Population Structure and Habitat Use of BENTHIC FISHES along the Missouri and Lower Yellowstone Rivers

Volume 4

Fish Growth, Mortality, Recruitment, Condition, and Size Structure

Project Volume

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PREFACE

POPULATION STRUCTURE AND HABITAT USE OF BENTHIC FISHES ALONG THE MISSOURI AND LOWER YELLOWSTONE RIVERS

This research is reported in the 12 volumes listed below. Reports are available through the U. S. Army Corps of Engineers, the primary contracting agency for the overall project. Contact: Becky Latka, U. S. Army Corps of Engineers, CENWO-PM-AE, 106 South 15th Street, Omaha, NE 68102, (rebecca.j.latka@usace.army.mil, 402/221-4602) for paper copies or access online in PDF format at: http://www.nwo.usace.army.mil/html/pd-e/planning.html. Anticipated date of publication is in (parentheses) for volumes not yet available. Please use the citation format suggested here without the email address when referencing Final Report volumes.

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EXECUTIVE SUMMARY

Population-level characteristics such as growth, condition, size-structure, survival and recruitment are important indicators of the well-being of fish populations. Measurement of population-level characteristics is a cornerstone of fishery management assessments. In contrast, biological studies for environmental assessment have focused more on community-level characteristics, such as species richness, evenness, diversity, proportions of functional groups, and composite indices based on the numbers or proportions of species or functional groups. Population-level assessments are an important partner with community-level approaches to fully characterize environmental quality and status as it relates to the biota.

Growth of fishes is a simple concept on the surface, but in practice it is a highly complex phenomenon because of the indeterminate nature and plasticity of growth throughout the life cycle of fishes. We used several approaches in this report to quantify, describe and compare growth in an attempt to satisfy a range of potential future uses for growth information.

Condition is commonly used in fish population assessment. Condition refers to the weight of a fish for its length, and thus is a measure of “plumpness”. Condition reflects various characteristics of fish, such as feeding history, reproductive state and health, as well as characteristics of the environment, such as water quality, habitat quality and food availability.

Size structure, particularly the proportional stock density (PSD) and relative stock density (RSD) indices, are also widely used in fish population assessment. PSD and RSD refer to proportions of the population of stock-length or greater fish that are also longer than quality length (PSD) or one of the larger length categories (RSD). Size structure reflects the growth and survival rates of unexploited populations; faster growth and greater survival both result in higher PSD and RSD values. Recreational and commercial harvest generally lowers size structure index values, since harvest usually targets the largest individuals. Differential mortality among size classes, for example size-selective predation mortality, can have variable effects on size structure values.

Survival and recruitment are related processes that are central to fish population dynamics studies. Survival is typically expressed as the proportion of individuals surviving for a specified period of time, usually a year. Survival may reflect natural environmental factors such as predation, resource availability, water quality and habitat quality, as well as recreational and commercial exploitation. Recruitment is the process by which new cohorts enter the population, and thus is a reflection of reproduction by the adult population and survival of the cohort. Year-to-year variability is a hallmark of many fish populations, and the magnitude of this variation is another potential response to environmental factors. One of the ways of expressing recruitment variation is the presence of missing year classes in a sample of the population.

This study is part of a comprehensive investigation of population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone Rivers. The goal of this study was to assess population-level characteristics of fifteen fish species in the Missouri and lower Yellowstone rivers, and explore spatial patterns of these characteristics in relation to natural environmental gradients, flow regimes, and human alteration. Our specific objectives were to: (1) quantify growth, condition, size structure, survival and

recruitment deficiencies among fifteen river segments, (2) analyze sources of variation in population-level characteristics, and (3) describe relationships with natural environmental gradients (e.g., distance from river mouth, temperature), flow regimes, and human alteration (e.g., reservoir influence, channelization).

The Missouri River flows 3,768 km from its origin at the confluence of the Gallatin, Madison and Jefferson rivers near Three Forks, Montana, generally east and south to its terminus with the Mississippi River just upstream from St. Louis, Missouri. It is the longest river in the conterminous United States with a catchment encompassing about 1,327,000 km^2, or about one-sixth of the conterminous United States.

The Missouri River is divided into three approximately equal length zones. The upper 1,241 km represents a “least-altered” zone relative to the remaining river. The 1,316-km-long middle or “inter-reservoir” zone was impounded between 1937 and 1963 by six large mainstem reservoirs (total gross volume: 90.7 km^2; total average annual discharge: 100.5 km^3 yr^{-1}). Flows in the 1,212 km long lower zone are also regulated by upstream reservoirs, although reductions in spring-summer high flows are somewhat offset in lowermost reaches by tributary input. In addition, channel-floodplain morphology in the lowermost zone from Sioux City, Iowa (km 1,178), to the mouth was altered by channelization, bank stabilization, and levee construction and encompasses the “channelized” zone.

To assess spatial variation in benthic fish population characteristics, we used a hierarchical framework to divide the river into segments and zones. Segments were contiguous stretches of river, separated by geomorphic, hydrologic and constructed features. Fifteen segments were sampled in this study. Zones were groups of segments similar in their degree of human alteration. Three zones were recognized in this study. The least-altered (LA) zone consisted of segments in the upper Missouri River and the Yellowstone River segment, characterized by relatively little flow regulation and habitat modification. The inter-reservoir (IR) zone consisted of segments located between or just downstream from the major main-stem reservoirs in the middle portion of the Missouri River, characterized by significant flow regulation and varying degrees of thermal and turbidity alteration. The channelized (CH) zone consisted of segments in the lower Missouri River, characterized by significant flow regulation and alteration of in-stream and floodplain habitat due to channelization.

For analyses of condition, size structure and mortality, we modified the zone classification to include two additional groups. The Yellowstone River segment (YS) was separated from the two Missouri River LA segments, and the lowermost IR segment (LC) was separated from the other IR segments. The five areas resulting from this classification are hereafter referred to as “groups”.

To assess variation in benthic fish population characteristics due to differences in flow regime, we divided the river into six hydrological units. Hydrological units were groups of segments exhibiting similar flow regimes as determined by an analysis of mean daily flow data from U.S. Geological Survey gauging stations. The upper unchannelized (UU) unit consisted of segments in the upper Missouri River, characterized by high flows per unit drainage area and relatively high flow variability. The inter-reservoir 1 (IR-1) unit consisted of the segments immediately downstream from Ft. Peck and Sakakawea Reservoirs, characterized by low flow variability and high flow constancy. The inter-reservoir 2 (IR-2) unit consisted of the segment located roughly midway between Ft. Peck and Sakakawea Reservoirs; this unit is similar to IR-1 except for much higher flow variability due to local tributary input. The unchannelized Yellowstone (UYS) unit consisted of the single segment on the Yellowstone River, characterized by high flow variability and low flow constancy. The channelized units in the lower Missouri River had higher flow contingency than the other units, but contrasted dramatically in their flow variability. The upper channelized (UC) unit consisted of the segments between Gavin's Point Dam and Kansas City, MO, characterized by low flow variability. In contrast the lower channelized (LC) unit, consisting of the segments between Kansas City, MO and the mouth, was characterized by much higher flow variability reflecting input from several large tributary rivers.

Fish were collected from each river segment using a standardized protocol designed to capture both small and large-bodied fish in all available macrohabitats. Five sampling gear types were used: bag seines, benthic trawls, boat electrofishers, stationary gill nets and drifted trammel nets. All collected fish were identified to species and enumerated. Additional information was obtained from 15 target species, including blue sucker *Cycleptus elongates*, brassy minnow *Hybognathus hankinsoni*, channel catfish *Ictalurus punctatus*, emerald shiner *Notropis atherinoides*, flathead catfish *Pylodictis olivaris*, flathead chub *Platygobio gracilis*, freshwater drum *Aplodinotus grunniens*, plains minnow *Hybognathus placitus*, river carpsucker *Carpiodes carpio*, sand shiner *Notropis stramineus*, sauger *Sander canadense*, shovelnose sturgeon *Scaphirhynchus platorhynchus*, sicklefin chub *Macrhybopsis meeki*, smallmouth buffalo *Ictiobus bubalus*, and western silvery minnow *Hybognathus argyritis*.

For ageing and back-calculation, scales, otoliths, pectoral spines or pectoral fin rays were removed from captured specimens, depending on species. Scales were used for blue sucker, brassy minnow, emerald shiner, flathead chub, plains minnow, river carpsucker, sand shiner, sicklefin chub, smallmouth buffalo and western silvery minnow. Otoliths were used for freshwater drum and sauger. Pectoral spines were used for channel and flathead catfish, and pectoral fin rays were used for shovelnose sturgeon. Radii and inter-annular distances on ageing structure preparations were measured using a dissecting microscope and a computerized video image analysis system. Two methods were used for back-calculating lengths at previous ages. For scales, we used the Fraser-Lee technique. For other ageing structures we used the Dahl-Lea method.

Using back-calculated lengths-at-age from individual fish we tabulated mean length-at-age for each species by segments, hydrological units and zones. We tested spatial (segment, hydrological unit and zone) and year effects on length at age-1 with ANOVA, and expressed the percentage of variance due to main effects and interactions in each test with variance components. We used two approaches to test for differences in length-at-age among specific spatial units when the main effect was significant. We used six planned contrasts to test for differences among groups of segments. One contrast tested for differences between the Missouri River LA segments and the lower Yellowstone River LA segment (3, 5 vs. 9). A contrast tested for differences between the Missouri River LA segments upstream from Ft. Peck Lake and the IR segments immediately below Ft. Peck Lake (3, 5 vs. 7, 8). A contrast tested for differences between the IR segments immediately below Ft. Peck

Lake and the lower Yellowstone River LA segment (7, 8 vs. 9). A contrast tested for differences between the IR segments above Lewis and Clark Lake and the IR segment below Gavins Point Dam (7, 8, 10, 12, 14 vs. 15). A contrast tested for differences between the IR segment below Gavins Point Dam and the CH segments (15 vs. 17, 19, 22, 23, 25, 27). Finally, a contrast tested for differences between the CH segments upstream of Kansas City, MO and the CH segments downstream of Kansas City (17, 19, 22 vs. 23, 25, 27). For pairwise comparison among segments, hydrological units and zones we used Tukey's tests.

To test for growth differences occurring throughout life, we used Weisberg's age-specific ANOVA method for testing spatial (segment, hydrological unit and zone), age and year effects on annual growth, as represented by annual growth increments on ageing structures. Percentages of variance due to main effects and interactions were determined using variance components analysis. The scope of these tests encompassed growth during the entire life history, "factoring out" the relatively large effect of fish age and enabling examinations of the more subtle effects of location and year.

