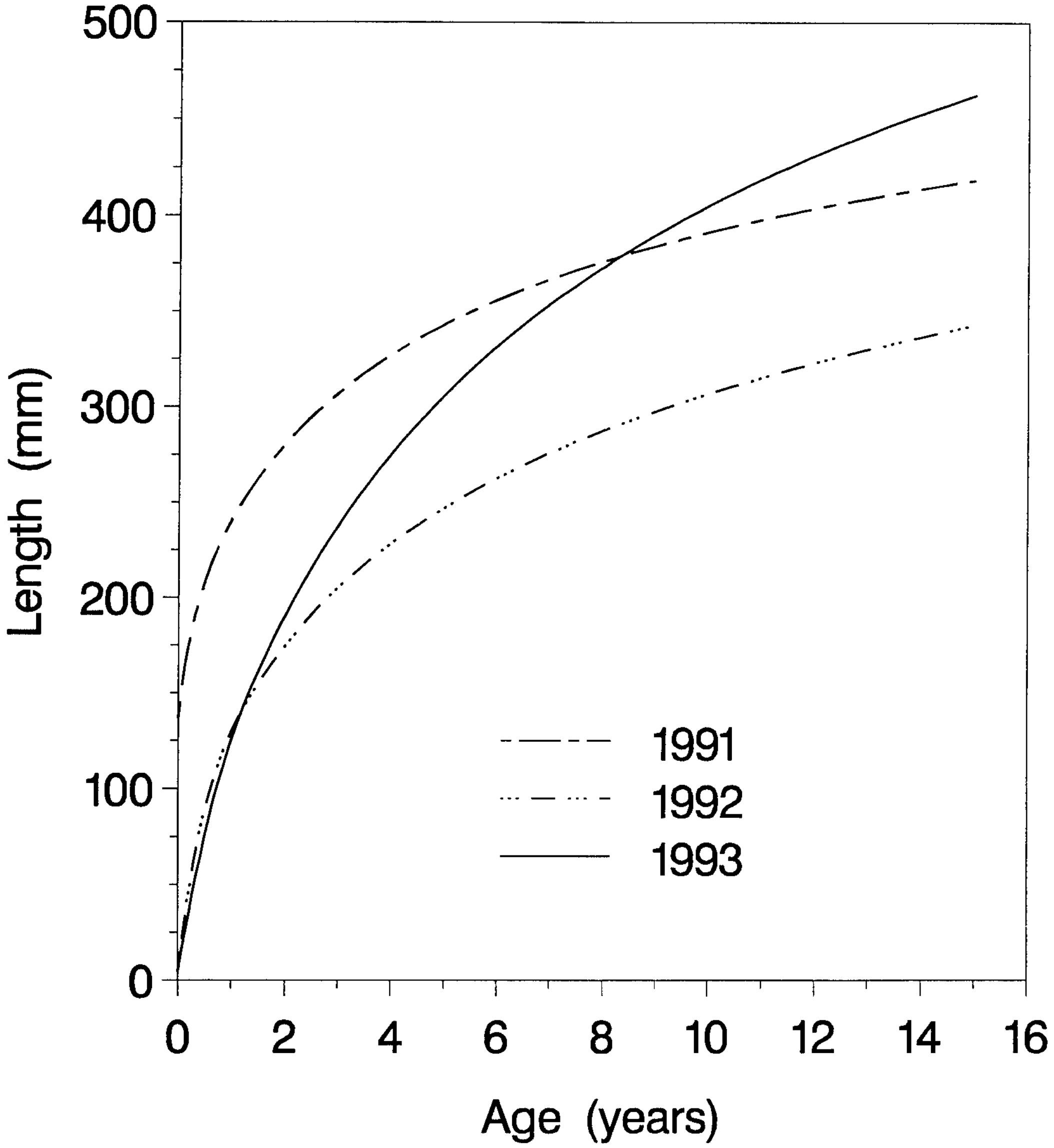
Figure 17. Estimated growth increments and initial length of freshwater drum, back-calculated from scale data. All fish were collected from Navigation Pool 8, upper Mississippi River.