We fit von Bertalanffy growth functions (VBGF) to describe increases in length-at-age for eight of the fifteen species by segment, hydrological unit and zone. The purpose of the VBGFs was to illustrate changes in length-at-age and to provide readers with VBGF parameter estimates, not to test for differences between spatial units.

We used locally weighted scatterplot smoothing (LOWESS) regression to model the size-specific growth responses for twelve of the fifteen species by segment, hydrological unit and zone. We used LOWESS regressions to estimate annual growth rate of each species at their length at maturity.

We used relative weight to index condition of common carp, channel catfish, flathead catfish, freshwater drum, river carpsucker, sauger, and shovelnose sturgeon. We calculated mean W_r by length category (S-Q, stock to quality; Q-P, quality to preferred; P-M, preferred to memorable; M-T, memorable to trophy).

Size structure was quantified using proportional stock density (PSD), relative stock density of preferred-length fish (RSD-P), and relative stock density of memorable-length fish (RSD-M) for common carp, channel catfish, flathead catfish, freshwater drum, river carpsucker, sauger, and shovelnose sturgeon

Total annual survival (1-A; e^{-z}) and theoretical maximum age were derived from catch curves (Ricker 1975) and calculated for channel catfish, flathead catfish, freshwater drum, river carpsucker, sauger, and shovelnose sturgeon.

Number of missing year classes in an age-structure sample was used to index year-class failure. Missing year classes were enumerated for a standardized age group by species (i.e., channel catfish, ages 1-5; freshwater drum, ages 0-5; river carpsucker, ages 1-5; sauger, ages 1-5; shovelnose sturgeon, ages 5-10).

The Serial Discontinuity Concept was used to express the effects of dams on growth, condition, survival, and number of missing year classes in inter-reservoir segments.

Canonical discriminant function analysis was used to illustrate the differences between population metrics and zones.

Our growth results showed complex mix of responses, varying among species, among sizes within species, and to a lesser extent in time. Year effects were statistically significant in many of our growth analyses, but in some cases these effects interacted with spatial groupings (segments, hydrological units or zones) and were difficult to interpret. However, length at age 1 varied significantly with years and consistently across one or more spatial groupings in emerald shiner, flathead catfish, freshwater drum, plains minnow, shovelnose sturgeon, sicklefin chub and western silvery minnow. First year growth appeared to be faster in older individuals than in fish collected at younger ages in two of the three long-lived species in this group, freshwater drum and shovelnose sturgeon. This pattern matches the well-known Lee's phenomenon, and thus should be interpreted cautiously because of the possibility that the pattern is a sampling or methodological artifact rather than a true representation of a temporal growth trend. First year growth was fastest in 1993 and slowest in 1996 in the other long-lived species, flathead catfish. There was no consistency in which years had the fastest and slowest first year growth among the short-lived species, emerald shiner, plains minnow, sicklefin chub and western silvery minnow. Only plains minnow had a significant year effect in our age-specific analyses of annual growth increments. Both analyses of plains minnow showed the same temporal pattern, fastest growth in 1996 and slowest in 1995. In summary, we found significant yearly growth variation in some species, but no consistent pattern was seen among species. Furthermore, growth of several species appeared not to vary significantly among years.

Location effects were statistically significant in several of our growth analyses, reflecting a variety of environmental influences. First year growth varied significantly among segments in freshwater drum, river carpsucker, sauger and smallmouth buffalo, and whereas growth declined with increasing distance from the mouth of the Missouri River in the first three species, it increased in smallmouth buffalo. Length at maturity varied significantly among segments in channel catfish, freshwater drum, river carpsucker, shovelnose sturgeon and smallmouth buffalo. Length declined with distance from the mouth in channel catfish, freshwater drum and shovelnose sturgeon, increased in smallmouth buffalo, and was not significantly related to distance from the mouth in river carpsucker.

Growth of several species showed relationships with temperature. First year growth of blue sucker, freshwater drum and sauger was positively correlated with temperature, but first year growth of smallmouth buffalo was negatively correlated with temperature. Growth rate at length of maturity of channel catfish, freshwater drum and sauger was positively correlated with temperature. Length at maturity of channel catfish, freshwater drum and shovelnose sturgeon was positively correlated with temperature.

Significant zone effects in blue sucker, channel catfish, freshwater drum, sauger and shovelnose sturgeon all reflect the following rank order in growth among zones: LA<IR<CH. Because this rank order corresponds to the latitudinal gradient and associated correlates, it is difficult to separate the potential effects of human alteration from natural environmental differences

Condition varied longitudinally, but patterns differed among species. For example, condition declined for shovelnose sturgeon and increased for sauger from upstream to downstream. Sauger was the only species that had an increasing trend in condition for all length categories from upstream to downstream. Longitudinal trends in condition varied among length categories for some species. Thus, factors influencing condition were not similar for length categories within a species.

Most species had highest condition values in the least-altered zone. Only

P-M common carp and sauger had higher condition values in the channelized zone. Longitudinal variation is also exhibited in prey fish; for example, gizzard shad *Dorosoma cepedianum*, a common prey item for sauger, is absent above Lake Oahe. The effects of reservoirs on condition were apparent in segments directly below reservoirs. Condition of shovelnose sturgeon was low below Ft. Peck Lake, Lake Sakakawea, and Lewis and Clark Lake. Interestingly, segment 10 below Ft. Peck Lake had higher condition values than predicted. Segment 10 is directly below the Yellowstone River and it is likely that the Yellowstone River is ameliorating the effects of Ft. Peck Lake on condition. Similarly, the Niobrara River enters at the bottom of segment 14, which had higher than predicted condition values for shovelnose sturgeon, and is ameliorating the disturbance from reservoirs.

Condition of saugers was influenced by reservoirs in all inter-reservoir segments. Tributaries did not appear to ameliorate the effects of reservoirs on sauger condition, and condition of sauger was atypically low in the least-altered zone

Condition appeared to be near or above 90 for all species except shovelnose sturgeon and sauger. Thus, channelization does not appear to have a profound detrimental effect on condition of common carp, river carpsucker, freshwater drum, channel catfish, or flathead catfish. Conversely, condition values of shovelnose sturgeon were below 90 in the channelized segments, except for segment 27 near the confluence with the Mississippi River. Importantly, shovelnose sturgeon is the only obligate main channel species we studied. Common carp, river carpsucker, freshwater drum, channel catfish, and flathead catfish are more generalist with respect to habitat use and are found in tributary mouths and secondary channels. Thus, low condition values observed in shovelnose sturgeon in channelized segments may be a function of changes in channel morphology caused by channelization. Low velocity habitat in main channel areas has been substantially reduced by strategic placement of dikes and revetments in the Missouri River below Sioux City, Iowa. Therefore, shovelnose sturgeon subjected to high velocities in the channelized portion of the river likely have increased metabolic costs for maintaining position and moving relative to fish in low-velocity areas.

Our a priori prediction was that condition would increase from upstream to downstream based on longitudinal increases in productivity and growing season, but would be negatively influenced by reservoirs. However, sauger was the only species that followed our prediction and this is likely a function of increased food availability (gizzard shad abundance), reduced competition with other percids, and an earlier switch to piscivory in lower segments of the Missouri River. High condition of fishes in the upper segments of the Missouri River could be a function of longevity and subsequent accumulation of energy reserves. If the mechanism influencing the variation in condition was only water temperature then we would predict shovelnose sturgeon to have high condition values below reservoirs with hypolimnetic release, but the opposite occurred.

Observed patterns in size structure were similar to condition; for example, size structure (especially RSD-P and RSD-M) values tended to be higher in upstream segments. Conversely, sauger and channel catfish had higher size structure values in the lower Missouri River. However, the longitudinal pattern in size structure was not as clear as for other population metrics (i.e., condition, survival, and recruitment), and many of the zone, group, and hydrological unit comparisons did not differ significantly because of sample size limitations and high variability. The effect of reservoirs on size structure was most pronounced above and below Ft. Peck Lake for river carpsucker, sauger, and shovelnose sturgeon.

Survival estimates clearly followed a longitudinal pattern from upstream to downstream for freshwater drum, sauger, and shovelnose sturgeon. However, sauger did not have an opposite pattern in survival relative to the other species as was observed in condition and size structure. Thus, the mechanism influencing survival of sauger differed from condition and size structure. There were no consistent patterns in survival estimates regarding the influence of reservoirs on riverine segments. Population survival estimates may be insensitive to changes to river morphology caused by dams. All species had declines in survival estimates in segments 22 and 23. These segments were near St. Joseph and Kansas City, Missouri. It is likely that anthropogenic factors associated with high-density urban areas influenced survival of the benthic species we studied.

Number of missing year classes (i.e., year-class failure) varied longitudinally. Similar to the data for condition and size structure, sauger exhibited an opposite pattern relative to channel catfish, freshwater drum, river carpsucker, and shovelnose sturgeon. That is, sauger had the highest number of missing year classes in the lower segments of the Missouri River. Similar to the other metrics, the large-scale longitudinal patterns in year-class failure are likely a function of water temperature. The "warmwater" species (i.e., channel catfish, freshwater drum, river carpsucker, and shovelnose sturgeon) had more year-class failures in the upper segments of the Missouri River; conversely, the "coolwater" species (i.e., sauger) had more year-class failures in the lower segments. Idiosyncrasies in the longitudinal pattern of year-class failure were related to reservoirs. For example, segment 12 (below Lake Sakakawea) had the highest deviations from the predicated number of missing year classes for channel catfish, river carpsucker, and sauger; and segment 14 (below Lake Francis Case) had the highest number of missing year classes for shovelnose sturgeon.

Correlation analyses and scatterplots of all variables by species identified several patterns in the relationships among growth, condition, size structure, survival and recruitment. Only 25% of the significant relationships between growth variables and condition variables were positive. All of the significant relationships between growth variables and size structure variables were positive. None of the significant relationships of growth variables with survival were positive. Because of the observational nature of this study and the fact that there were several non-significant relationships not accounted for in these percentages, their generality is uncertain.

Population metrics pooled for the benthic fishes moderately discriminated among the least-altered, inter-reservoir, and channelized zones. Relative weight, size structure indices, survival, number of missing year classes, mean back-calculated length at age 1, and mean back-calculated length at age of maturity were useful in discriminating among zones when individual species were examined. We were able to discriminate among zones for freshwater drum, river carpsucker, and shovelnose sturgeon. The ordination of zones using population metric data illustrates the unique population characteristics among species along the Missouri River. We surmise that longitudinal variation was evident prior to construction of dams and channelization, and population metrics varied along a continuum rather than exhibiting discrete zonation. However, population characteristics now exhibit zonation because of reservoirs fragmenting populations and changing the physical characteristics of the Missouri River.