200
150
100
50
0
Growth Increment (mm)
0
100
200
300
400
500
Initial Fish Length (mm)
1991
1992
1993

length of about 260 mm TL; fish grew about 25 mm more in 1993 than in 1992.

The potential effect of constant hydrologic regimes on freshwater drum growth was estimated with length-at-age curves to demonstrate effects on fish size if each of the three growth patterns were constant over time (Figure 18). The magnitude of potential differences due to hydrologic regime was greater for freshwater drum than for bluegill and black crappie. For drum up to age 8, the 1991 flow regime would produce the largest fish. Although the 1991 curve appears to intercept the y-axis at 150 mm, all three curves intercept at 5 mm. The growth rates exhibited in 1993 (flood regime) would eventually produce larger fish than growth rates from 1991 if the observed growth pattern could be sustained for more than 8 years. After 8 years, growth rates from the 1991 and 1993 flow regimes would produce fish about 100 mm longer than growth rates from 1992.

Figure 18. Estimated length-at-age of freshwater drum collected under different hydrologic regimes from Navigation Pool 8, upper Mississippi River.



500
400
300
200
100
0
Length (mm)
0
2
4
6
8
10
12
14
16
Age (years)
1991
1992
1993

DISCUSSION

Growth of Fish in Relation to Flow Regimes

Flood Responses. The patterns of fish growth observed in my study were consistent with some of the basic tenets of the FPC. Size-specific growth rates of bluegill were significantly greater during the flood of 1993 than during three previous growing seasons and were directly related to water surface elevations during the growing season. Growth rates for black crappie were greater during the flood year only when the drought year was added to the comparison. Growth of freshwater drum during the flood year was intermediate to that during the two prior years. This gradient of fish growth patterns in relation to water level regimes was expected and is consistent with the expected level of floodplain use and vegetation association by each species.

The FPC hypothesizes that river fish are adapted to take advantage of favorable floodplain conditions during flood pulses. Presumably their ability to exploit food resources that are temporarily abundant during floods is an adaptation that would result in increased biomass. During a flood, inundated terrestrial vegetation becomes an available substrate for production of aquatic macroinvertebrates as the ATTZ moves across the floodplain. This should provide opportunities for short-term increases in macroinvertebrate populations. Terrestrial macroinvertebrates also become available as food sources to fish. Thus, abundant macroinvertebrates should provide abundant food for fish adapted to these flooded terrestrial habitats.

For bluegill, increases in growth could be attributed to increased food availability if macroinvertebrate populations increased during the flood. Small bluegill are restricted to littoral areas (Mittlebach 1981, 1984) and feed almost exclusively on invertebrates. Larger bluegill often have a diversified diet and feed on zooplankton (Mittlebach 1981), insects and small fish (Becker 1983), and plants (Seaburg and Moyle 1964). Additionally, small bluegill seem to be more efficient than large bluegill at competing for invertebrates (Seaburg and Moyle 1964). This may explain the greater increases in growth rates during the flood for small and medium but not large bluegill.

Growth of black crappie during the flood was greater than during the drought year, but was not greater than growth during normal flow years. Also, the greater growth rates were only evident for very large black crappie. Reasons for this departure from the patterns observed for bluegill may have been related to slight differences in habitat and food preference between the two species. Black crappie eat fish, insects, and other invertebrates (Seaburg and Moyle 1964, Becker 1983), but fish often make up a majority of the diet (Becker 1983). The density of small fishes as food for black crappie probably decreased during the flood year, due to the dilution factor of the higher water levels. In addition, black crappie tend to maintain their position above the bottom in deep water (Becker 1983); therefore the greater macroinvertebrate populations associated with flooded vegetation may not have been as readily available to them. The combination of these two factors during the flood may have been responsible for the maintenance of growth rates only at or slightly above normal.

As expected, freshwater drum did not clearly exhibit greater growth during the flood. Growth of small drum during the flood year was apparently less than that of 1991 and 1992, but large drum grew faster during the flood year than in either previous year. This may indicate that large fluctuations in growth are normal for freshwater drum or that drum actually showed a response to the flood pulse. The smaller sample size for freshwater drum and the narrow range of fish length in the 1991 collection made interpretation of growth effects more uncertain than for bluegill and black crappie. A larger sample and more complete size distribution in the sample may have indicated growth patterns more clearly. Because the magnitude of change in food supply would be less in channel than backwater areas I hypothesized that freshwater drum, as a channel-oriented species, would have been less likely to show a growth response to a flood pulse than backwater-oriented fishes. Perhaps freshwater drum were adaptable enough to switch habitat preferences to take advantage of the potentially large increase in macroinvertebrate populations in the flooded backwater areas. The likely benefits of a large flood pulse to the growth of a channel-oriented species would further support the FPC.