We found that anthropogenic modifications to the river (i.e., dams) can alter population metrics independently of latitudinal effects. The effects of reservoirs on population metrics were clear for many species; however, major tributaries (i.e., Yellowstone River, Niobrara River) ameliorated the effects of reservoirs on population metrics for the species that could use those tributaries during their life cycle. Many of the population metrics in Segment 12 were unfavorable relative to other segments. Segment 12 is the most isolated segment in the Missouri River; that is, there are no tributaries that enter the segment at the scale of the Yellowstone, Niobrara, Platte, or Kansas rivers. Despite that segment 15 is the only unchannelized area of the lower Missouri River, condition and recruitment of shovelnose sturgeon were lower than expected. The patterns observed in the population metrics below segment 15 may be related to the cumulative effects of reservoirs on river function.

The goal of this study was to assess population-level characteristics of fifteen fish species in the Missouri and lower Yellowstone rivers, and explore spatial patterns of these characteristics in relation to natural environmental gradients, flow regimes, and human alteration. This study is the largest of it's kind ever attempted, both in spatial scale and breadth of species included. We accomplished our objectives and provided a wealth of data to dissect the myriad patterns and relationships exhibited by a diverse fish assemblage exposed to a highly complex mix of environmental factors, both natural and anthropogenic. Understanding these patterns and relationships in large rivers is critical for management and restoration.

Previous research suggests that the population status of fishes at risk within the Missouri River varies geographically. The healthiest populations of most species occur in the upper, least-altered Missouri River and its major tributaries. The section of greatest population decline is the middle and lower Missouri River in areas of degraded channels downstream from mainstem reservoirs. Although we conclude that the fish population metrics we measured were not profoundly affected in the lower channelized area, they may not be the best measures of the impacts of channelization. Tributaries in the lower Missouri River may provide refugia for fish populations, partially offsetting the negative effects of a degraded main channel. Relative abundance and diversity of obligate main channel species are apparently more sensitive indicators of negative impacts of channelization and impoundment than the populations characteristics we measured are. We surmise that fish populations below reservoirs are the most negatively affected, especially those areas without large tributaries. Tributaries are critical to maintaining healthy fish populations in the Missouri River. Additional degradation of tributaries such as the Yellowstone, Platte and Kansas rivers could further jeopardize fish populations in the Missouri River ecosystem.

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INTRODUCTION

Population-level characteristics such as growth, condition, size-structure, survival and recruitment are important indicators of the well-being of fish populations, and may reflect a variety of physical, chemical and biological influences (Busacker et al. 1990; Anderson and Neumann 1996; DeVries and Frie 1996; Ney 1999; Van Den Avyle and Hayward 1999). Measurement of population-level characteristics is a cornerstone of fishery management assessments, and it is widely accepted practice to base management of fish populations on the results of such assessments (Kohler and Hubert 1999). In contrast, biological studies for environmental assessment have focused more on community-level characteristics, such as species richness, evenness, diversity, proportions of functional groups, and the variety of composite indices (e.g., IBI) based on the numbers or proportions of species or functional groups (Crowder 1990; Simon 1998). Although these community-level analyses have made important contributions to environmental assessment, they provide little or no insight into the direct mechanisms by which fish communities are affected. In contrast, population-level characteristics provide direct evidence for the success or failure of species because they describe basic biological or demographic phenomena. We believe that to fully characterize environmental quality and status as it relates to the biota, population-level assessments are an important partner with community-level approaches.

Growth of fishes is a simple concept on the surface, but in practice it is a highly complex phenomenon because of the indeterminate nature and plasticity of growth throughout the life cycle of fishes (Weatherley and Gill 1987). Furthermore, growth data are typically derived from a complicated protocol, involving numerous assumptions and intermediate calculations leading ultimately to numerical estimates of growth (Busacker et al. 1990; DeVries and Frie 1996). Finally, the range of desired insights into growth differ greatly. For example, the initial question, "In which river segment do fish grow the fastest?", could be rephrased into several more specific questions, including, "In which river segment do fish grow the fastest in the juvenile life-history stage?", "In which river segment do fish grow the fastest in the adult life-history stage?", "In which river segment do fish attain the largest body size in five years?", "In which river segment do fish reach the largest maximum body size?", and so on. These are different questions, and each has relevance to a different line of inquiry about fish populations. In this report we used several approaches to quantify, describe and compare growth in an attempt to satisfy a range of potential future uses for growth information.

Condition is commonly used in fish population assessment (Anderson and Neumann 1996). Condition refers to the weight of a fish for its length, and thus is a measure of "plumpness". Condition reflects various characteristics of fish, such as feeding history, reproductive state and health, as well as characteristics of the environment, such as water quality, habitat quality and food availability. Another reason condition is widely used in assessments is that it is easily calculated from simple length and weight measurements and requires few analytical assumptions.

Size structure, particularly the proportional stock density (PSD) and relative stock density (RSD) indices, are also widely used in fish population assessment (Willis et al. 1993; Anderson and Neumann 1996). PSD and RSD refer to proportions of the population of stock-length or greater fish that are also longer than quality length

(PSD) or one of the larger length categories (RSD). Size structure reflects the growth and survival rates of unexploited populations; faster growth and greater survival both result in higher PSD and RSD values. Recreational and commercial harvest generally lowers size structure index values, since harvest usually targets the largest individuals. Differential mortality among size classes, for example size-selective predation mortality, can have variable effects on size structure values. Like condition, size structure indices are widely used because the calculations are simple and they require only counts and length measurements. A drawback to size structure indices is the assumption of unbiased sampling and the difficulty of obtaining unbiased samples in practice.

Survival and recruitment are related processes that are central to fish population dynamics studies (Van Den Avyle and Hayward 1999). Survival is typically expressed as the proportion of individuals surviving for a specified period of time, usually a year. Survival may reflect natural environmental factors such as predation, resource availability, water quality and habitat quality, as well as recreational and commercial exploitation. Recruitment is the process by which new cohorts enter the population, and thus is a reflection of reproduction by the adult population and survival of the cohort. Year-to-year variability is a hallmark of many fish populations (Rothschild 1986), and the magnitude of this variation is another potential response to environmental factors. One of the ways of expressing recruitment variation is the presence of missing year classes in a sample of the population.

This study is part of a comprehensive investigation of population structure and habitat use of benthic fishes along the Missouri and lower Yellowstone Rivers. Other final reports from this study examine the overall background, design and rationale (Berry and Young 2001), habitat conditions (Galat et al. 2001), fish distribution and abundance (Berry et al. 2003), life history patterns (Braaten 2000), sicklefin chub ecology (Dieterman 2000), flow variation and fish responses (Pegg 2000), emerald shiner ecology (Young 2000), and community relationships (Welker 2000). The goal of this study was to assess population-level characteristics of fifteen fish species in the Missouri and lower Yellowstone rivers, and explore spatial patterns of these characteristics in relation to natural environmental gradients, flow regimes, and human alteration. Our specific objectives were to: (1) quantify growth, condition, size structure, survival and recruitment deficiencies among fifteen river segments, (2) analyze sources of variation in population-level characteristics, and (3) describe relationships with natural environmental gradients (e.g., distance from river mouth, temperature), flow regimes, and human alteration (e.g., reservoir influence, channelization).

STUDY AREA[2]

The Missouri River flows 3,768 km from its origin at the confluence of the Gallatin, Madison and Jefferson rivers near Three Forks, Montana, generally east and south to its terminus with the Mississippi River just upstream from St. Louis, Missouri (Figure.1). It is the longest river in the conterminous United States with a catchment encompassing about 1,327,000 km^2, or about one-sixth of the conterminous United States. Four physiographic provinces comprise its catchment: 142,000 km^2 of the Rocky Mountains in the west, 932,000 km^2 of the Great Plains in the center of the basin, 228,000 km^2 of Central

[2]This section is from Galat et al. 2001.

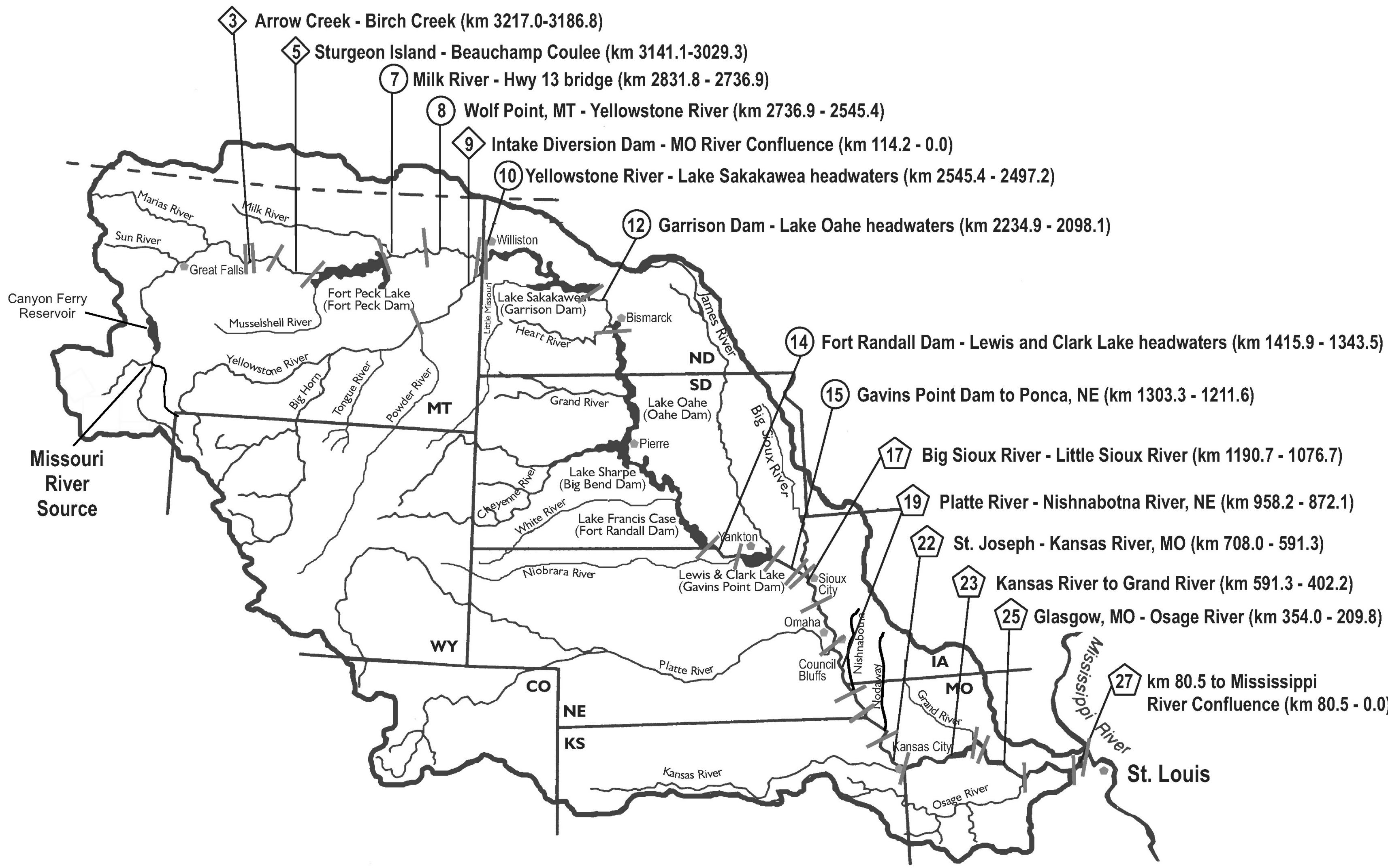

Figure 1. Map of the Missouri and Yellowstone rivers, with locations of major reservoirs, tributaries and cities. Study segments are numbered, labeled and delimited by thick bars perpendicular to the river channel. Symbols used for numbering segments indicate zone affiliation as follows: diamonds=least-altered (LA), circles=inter-reservoir (IR), pentagons=channelized (CH).