Drought Responses. The negative growth response exhibited by bluegill and black crappie to the drought of 1989 adds significantly to the discussion of growth responses of riverine fish to fluctuating water levels. For bluegill and black crappie, the effects of the drought were apparently greater than the effects of the flood. This is demonstrated by the magnitude of differences between the Gompertz curves for flow regimes of flood, normal, and drought years. Although effects of the flood were observed for both species, they were not statistically significant for black crappies. The implications may be that ecological effects of a severe drought are potentially greater than those of a severe flood, however little work has been done on the effects of drought on the ecology of large floodplain rivers. This is an area that merits attention. Moreover, studies are needed to evaluate (1) the thresholds of flood pulse required to change fish growth rates and (2) if this threshold differs among species. A long term data set will be important to discern if the growth of fish is enhanced by floods, suppressed by droughts, or if my data reflect random coincidence.

Practical Signifcance of Growth Responses. Differences in total length of fish projected from growth rates under each hydrologic regime are subtle for bluegill and black crappie, i.e. projected to be less than 25 mm per year. In contrast, the magnitude of differences in growth of freshwater drum were greater among years (up to 100 mm), but lengths of drum were also greater than those of bluegill and black crappie. These projected differences would become apparent only if the growth patterns of each flow regime were repeated over time. The range of estimates of growth for the three species in this study are similar to those previously reported for the UMR (Becker 1983). The growth rates for bluegill during the flood, however, were greater than average. These differences in growth may be meaningful because greater growth may reduce over-winter mortality, increase egg production, or enhance the ability to escape predators. Even if natural mortality rates of bluegill were constant for all sizes, say 20% annually, the observed differences in growth of bluegill between 1989 and 1993 would result in at least a 20% difference in the abundance of quality size (150 mm) fish.

Other Factors That May Influence Growth

Factors other than hydrology must also be considered in future studies to address the mechanisms that affect growth. For example, changes in mean monthly water conductivity values had the same pattern as flow and growth rates, but mean monthly water temperatures were similar from year to year. Although conductivity is only vaguely related to nutrient levels, the relationship between concentrations of dissolved ionic nutrients, primary and secondary producers is likely a key in understanding how river hydrology affects growth rates of riverine fishes. If the abundance of primary producers is linked to the flood pulse by nutrient supply, then the invertebrates that feed upon the primary producers, as well as the fish that feed upon the invertebrates, will also be affected. Putman et al. (1995) found that biological, physical, and chemical variables could account for 67-99% of the variation in growth of several combinations of species and sizes of fish. The challenge remains to identify and adequately measure pertinent environmental variables that influence growth of fish in large floodplain rivers.

In conjunction with physical factors, ecological variables such as fish density probably affect growth of riverine fish. If changes to the prey base, due to drought, limit availability of food, competition among predators for scarce resources may increase. Conversely, competition among predators may decrease if predator populations become diluted and prey communities flourish under FPC effects. Water elevation changes, and therefore changes in the volume of aquatic area, may affect growth through density-dependent mechanisms mediated by differential dilution of predators and prey. For example, electrofishing catch rates for bluegills have declined in Pool 8 from 1989 to 1993 (author, unpublished data). The combination of reduced density of fish between the drought of 1989 and the flood of 1993, coupled with greater production of invertebrates since the drought, may have contributed to the growth I observed. Moreover, low water levels during the drought probably magnified density-dependent ecological effects. Crowding affects not only somatic growth but also fecundity, egg deposition, predator/prey relationships, behavior, and fitness (Goodyear 1980). These factors almost certainly act in combination, and could have influenced the fish community during and after the drought. Examples of these influences include increased competition for spawning sites and overwintering habitat, increased displacement and exposure to predators, and increased metabolism and stress due to agonistic behavior.