Lowlands in the north lower basin, and 24,500 km^2 of the Interior Highlands in the south lower basin (Slizeski et al. 1982). Range of latitude of the Missouri River varies from about 48E 03' N to 38E 47' N (Braaten 2000).

The size of the Missouri River puts it into to a small sub-class of the world's large rivers categorized as *great* rivers (Simon and Emory 1995). Stalnaker et al. (1989) defined large rivers as having an average depth >1 m and requiring that measurements be taken from a boat. Simon and Emory (1995) defined great rivers as hydrologic units with catchments >3200 km^2. Other great rivers in the United States include the Mississippi, Ohio, Colorado, and Columbia. The Amazon (South America), Danube (Europe), Mekong (Asia), and Murray-Darling (Australia) are examples of great rivers from other continents. Great rivers are distinctive in that they are few in number, interjurisdictional, comprise the largest component of the continental river resource, and are disproportionally degraded (Gammon and Simon 2000).

The highly regulated Missouri River is divided into three approximately equal length zones. The upper 1,241 km represents a "least-altered" zone relative to the remaining river. Although several mainstem dams and reservoirs are present above Ft. Peck Lake, (e.g., Canyon Ferry Hauser, and Holter), their usable capacity (ca. 2.7 km^3) is only 3% of the downriver mainstem reservoirs. The 1,316-km-long middle or "inter-reservoir" zone was impounded between 1937 and 1963 by six large mainstem reservoirs (total gross volume: 90.7 km^2; total average annual discharge: 100.5 $km^3\ yr^{-1}$). Flows in the 1,212 km long lower zone are also regulated by upstream reservoirs, although reductions in spring-summer high flows are somewhat offset in lowermost reaches by tributary input (Galat and Lipkin 2000). In addition, channel-floodplain morphology in the lowermost zone from Sioux City, Iowa (km 1,178), to the mouth was altered by channelization, bank stabilization, and levee construction and encompasses the "channelized" zone.

METHODS

Sampling Design

To assess spatial variation in benthic fish population characteristics, we used a hierarchical framework (sensu Frissell et al. 1986) to divide the river into segments and zones. Segments were contiguous stretches of river, separated by geomorphic, hydrologic and constructed features. Fifteen segments were sampled in this study (Figure 1, Table 1). Zones were groups of segments similar in their degree of human alteration. Three zones were recognized in this study. The least-altered (LA) zone consisted of segments in the upper Missouri River and the Yellowstone River segment, characterized by relatively little flow regulation and habitat modification. The inter-reservoir (IR) zone consisted of segments located between or just downstream from the major main-stem reservoirs in the middle portion of the Missouri River, characterized by significant flow regulation and varying degrees of thermal and turbidity alteration. The channelized (CH) zone consisted of segments in the lower Missouri River, characterized by significant flow regulation and alteration of in-stream and floodplain habitat due to channelization. See Berry et al. (2001) and Galat et al. (2001) for more detailed descriptions of the rationale for our spatial design and the characteristics of various segments and zones.

For analyses of condition, size structure and mortality, we modified the zone classification to include two additional groups. The Yellowstone River segment (YS) was

Table 1. Location information for Missouri and lower Yellowstone river zones and segments where fish were sampled, 1996-1998, and corresponding U. S. Geological Survey (USGS) flow gages. Zones: least altered (LA), inter reservoir (IR), channelized (CH). Reservoir names are also in **bold** and reservoirs lengths are approximate.

			River kilometer				USGS gage location		
Zone	Segment	Location	Upper	Lower	Midpoint	Length	Name	Number	km
LA	3	Arrow Creek - Birch Creek, MT	3217	3186.8	3201.9	30.2			
LA	5	Sturgeon Island - Beauchamp Coulee, MT	3141.1	3029.3	3085.2	111.8	Landusky	6115200	3092
		Ft. Peck Lake	3029.3	2847.9	3120	181.4			
IR	**7**	Milk River - Hwy 13 bridge (Wolf Point), MT	2831.8	2736.9	2784.4	94.9	Wolf Point	6177000	2738
IR	**8**	Wolf Point - above Yellowstone River, MT	2736.9	2545.4	2641.2	191.5	Culbertson	6185500	2618
LA	9	Intake Diversion Dam - MO River Confluence, MT	114.2	0	57.1	114.2	Sidney	6329500	47
IR	**10**	Yellowstone River, MT - L Sakakawea Headwaters, ND	2545.4	2497.2	2521.3	48.3			
		Lake Sakakawea	2469.8	2234.9	2352.4	234.9			
IR	**12**	Garrison Dam - Lake Oahe Headwaters, ND	2234.9	2098.1	2166.5	136.8	Bismarck	6342500	2115
		Lakes Oahe, Sharpe, and Francis Case	2051.5	1415.9	1733.7	635.6			
IR	**14**	Fort Randall Dam - Lewis & Clark L. Headwaters, SD	1415.9	1343.5	1379.7	72.4			
		Lewis and Clark Lake	1343.5	1303.3	1323.4	40.2			
IR	**15**	Gavins Point Dam, SD - Ponca, NE	1303.3	1211.6	1257.4	91.7			
CH	*17*	below Big Sioux River, SD - Little Sioux River, IA	1190.7	1076.7	1133.7	113.9	Sioux City	6486000	1164
CH	*19*	Platte River, NE - Nishnabotna River, IA	958.2	872.1	915.1	86.1	Nebraska City	6807000	905
CH	*22*	St. Joseph - Kansas River, MO	708	591.3	649.6	116.7	St. Joseph	6818000	721
CH	*23*	below Kansas River - Grand River, MO	591.3	402.2	496.8	189.1	Waverly	6895500	472
CH	*25*	Glasgow - Osage River, MO	354	209.8	281.9	144.2	Boonville	6909000	317
CH	*27*	km 80.5 - Mississippi River Confluence, MO	80.5	0	40.2	80.5	Hermann	6934500	158

separated from the two Missouri River LA segments, and the lowermost IR segment (LC) was separated from the other IR segments. The five areas resulting from this classification are hereafter referred to as "groups".

To assess variation in benthic fish population characteristics due to differences in flow regime, we divided the river into six hydrological units. Hydrological units were groups of segments exhibiting similar flow regimes as determined by an analysis of mean daily flow data from U.S. Geological Survey gauging stations (Pegg and Pierce 2002a). The upper unchannelized (UU) unit consisted of segments in the upper Missouri River, characterized by high flows per unit drainage area and relatively high flow variability. The inter-reservoir 1 (IR-1) unit consisted of the segments immediately downstream from Ft. Peck and Sakakawea Reservoirs, characterized by low flow variability and high flow constancy. The inter-reservoir 2 (IR-2) unit consisted of the segment located roughly midway between Ft. Peck and Sakakawea Reservoirs; this unit is similar to IR-1 except for much higher flow variability due to local tributary input. The unchannelized Yellowstone (UYS) unit consisted of the single segment on the Yellowstone River, characterized by high flow variability and low flow constancy. The channelized units in the lower Missouri River had higher flow contingency than the other units, but contrasted dramatically in their flow variability. The upper channelized (UC) unit consisted of the segments between Gavin's Point Dam and Kansas City, MO, characterized by low flow variability. In contrast the lower channelized (LC) unit, consisting of the segments between Kansas City, MO and the mouth, was characterized by much higher flow variability reflecting input from several large tributary rivers. See Pegg and Pierce (2002a) for more detailed descriptions of the hydrological analysis and resulting hydrologic units.

To apportion our sampling effort within segments, we identified six macrohabitats representing major habitat zones found throughout the river. All six macrohabitats were sampled with at least two different sampling gear types to maximize the chances of capturing species where they occurred. For this study, fish captured in all macrohabitats were combined within segments. See Berry et al. (2001) and Galat et al. (2001) for more detailed descriptions of the macrohabitats.

Sampling was conducted in all segments during the late summer to early fall period, roughly late July through late September, 1996-1998. See Berry et al. (2001, 2003) and Galat et al. (2001) for more detailed descriptions of the rationale for the temporal sampling design and specific sampling dates.

Fish Collection

Fish were collected from each river segment using a standardized protocol designed to capture both small and large-bodied fish in all available macrohabitats. Five sampling gear types were used: bag seines, benthic trawls, boat electrofishers, stationary gill nets and drifted trammel nets. See Berry et al. (2001) for the rationale, and Sappington et al. (1998) and Berry et al. (2003) for detailed descriptions of the sampling gear types and deployment methods used in each macrohabitat type.

Fish Handling

All collected fish were identified to species and enumerated. Additional information was obtained from 15 target species, including blue sucker *Cycleptus elongates*, brassy minnow *Hybognathus hankinsoni*, channel catfish *Ictalurus punc-*

tatus, emerald shiner *Notropis atherinoides*, flathead catfish *Pylodictis olivaris*, flathead chub *Platygobio gracilis*, freshwater drum *Aplodinotus grunniens*, plains minnow *Hybognathus placitus*, river carpsucker *Carpiodes carpio*, sand shiner *Notropis stramineus*, sauger *Sander canadense*, shovelnose sturgeon *Scaphirhynchus platorhynchus*, sicklefin chub *Macrhybopsis meeki*, smallmouth buffalo *Ictiobus bubalus*, and western silvery minnow *Hybognathus argyritis*. Individuals of the fifteen target species were measured for body length, wet weighed and sampled for one or more ageing structures. Body length measurements were made to the nearest 1 mm; total length (TL) was measured for all species except shovelnose sturgeon, which were measured for fork length (FL). Wet weight measurements for individuals weighing < 1200 g were made to the nearest 0.1 g with an electronic balance and larger individuals were weighed to the nearest 50 g with a spring balance. See Sappington et al. (1998) for detailed descriptions of fish handling, data collection and QA/QC procedures.