Data from other reaches of the UMR must be examined to determine the extent of flood effects and the generality of my results. For example, the magnitude and duration of the 1993 flood were lesser in Pool 8 than in downstream reaches, which may suggest that effects on growth should have been magnified downstream as the scale of the flood increased. Rutherford et al. (1995) examined four common riverine fishes in the lower Mississippi River, where the area of the floodplain has been reduced by levee construction, and found no relationship between flood events and fish growth. The data of Rutherford et al. (1995) and my data might suggest that the upper, unleveed reach of the UMR is the only remaining section of this river where the FPC is still operating. A record of growth over time from several reaches would allow for better comparisons of relative changes in growth due to floods; however, differences in length of growing season would confound direct annual comparisons for different reaches of the river.

Future Directions of Hydrologic Management

This study also raises the question of whether there are strategies for water level management that may be beneficial to biota of the river. The data presented here are consistent with FPC predictions and suggest that the differences in observed growth rates of some riverine fishes may have been due to differences in annual hydrographs. Refined knowledge of the causal mechanisms involved in regulating fish growth will eventually lead to better management to achieve the water levels required for navigation and flood control, while simultaneously benefitting fish and wildlife. It may be possible to mimic the natural hydrograph and still maintain multiple-use management of the UMRS. I recommend that the water-level experiments presently occurring in the downstream reaches of the river be expanded to the upstream reaches. This experimental approach would be superior to waiting for opportunities to study future floods and droughts.

The unanswered questions that remain illustrate the need to remain inquisitive. Events that have the potential to affect whole ecological systems are usually unpredictable. Large floodplain rivers are particularly unpredictable because major disturbances anywhere in the watershed can affect the mainstem. To effectively study disturbances like floods or droughts, basic data must be routinely collected on both organisms and processes. For example, a hypothesis based on data from this study might be that reproductive output of fish is enhanced in the immediate years following a flood, due to increased size and fitness of fish. Another hypothesis could be that some species are more able than others to benefit from flood pulses based upon their ability to switch food sources. Special studies would be of little value in these cases because no baseline data would be available. This is why monitoring is important. However, monitoring must be desgined to collect data that can answer specific questions, in addition to providing baseline, general data. Theories such as the FPC and events like the drought of 1989 or the flood of 1993 should serve to stimulate discussion among biologists on what data are needed to better understand riverine ecological processes, and how best to collect those data.

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13. ABSTRACT (Maximum 200 words)

Size-specific growth of bluegill, black crappie, and freshwater drum was significantly different over four years in Navigation Pool 8 of the upper Mississippi River. Differences in growth were positively related to annual hydrographs for bluegill but less related to hydrographs for black crappie and freshwater drum. These results are consistent with predictions of the Flood Pulse Concept. Extensions of analysis of covariance (ANCOVA) models were used to account for differences in growth due to the size of fish and tested for annual differences in growth rates. Planned comparisons examined differences in growth among years with a large flood event, two years of normal hydrology, and a drought. Some sizes of bluegill and freshwater drum, but not black crappie, grew significantly faster during the flood year than during years of normal flow. Some sizes of bluegill and black crappie grew slower during the drought year when freshwater drum were not sampled. Growth curves for bluegill and black crappie indicate that the magnitude of the effects on growth rate was greater for the drought year than for the flood year. Differences in growth rate among years were most apparent for bluegill from 50 - 100 mm, black crappie greater than 200 mm, and drum longer than 100 mm. These data suggest that (1) patterns in growth for some riverine fishes are consistent with the Flood Pulse Concept, (2) droughts may be of greater consequence than floods to riverine communities, and (3) growth responses related to hydrology are size- and species-specific.

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The Long Term Resource Monitoring Program (LTRMP) for the Upper Mississippi River System was authorized under the Water Resources Development Act of 1986 as an element of the Environmental Management Program. The mission of the LTRMP is to provide river managers with information for maintaining the Upper Mississippi River System as a sustainable large river ecosystem given its multiple-use character. The LTRMP is a cooperative effort by the U.S. Geological Survey, the U.S. Army Corps of Engineers, and the States of Illinois, Iowa, Minnesota, Missouri, and Wisconsin.