Ageing Structures

For ageing and back-calculation, scales, otoliths, pectoral spines or pectoral fin rays were removed from captured specimens, depending on species. Scales were used for blue sucker, brassy minnow, emerald shiner, flathead chub, plains minnow, river carpsucker, sand shiner, sicklefin chub, smallmouth buffalo and western silvery minnow. Otoliths were used for freshwater drum and sauger. Pectoral spines were used for channel and flathead catfish, and pectoral fin rays were used for shovelnose sturgeon. Preparations of ageing structures were linked to the fish they were obtained from to allow comparison of age determination and radial and inter-annular measurements with fish size at capture. During the first year of the study, otoliths were examined from subsamples of the species in which scales were used. Age determinations from these otoliths verified the adequacy of using scales to age these species. See Sappington et al. (1998) and Braaten and Guy (2002) for detailed descriptions of ageing structure removal and preparation.

Ageing

Ageing structure preparations were viewed under a dissecting microscope at 12.5x to 50x magnification, depending on size. Each preparation was independently aged by two workers. Preparations aged differently were viewed a second time by both workers, and if the second viewing failed to produce agreement the fish was discarded from the analysis. This procedure resulted in omission of as few as <5% (e.g., channel catfish) to >20% (e.g., shovelnose sturgeon) of the preparations. See Sappington et al. (1998) and Braaten and Guy (2002) for detailed descriptions of ageing procedures.

Growth

Measurement of Radii and Inter-Annular Distances

Radii and inter-annular distances on ageing structure preparations were measured using a dissecting microscope (12.5x to 50x magnification) and a computerized video image analysis system. For scale preparations, five individual scales were measured and averaged (Newman and Weisberg 1987). Scale measurements were made along the longest possible axis from the focus to the anterior edge, except for blue sucker and river carpsucker scales which were measured from the focus along a horizontal line to the lateral edge. For pectoral spine and pectoral fin ray preparations, measurements were made along the longest possible axis from the origin to the edge of the largest lobe. Freshwater drum otoliths were first sanded along the dorsoventral axis and then measured along the axis from the nucleus along the sulcal groove to the edge. Whole sauger otoliths were measured along the axis from the nucleus to the tip. See Sappington et al. (1998) and Braaten and Guy (2002) for detailed descriptions of ageing structure measurement.

Back-Calculation of Lengths at Previous Ages

We used two methods for back-calculating lengths at previous ages (DeVries and Frie 1996). For scales, we used the Fraser-Lee technique for back-calculation of lengths at previous ages based on inter-annular increments. The Fraser-Lee formula is

$$L_i = c + (L_c - c)(S_i/S_c),$$

where L_i = back-calculated fish body length at age *i*, L_c = fish body length at capture, S_i = mean scale length at annulus *i*, S_c = mean scale radius length, and *c* = intercept from the regression of fish body length vs. mean scale radius. Intercepts (*c*) were generated from data pooled across all segments. For other ageing structures we used the Dahl-Lea method because the structures are present at hatching and thus a correction (*c* term in Fraser-Lee formula) for body length when the structure first appears is not applicable. The Dahl-Lee formula is

$$L_i = (S_i/S_c)L_c.$$

See Sappington et al. (1998) and Braaten and Guy (2002) for detailed descriptions of back-calculation.

Age-Specific Analyses

Fish growth studies typically use an age-specific approach, where annual growth is tabulated or plotted graphically by fish age. Length-at-age tables, statistical comparisons of mean length-at-age and von Bertalanffy growth curves are examples of this common approach to presenting and analyzing fish growth data, and we used all of these methods. Using back-calculated lengths-at-age from individual fish we tabulated mean length-at-age for each species by segments, hydrological units and zones. We tested spatial (segment, hydrological unit and zone) and year effects on length at age-1 with ANOVA, and expressed the percentage of variance due to main effects and interactions in each test with variance components. We tested spatial effects only on length at age of maturity, since growth to length at age of maturity spanned different sequences of years for each individual fish. Age of maturity for each species was obtained from Pegg and Pierce (2001b). These tests compared lengths at two important points in the life history, but did not address growth occurring throughout life. We used SAS PROC GLM and PROC VARCOMP (SAS Institute 1988) for these analyses. Following Galat et al. (2001), we used the dual criteria of $\alpha<0.05$ and % variance>=10% for significance.

We used two approaches to test for differences in length-at-age among specific spatial units when the main effect was significant. We used six planned contrasts to test for differences among groups of segments, following the general approach of Galat et al. (2001) and Berry et al. (2004). One contrast tested for differences between the Missouri River LA segments and the lower Yellowstone River LA segment (<u>3</u>, <u>5</u> vs. <u>9</u>). A contrast tested for differences between the Missouri River LA segments upstream from Ft. Peck Lake and the IR segments immediately below Ft. Peck Lake (<u>3</u>, <u>5</u> vs. **7**, **8**). A contrast tested for differences between the IR segments immediately below Ft. Peck Lake and the lower Yellowstone River LA segment (**7**, **8** vs. <u>9</u>). A contrast tested for differences between the IR segments above Lewis and Clark Lake and the IR segment below Gavins

Point Dam (**7**, **8**, **10**, **12**, **14** vs. **15**). A contrast tested for differences between the IR segment below Gavins Point Dam and the CH segments (**15** vs. *17*, *19*, *22*, *23*, *25*, *27*). Finally, a contrast tested for differences between the CH segments upstream of Kansas City, MO and the CH segments downstream of Kansas City (*17*, *19*, *22* vs. *23*, *25*, *27*). For pair-wise comparison among segments, hydrological units and zones we used Tukey's tests. Results of all contrasts and pair-wise comparisons were tabulated, but they were interpreted only in cases where the ANOVA main effect was considered significant (i.e., $\alpha<0.05$ and % variance>=10%). We used SAS PROC GLM (SAS Institute 1988) for these analyses.

To test for growth differences occurring throughout life, we used Weisberg's age-specific ANOVA method (Weisberg 1993; as modified by Krause 1999) for testing spatial (segment, hydrological unit and zone), age and year effects on annual growth, as represented by annual growth increments on ageing structures. Percentages of variance due to main effects and interactions were determined using variance components analysis. The scope of these tests encompassed growth during the entire life history, "factoring out" the relatively large effect of fish age and enabling examinations of the more subtle effects of location and year. We used SAS PROC MIXED and PROC VARCOMP (SAS Institute 1988) for these analyses. Following Galat et al. (2001), we used the dual criteria of $\alpha<0.05$ and % variance>=10% for significance.

We fit von Bertalanffy growth functions (VBGF) (van den Avyle and Hayward 1999) to describe increases in length-at-age for eight of the fifteen species by segment, hydrological unit and zone. The purpose of the VBGFs was to illustrate changes in length-at-age and to provide readers with VBGF parameter estimates, not to test for differences between spatial units. We used mean lengths-at-age, and only included means calculated from at least two individual back-calculated lengths. VBGFs were not fit for short-lived species, nor were they fit for flathead catfish due to few older individuals in our collections. The usual VBGF is

$$L_t = L_\infty[1 - e^{-K(t - t_o)}],$$

where L_t = length at age t, L_∞ = asymptotic length, K = rate at which L_∞ is approached, and t_o is a constant theoretically representing the age at which fish length is zero. However, this formulation of the VBGF results in strong negative autocorrelation of L_∞ and K, which reduces their value for statistical comparisons. To avoid this problem, Gallucci and Quinn (1979) recommended using a reparameterized VBGF of the form

$$L_t = (\omega/K)[1 - e^{-K(t - t_o)}].$$

In this form of the VBGF, ω is the product of L_∞ and K. Gallucci and Quinn (1979) recommended using ω for statistically comparing VBGFs among populations. We used SAS PROC NLIN (SAS Institute 1988) for these analyses.

Size-Specific Analyses

Size-specific approaches relate growth to body size rather than fish age during the time interval growth occurred. Because of the plasticity of fish growth, individuals of the same age can vary greatly in size. Many aspects of the ecology of fishes are size-dependent, and thus comparing growth rates of similarly sized individuals may be more meaningful than comparing growth of similar aged individuals in many instances (Gerking and Raush 1979; Werner and Gilliam 1984). This rationale has been supported by several more recent studies (e.g., Gutreuter 1987; Osenberg et al. 1988; Putman et al.1995; Gutreuter et al. 1999).

We used a regression approach to model the size-specific growth responses for twelve of the fifteen species by segment, hydrological unit and zone. Using differences between successive back-calculated lengths as estimates of annual growth, we regressed annual growth vs. length at the start of the growing season. We used literature estimates of length at hatching (Winemiller and Rose 1992; Poff and Allan 1995) as length at the start of the growing season for age-0 fish, and back-calculated length at the beginning of each year for older fish. See Putman et al. (1995) for a detailed description and example of this approach.

Scatterplots of annual growth vs. length at the start of the growing season suggested that most of the relationships were nonlinear, but the patterns and dispersion of points were highly variable. Because these relationships were poorly suited for traditional parametric approaches such as polynomial regression, we followed the advice of Trexler and Travis (1993) and used locally weighted scatterplot smoothing (LOWESS) regression. LOWESS regression is a nonparametric regression method appropriate where the data suggest no particular model form (Cleveland 1979). LOWESS calculates a smoothed fit to the data by performing local regressions for each data point using a proportion of the entire data set and weighting the influence of other points as decreasing functions of their distance from the central point. The proportion of points used for each local regression is called the smoothing parameter; greater percentages of points used lead to greater smoothing. Local regressions can be either linear or quadratic. Inspection of several preliminary LOWESS fits and associated residual plots (Cleveland 1985) suggested that a smoothing parameter of 0.8 and quadratic local regressions provided smoothed fits that accurately represented the size-specific growth patterns evident in the entire data sets without being unduly influenced by individual variation and outliers. We used SAS PROC LOESS (SAS Institute 1988) for these analyses.

The resulting LOWESS regressions represent the “average” annual growth rate of fish at different sizes during their life history. As such, they can be used to generate estimates of the expected annual growth for any size. We used LOWESS regressions to estimate annual growth rate of each species at their length at maturity (Pegg and Pierce 2002b). At age-0, age-specific and size-specific annual growth estimates are essentially identical, since fish begin this growing interval at a fairly consistent hatching length. Therefore, we estimated annual growth rate at length-at-hatching as the mean length at age-1.

Growth Relationships

We selected three growth variables to explore relationships of growth among species, with major geomorphic and environmental factors, and with condition, size structure, survival and recruitment. Annual growth at age-0 (AG-0) is both an age-specific and size-specific measure of growth in the first year, since growth is assumed to commence at a common size-at-hatching. Annual growth at length of maturity (AG-m) is a size-specific measure of growth obtained from the LOWESS regressions. AG-0 and AG-m are independent estimates of growth at different points in the life history, comparing growth of similarly sized fish. Length at age of maturity (L-m) is the mean back-calculated length at age of maturity, which allows comparison of lengths attained by fish at a common age (their age of first reproduction) among spatial units. Whereas AG-0 and AG-m are point estimates of growth and are independent of each other, L-m is a cumulative measure of all growth occurring up to the age of maturity. These three variables were calculated by segment. Relationships of these variables were examined by correlation analysis and scatterplots. We used SAS PROC CORR (SAS Institute 1988) for correlation analyses, with the criterion of α<0.05 for significance.

Condition

We used relative weight (W_r=100 x individual fish weight/standard weight; Anderson and Neumann 1996) to index condition of common carp, channel catfish, flathead catfish, freshwater drum, river carpsucker, sauger, and shovelnose sturgeon. The standard weight equations used were reported in the literature by Anderson and Neumann (1996), , Quist (1998), and Bister et al. (2000; Table 2). According to recommendations by Murphy et al. (1991) we calculated mean W_r by length category (S-Q, stock to quality; Q-P, quality to preferred; P-M, preferred to memorable; M-T, memorable to trophy; Table 2). Low sample size (N < 5) precluded analysis of W_r for the M-T length category for all species except shovelnose sturgeon. Similarly, low sample size (N < 5) prevented calculating reliable W_r values for Q-P and P-M length flathead catfish.

We were not interested in temporal variation in W_r, thus W_r values were pooled among years. Relative weight values for each fish were the sampling unit and independent among fish, thus N in the zone, group, and hydrological unit comparisons was number fish within each category. One-way analysis of variance (ANOVA) was used to test for differences in relative weight values among segments, zones, groups, and hydrological units. When one-way ANOVA models were significant, multiple comparisons were conducted using least-squared means. Relation between

Table 2. Parameters for $\log_{10}$ weight-$\log_{10}$ length regression equations for species used in relative weight (W_r=100 x individual fish weight/standard weight) analyses. Values for the intercept and slope are for metric equations where length is in millimeters and weight is in grams. Length categories (centimeters) used to calculate size structure indices (i.e., proportional stock density [PSD], relative stock density of preferred-length fish [RSD-P], and relative stock density of memorable-length fish [RSD-M]) for species used in size structure analyses.

	W_s equation parameters		Length category				
Species	Intercept	Slope	Stock	Quality	Preferred	Memorable	Trophy
Common carp[a]	-4.639	2.920	28	41	53	66	84
Channel catfish[b]	-5.800	3.294	28	41	61	71	91
Flathead catfish[a]	-5.542	3.230	35	51	71	86	102
Freshwater drum[b]	-5.419	3.204	20	30	38	51	63
River carpsucker[a]	-4.839	2.992	18	28	36	46	56
Sauger[b]	-5.492	3.187	20	30	38	51	63
Shovelnose sturgeon[c]	-6.287	3.330	25	38	51	64	81

[a]Bister et al. (2000).
[b]Anderson and Neumann (1996).
[c]Quist et al. (1998).

river kilometer and W_r values was evaluated by visually examining bivariate plots and modeled using linear and non-linear regression techniques.

Size Structure

Size structure was quantified using proportional stock density (PSD), relative stock density of preferred-length fish (RSD-P), and relative stock density of memorable-length fish (RSD-M; Anderson and Neumann 1996) for common carp, channel catfish, flathead catfish, freshwater drum, river carpsucker, sauger, and shovelnose sturgeon. Size structure indices were calculated only from the gear that captured the greatest number of a given species because of length biases associated with sampling gear. Data from boat electrofishing were used to calculate size structure values for common carp, freshwater drum, river carpsucker, and sauger; stationary gill nets for channel catfish; and drifting trammel nets for shovelnose sturgeon. Proportional stock density is the percentage of stock-length fish that are also quality length; RSD-P is the percentage of stock-length fish that are preferred length; RSD-M is the percentage of stock-length fish that are memorable length (see Anderson and Neumann 1996 for formulas). See Table 2 for minimum stock (S), quality (Q), preferred (P), and memorable (M) lengths by species. Similar to the relative weight data, we were not interested in temporal variation, thus size structure data were pooled among years. Size structure data were not statistically tested among segments because there was no measure of variation within segment. However, one-way analysis of variance (ANOVA) was used to test for differences in size structure values among zones, groups, and hydrological units. Segments within zones, groups, and hydrological units were the sampling unit and considered independent, thus N in the zone, group, and hydrological unit comparisons was number of segments within each category. When one-way ANOVA models were significant, multiple comparisons were conducted using least-squared means. Relation between river kilometer and size structure was evaluated by visually examining bivariate plots and modeled using linear and non-linear analyses regression techniques.

Survival

Total annual survival (1-A; e^{-z}) and theoretical maximum age were derived from catch curves (Ricker 1975) and calculated for channel catfish, flathead catfish, freshwater drum, river carpsucker, sauger, and shovelnose sturgeon. Catch curve analyses were conducted using the software program Fishery Analyses and Simulation Tools (FAST) developed by Slipke and Maceina (2000). Unweighted catch curves were used because survival estimates did not vary from weighted catch curves (Maceina 1997). Ages used for the catch curve represented those fully recruited to the sampling gear (i.e., the descending right limb of the curve) and maximum age present in the samples. Constant recruitment is one assumption of the catch curve analysis, but is often violated. However, Ricker (1975) suggests that the influence of variable recruitment on survival estimates from catch curves can be reduced by pooling several years of data. Thus, the number-at-age data were pooled by species from 1996-1998 to obtain a single survival estimate. Slopes of the catch-curve regression line were compared using analysis of covariance. Relation between river kilometer and survival estimates was evaluated by visually examining bivariate plots and modeled using linear and non-linear regression techniques.

Recruitment Deficiencies

Number of missing year classes in an age-structure sample was used to index year-class failure. Missing year classes were enumerated for a standardized age group by species (i.e., channel catfish, ages 1-5; freshwater drum, ages 0-5; river carpsucker, ages 1-5; sauger, ages 1-5; shovelnose sturgeon, ages 5-10). Missing year classes were calculated for samples from 1996-1998 (few samples were used from the 1996 data due to low sample size), each year was considered a subsample because the same missing year class could be present in all samples. Thus, the data were not independent among years. Number of missing year classes was estimated by segment and zone. One-way analysis of variance (ANOVA) was used to test for differences in number of missing year classes among zones. When one-way ANOVA models were significant, multiple comparisons were conducted using least-squared means. Relation between river kilometer and number of missing year classes was evaluated by visually examining bivariate plots and modeled using linear and nonlinear regression techniques.

Serial Discontinuity Analyses

The Serial Discontinuity Concept proposed by Ward and Stanford (1983) was used to express the effects of dams on growth, condition, survival, and number of missing year classes in inter-reservoir segments. Following Galat et al. (2001), we first tested for relationships of variables with distance from the mouth of the Missouri River, using only the LA and CH segments. If a significant linear relationship existed, we then calculated parameter intensity (PI) and discontinuity distance (DD) for the IR segments, which would be expected to exhibit serial discontinuity. PI is the difference in a given metric from what would be predicted by the LA and CH segments. DD is the longitudinal shift in a given metric from what would be predicted from the LA and CH segments. See Galat et al. (2001) for a detailed description of the rationale and calculations of PI and DD.

The following variables and species had significant linear relationships with distance from the mouth of the Missouri River, and therefore were included in serial discontinuity analysis: AG-0 (freshwater drum, sand shiner, sauger and smallmouth buffalo), AG-m (shovelnose sturgeon), L-m (freshwater drum and shovelnose sturgeon), W_r (shovelnose sturgeon and sauger), survival (freshwater drum, sauger, and shovelnose sturgeon), and number of missing year classes (channel catfish, river carpsucker, sauger, and shovelnose sturgeon).

Multivariate Analyses

Canonical discriminant function analysis was used to illustrate the differences between population metrics and zones. Zone classification was established a priori. Canonical discriminant function analysis was first conducted for all species pooled to determine if population metrics for all species discriminated among zones. Canonical discriminant function analysis was also conducted by species to illustrate varying patterns among species. Distances (i.e., Mahalanobis distances) between centroids for each zone were compared using ANOVA.

RESULTS

Length-at-Age

Segment Comparisons

We tested for significant differences in length at age 1 and length at age of maturity, and expressed the percentages of variance due to main effects, interactions and error in each test (Table 3). We reported length-at-age values for all fifteen species (Table 4), although not all species were collected in all segments and age ranges encountered for a species varied widely among segments. Length-at-age values are reported in all fifteen segments for channel catfish, emerald shiner, river carpsucker, shovelnose sturgeon and smallmouth buffalo. Length-at-age values are reported in only one segment for brassy minnow. Length-at-age values are reported up to age 37 in shovelnose sturgeon, but only to age 1 in brassy minnow, plains minnow and sand shiner. Tukey's tests for pair-wise comparison among segments are reported in Table 4. Planned contrasts are reported in Table 5.

The year main effect was significant for age-1 blue sucker, but this was difficult to interpret due to a significant segment by year interaction reflecting differences in the rank order of segments from 1992-1997. Length at age of maturity differed among segments for channel catfish, with the shortest lengths occurring in segments 9 and 10, and the greatest lengths occurring in segment 19. Contrasts for length at age of maturity in channel catfish indicated the following significant differences: 3, 5 > 9; 3, 5 > **7**, **8**; **7**, **8**, **10**, **12**, **14** < **15**; **15** < *17*, *19*, *22*, *23*, *25*, *27*. Length at age 1 differed among segments for emerald shiner, but this was difficult to interpret due to a non-significant interaction with year. Length at age 1 differed among years for flathead catfish, with the greatest lengths attained after the 1993 growth year and the shortest lengths attained after the 1996 growth year. There was a significant segment by year interaction for age 1 flathead chub. Both segment and year effects were significant for age 1 freshwater drum. Freshwater drum length at age 1 was lowest in segment 8 and greatest in segment 19. Contrasts for length at age 1 in freshwater drum indicated the following significant differences: 3, 5 < 9; 3, 5 < **7**, **8**; *17*, *19*, *22* > *23*, *25*, *27*. Freshwater drum length at age 1 tended to be greater in the early and mid 1990s and lower in the 1980s and 1970s. Length at age of maturity differed among segments for freshwater drum, with the shortest lengths occurring in segments 3, 5, 8 and 14, and the greatest lengths occurring in segment 22. Contrasts for length at age of maturity in freshwater drum indicated the following significant differences: **7**, **8**, **10**, **12**, **14** < **15**; *17*, *19*, *22* > *23*, *25*, *27*. Length at age 1 differed among years for plains minnow, with greater lengths attained after the 1996 and 1997 than the 1995 growth year. Length at age 1 differed among segments for river carpsucker, with the shortest lengths occurring in segments 3, 9, and 10, and the greatest lengths occurring in segments 5, 25 and 27. Contrasts for length at age 1 in river carpsucker indicated the following significant differences: **7**, **8** > 9; **15** < *17*, *19*, *22*, *23*, *25*, *27*; *17*, *19*, *22* < *23*, *25*, *27*. Length at age of maturity differed among segments for river carpsucker, with the shortest lengths occurring in segments 9, 10, 14, 15 and 22, and the greatest lengths occurring in segment 5. Contrasts for length at age of maturity in river carpsucker indicated the following significant differences: 3, 5 > 9; 3, 5 > **7**, **8**. Length at age 1 differed among segments for sauger, with the shortest lengths occurring in segment 12 and the greatest lengths occurring in segment 22. Contrasts for length at age 1 in sauger indicated the following significant difference: **7**, **8**, **10**, **12**, **14** < **15**. Length at age 1 differed among years for shovelnose sturgeon and although there was year-to-year variation, the underlying pattern was of decreasing length with increasing age at capture. Length at age at maturity differed among segments for

Table 3. Summary of ANOVAs testing the effects of spatial units and year on length-at-age of fifteen species of benthic fishes in the Missouri and Lower Yellowstone rivers. Total body lengths back-calculated from corresponding annual growth increments on calcified structures were used in analyses. Year refers to calendar year when growth occurred. Separate ANOVAs were used for each of three spatial units: segments, hydrological units and zones. N refers to the number of individual back-calculated body lengths used in analyses. F-ratios and P-values are based on Type III tests from ANOVAs using Proc GLM (SAS Institute Inc. 1997). Percentages of variance (% Var.) were calculated using Proc VARCOMP (SAS Institute Inc. 1988). Tukey's tests shown in Tables 4 and 6. Error variance percentages are roughly equivalent to $1\text{-}R^2$. Dashes (-) indicate insufficient data to evaluate effect.

		Segments				Hydrological Units				Zones			
Age	N	Effect	F	P	% Var.	Effect	F	P	% Var.	Effect	F	P	% Var.
						Blue sucker							
1	136	Segment (S)	1.3	0.23	<0.1	Unit (U)	0.3	0.90	24.5	Zone (Z)	0.2	0.81	20.9
		Year (Y)	3.5	0.001	31.0	Year (Y)	2.2	0.02	9.0	Year (Y)	2.2	0.02	6.9
		S x Y	2.1	0.01	17.0	U x Y	1.0	0.42	<0.1	Z x Y	2.2	0.04	6.6
		Error			52.0	Error			66.5	Error			66.3
6	12	Segment (S)	2.9	0.13	46.6	Unit (U)	1.1	0.42	3.6	Zone (Z)	5.6	0.04	44.2
		Error			53.4	Error			96.4	Error			55.8
						Brassy minnow							
1	-	Segment (S)	-	-	-	Unit (U)	-	-	-	Zone (Z)	-	-	-
		Year (Y)	-	-	-	Year (Y)	-	-	-	Year (Y)	-	-	-
		S x Y	-	-	-	U x Y	-	-	-	Z x Y	-	-	-
		Error			-	Error			-	Error			-
2	-	Segment (S)	-	-	-	Unit (U)	-	-	-	Zone (Z)	-	-	-
		Error			-	Error			-	Error			-
						Channel catfish							
1	1449	Segment (S)	2.6	0.001	1.6	Unit (U)	4.2	0.0008	2.5	Zone (Z)	0.2	0.82	<0.1
		Year (Y)	4.0	<0.0001	5.6	Year (Y)	1.9	0.02	4.3	Year (Y)	7.4	<0.0001	4.8
		S x Y	2.0	<0.0001	9.8	U x Y	2.2	<0.0001	8.8	Z x Y	3.2	<0.0001	5.7

		Segments				Hydrological Units				Zones			
Age	N	Effect	F	P	% Var.	Effect	F	P	% Var.	Effect	F	P	% Var.
		Error			83.1	Error			84.4	Error			89.6
4	844	Segment (S)	22.5	<0.0001	34.3	Unit (U)	40.9	<0.0001	26.5	Zone (Z)	63.4	<0.0001	24.3
		Error			65.7	Error			73.5	Error			75.7
						Emerald shiner							
1	1730	Segment (S)	6.5	<0.0001	11.8	Unit (U)	5.0	0.0001	3.1	Zone (Z)	0.6	0.53	0.4
		Year (Y)	8.9	0.0001	9.6	Year (Y)	1.4	0.26	8.9	Year (Y)	31.2	<0.0001	11.5
		S x Y	5.7	<0.0001	7.7	U x Y	4.9	<0.0001	11.0	Z x Y	1.1	0.38	0.3
		Error			70.9	Error			77.0	Error			87.7
2	21	Segment (S)	1.8	0.17	21.2	Unit (U)	4.5	0.12	71.7	Zone (Z)	2.0	0.16	20.2
		Error			78.8	Error			28.3	Error			79.8
						Flathead catfish							
1	677	Segment (S)	1.0	0.43	0.3	Unit (U)	0.4	0.52	<0.1	Zone (Z)	2.0	0.16	<0.1
		Year (Y)	5.1	<0.0001	19.2	Year (Y)	5.2	<0.0001	18.8	Year (Y)	4.8	<0.0001	18.6
		S x Y	1.2	0.24	0.1	U x Y	0.7	0.64	0.1	Z x Y	1.0	0.44	<0.1
		Error			80.3	Error			81.1	Error			81.4
5	40	Segment (S)	2.2	0.07	21.1	Unit (U)	0.4	0.55	<0.1	Zone (Z)	1.0	0.32	0.1
		Error			78.9	Error			>99.9	Error			99.9
						Flathead chub							
1	361	Segment (S)	1.8	0.11	<0.1	Unit (U)	1.2	0.31	<0.1	Zone (Z)	<0.1	0.87	<0.1
		Year (Y)	3.4	0.002	3.3	Year (Y)	4.2	0.0002	3.8	Year (Y)	2.7	0.01	4.0
		S x Y	2.4	0.0008	13.1	U x Y	2.3	0.005	13.9	Z x Y	1.2	0.30	<0.1
		Error			83.6	Error			82.3	Error			96.0
2	108	Segment (S)	0.4	0.88	<0.1	Unit (U)	0.8	0.52	<0.1	Zone (Z)	0.1	0.73	<0.1
		Error			>99.9	Error			>99.9	Error			>99.9

		Segments				Hydrological Units				Zones			
Age	N	Effect	F	P	% Var.	Effect	F	P	% Var.	Effect	F	P	% Var.
						Freshwater drum							
1	538	Segment (S)	15.6	<0.0001	24.1	Unit (U)	22.7	<0.0001	29.7	Zone (Z)	28.4	<0.0001	27.3
		Year (Y)	11.1	<0.0001	40.6	Year (Y)	12.4	<0.0001	31.5	Year (Y)	8.9	<0.0001	36.3
		S x Y	2.2	<0.0001	5.5	U x Y	1.4	0.13	1.8	Z x Y	1.7	0.04	3.0
		Error			29.9	Error			36.9	Error			33.5
4	271	Segment (S)	36.3	<0.0001	68.7	Unit (U)	86.5	<0.0001	62.6	Zone (Z)	127.0	<0.0001	55.5
		Error			31.3	Error			37.4	Error			44.5
						Plains minnow							
1	38	Segment (S)	1.5	0.21	0.9	Unit (U)	2.3	0.10	0.4	Zone (Z)	2.8	0.11	20.7
		Year (Y)	7.4	0.003	54.2	Year (Y)	12.0	0.0001	55.3	Year (Y)	7.1	0.002	38.0
		S x Y	2.6	0.07	18.0	U x Y	5.7	0.008	22.0	Z x Y	1.2	0.29	<0.1
		Error			26.9	Error			22.4	Error			41.3
2	-	Segment (S)	-	-	-	Unit (U)	-	-	-	Zone (Z)	-	-	-
		Error			-	Error			-	Error			-
						River carpsucker							
1	1078	Segment (S)	3.6	<0.0001	10.2	Unit (U)	5.2	0.0001	11.4	Zone (Z)	5.1	0.006	8.1
		Year (Y)	2.6	0.004	1.7	Year (Y)	1.8	0.06	1.3	Year (Y)	2.4	0.009	2.0
		S x Y	1.2	0.17	1.1	U x Y	1.1	0.35	0.4	Z x Y	1.3	0.18	1.3
		Error			86.9	Error			86.9	Error			88.6
4	559	Segment (S)	4.6	<0.0001	11.6	Unit (U)	10.2	<0.0001	14.3	Zone (Z)	2.3	0.10	0.8
		Error			88.4	Error			85.7	Error			99.2
						Sand shiner							
1	132	Segment (S)	0.8	0.57	2.4	Unit (U)	<0.1	0.86	<0.1	Zone (Z)	6.2	0.01	19.1

		Segments				Hydrological Units				Zones			
Age	N	Effect	F	P	% Var.	Effect	F	P	% Var.	Effect	F	P	% Var.
		Year (Y)	6.5	0.002	8.2	Year (Y)	9.7	0.0001	<0.1	Year (Y)	2.8	0.07	<0.1
		S x Y	1.8	0.12	10.4	U x Y	7.0	0.009	18.9	Z x Y	2.1	0.15	5.0
		Error			79.0	Error			81.1	Error			75.9
2	-	Segment (S)	-	-	-	Unit (U)	-	-	-	Zone (Z)	-	-	-
		Error			-	Error			-	Error			-
						Sauger							
1	285	Segment (S)	15.7	<0.0001	52.4	Unit (U)	22.0	<0.0001	53.6	Zone (Z)	31.4	<0.0001	42.3
		Year (Y)	2.8	0.004	4.9	Year (Y)	2.4	0.01	4.1	Year (Y)	3.9	0.0001	5.4
		S x Y	1.4	0.06	4.3	U x Y	1.5	0.10	4.3	Z x Y	1.8	0.05	3.2
		Error			38.4	Error			38.0	Error			49.1
5	35	Segment (S)	1.9	0.10	23.0	Unit (U)	3.4	0.02	28.5	Zone (Z)	2.6	0.09	<0.1
		Error			77.0	Error			71.5	Error			>99.9
						Shovelnose sturgeon							
1	1318	Segment (S)	3.2	<0.0001	3.7	Unit (U)	0.6	0.69	0.3	Zone (Z)	0.7	0.48	<0.1
		Year (Y)	4.7	<0.0001	22.3	Year (Y)	3.4	<0.0001	20.5	Year (Y)	5.7	<0.0001	21.1
		S x Y	1.1	0.12	1.7	U x Y	1.3	0.05	2.4	Z x Y	1.5	0.02	3.7
		Error			72.3	Error			76.8	Error			75.1
7	904	Segment (S)	14.3	<0.0001	18.1	Unit (U)	26.1	<0.0001	14.0	Zone (Z)	70.4	<0.0001	17.2
		Error			81.9	Error			86.0	Error			82.8
						Sicklefin chub							
1	260	Segment (S)	3.5	0.0007	<0.1	Unit (U)	4.4	0.002	<0.1	Zone (Z)	0.4	0.67	<0.1
		Year (Y)	37.5	<0.0001	32.4	Year (Y)	39.2	<0.0001	33.1	Year (Y)	33.2	<0.0001	40.9
		S x Y	4.4	<0.0001	25.3	U x Y	4.5	<0.0001	26.4	Z x Y	1.1	0.38	<0.1
		Error			42.3	Error			40.5	Error			59.1

		Segments				Hydrological Units				Zones			
Age	N	Effect	F	P	% Var.	Effect	F	P	% Var.	Effect	F	P	% Var.
2	42	Segment (S)	0.8	0.59	0.5	Unit (U)	0.9	0.47	3.1	Zone (Z)	1.1	0.34	3.2
		Error			99.5	Error			96.9	Error			96.8
Smallmouth buffalo													
1	226	Segment (S)	5.0	<0.0001	26.5	Unit (U)	7.4	<0.0001	24.6	Zone (Z)	4.3	0.02	9.6
		Year (Y)	1.4	0.19	<0.1	Year (Y)	1.1	0.41	0.9	Year (Y)	0.9	0.53	<0.1
		S x Y	1.1	0.34	<0.1	U x Y	1.2	0.29	3.4	Z x Y	1.4	0.18	2.7
		Error			73.5	Error			71.1	Error			87.6
4	135	Segment (S)	3.3	0.0002	20.4	Unit (U)	3.3	0.009	10.8	Zone (Z)	3.8	0.02	7.4
		Error			79.6	Error			89.2	Error			92.6
Western silvery minnow													
1	287	Segment (S)	3.4	0.003	4.6	Unit (U)	3.9	0.004	12.5	Zone (Z)	1.7	0.19	3.8
		Year (Y)	4.1	0.003	26.8	Year (Y)	2.4	0.05	24.1	Year (Y)	4.8	0.001	33.6
		S x Y	2.6	0.01	7.9	U x Y	1.0	0.45	1.4	Z x Y	0.07	0.93	<0.1
		Error			60.7	Error			62.0	Error			62.6
2	-	Segment (S)	-	-	-	Unit (U)	-	-	-	Zone (Z)	-	-	-
		Error			-	Error			-	Error			-

Table 4. Mean length-at-age of fifteen species of benthic fishes in segments of the Missouri and Lower Yellowstone rivers. Lengths are means of total body lengths (mm) back-calculated from corresponding annuli on calcified structures for all species except shovelnose sturgeon, which are fork length. Numbers below mean lengths are (±) 95% confidence interval and sample size, respectively. Asterisks indicate ages tested for significant differences among segments; segment means sharing a letter are not significantly different (Tukey's test, α=0.05). Dashes (-) indicate insufficient data to calculate confidence interval. Empty cells indicate no data.

	Segment														
Age	3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
							Blue sucker								
1*	127b	106b	134b	119b	127b		140b		165ab	175ab	190ab	194ab	194ab	245a	168ab
	-, 1	-, 1	51, 3	26, 3	19, 5		233, 2		16, 26	11, 49	28, 8	31, 12	18, 22	-, 1	63, 5
2	209	181	240	225	211		241		308	327	340	325	348	331	332
	-, 1	-, 1	57, 3	10, 3	23, 5		422, 2		20, 25	13, 47	68, 6	46, 8	64, 9	-, 1	85, 5
3	282	239	322	310	300		334		408	438	447	450	471	491	396
	-, 1	-, 1	97, 3	36, 3	48, 5		378, 2		21, 21	14, 38	88, 3	46, 6	68, 8	-, 1	853, 2
4	342	318	393	400	391		430		484	498	534	538	541	579	496
	-, 1	-, 1	162, 3	98, 3	59, 5		131, 2		38, 14	18, 17	-, 1	69, 3	136, 4	-, 1	564, 2
5	415	377	471	491	414		557		508	588		618	517		575
	-, 1	-, 1	187, 3	137, 3	81, 3		-, 1		85, 5	24, 6		52, 2	-, 1		-, 1
6*	492a	420a	496a	531a	479a		632a		541a						
	-, 1	-, 1	85, 2	289, 2	58, 3		-, 1		708, 2						
7	561	476	553	582	543				534						
	-, 1	-, 1	176, 2	-, 1	95, 2				-, 1						
8	621	544		646	587										
	-, 1	-, 1		-, 1	146, 2										
9	682				626										
	-, 1				-, 1										
10					668										
					-, 1										
11					703										
					-, 1										

	Segment														
Age	3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
								Brassy minnow							
1									44						
									1, 10						
								Channel catfish							
1*	82ab	85a	79abcd	77abcd	64cd	62d	79abcd	81abc	72abcd	67bcd	73abcd	71abcd	69abcd	64d	71abcd
	7, 52	5, 101	6, 59	8, 51	3, 201	4, 105	8, 23	4, 269	6, 145	8, 66	10, 51	7, 97	6,89	7, 44	6, 97
2	156	166	147	138	126	126	143	166	166	158	186	189	173	154	177
	10, 52	6, 101	10, 59	12, 48	6, 181	8, 85	14, 23	7, 248	8, 118	19, 28	28, 19	19, 43	16, 46	20, 30	13, 71
3	239	248	213	211	191	191	210	242	243	235	284	282	271	249	265
	11, 52	9, 99	10, 59	13, 46	7, 164	10, 67	14, 23	7, 206	9, 91	27, 20	25, 14	23, 34	18, 41	26, 25	15, 65
4*	305cd	306cd	267de	272de	251e	250e	266de	295cd	301cd	296cd	373a	361ab	352ab	329bc	320bc
	15, 52	9, 97	10, 59	12, 45	9, 133	9, 62	17, 23	9, 149	11, 65	33, 17	50, 10	31, 25	24, 34	28, 21	18, 53
5	361	362	309	314	306	295	306	344	361	361	444	446	449	381	378
	14, 47	12, 78	10, 59	12, 44	10, 105	9, 59	18, 23	10, 119	15, 55	36, 14	69, 6	38, 14	30, 19	32, 16	22, 37
6	427	419	344	349	354	337	343	383	407	414	506	519	528	444	426
	23, 33	18, 51	11, 57	14, 40	11, 88	9, 53	21, 23	12, 99	28, 27	51, 9	228, 3	76, 5	47, 10	59, 8	26, 23
7	495	474	366	392	406	375	379	414	473	419	450	580	615	455	477
	32, 22	21, 39	14, 39	17, 31	18, 50	14, 37	24, 23	15, 73	43, 11	558, 2	-, 1	79, 4	-, 1	107, 5	36, 16
8	544	557	395	421	454	423	411	440	546			570		515	486
	43, 13	38, 16	20, 27	23, 16	26, 29	21, 19	25, 22	19, 51	47, 8			275, 2		1267, 2	64, 7
9	614	604	425	449	508	461	437	469	571			599			531
	44, 8	80, 6	38, 18	30, 10	28, 17	26, 12	26, 21	23, 35	35, 4			338, 2			-, 1
10	654	631	444	481	540	500	459	487	599						
	48, 8	108, 5	45, 11	38, 9	31, 14	31, 9	34, 15	27, 20	30, 2						
11	675	740	421	503	571	545	482	506	638						
	51, 6	156, 2	55, 6	57, 7	31, 14	52, 5	34, 12	45, 11	-, 1						
12	711	769	411	524	611	576	496	551	653						
	55, 4	-, 1	62, 4	879, 2	36, 8	57, 5	68, 6	43, 4	-, 1						
13	729		427		642	595	463								
	66, 3		140, 3		93, 4	39, 3	519, 2								
14			389			602									

	Segment														
Age	<u>3</u>	<u>5</u>	**7**	**8**	<u>9</u>	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
			-, 1			-, 1									
Emerald shiner															
1*	47abc	49ab	47abc	44abc	42bc	43bc	43bc	53a	44abc	48abc	41bc	44bc	45abc	41bc	39c
	1, 195	1, 355	2, 28	4, 13	1, 151	2, 59	61, 2	1, 233	1, 431	4, 113	3, 21	2, 49	1, 52	3, 13	3, 15
2*	73a			85a	72a	79a		74a	74a	69a					
	-, 1			-, 1	39, 2	7, 3		3, 11	-, 1	21, 2					
Flathead catfish															
1*								95a	81a	83a	82a	79a	79a	78a	83a
								-, 1	4, 91	3, 94	2, 157	4, 70	3, 111	5, 57	3, 98
2								163	178	165	176	183	159	157	162
								-, 1	10, 47	11, 28	7, 57	13, 24	10, 30	12, 22	14, 29
3								261	270	259	254	273	247	266	266
								-, 1	17, 30	14, 15	18, 23	21, 13	27, 14	28, 11	42, 12
4								384	350	327	309	337	327	381	303
								-, 1	22, 24	30, 6	21, 10	67, 5	41, 9	107, 4	97, 5
5*									425a	427a	349a	410a	422a	487a	353a
									37, 17	259, 2	30, 6	535, 2	55, 7	254, 3	150, 3
6									499	460	388	383	468	588	349
									64, 13	-, 1	77, 4	-, 1	104, 5	271, 3	267, 2
7									583		352		494		392
									156, 8		-, 1		946, 2		95, 2
8									754		364				443
									464, 4	-, 1	-, 1				-, 1
9									796						480
									490, 4						-, 1
10									817						
									2907, 2						
11									615						
									-, 1						
12									648						

	Segment														
Age	3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
									-, 1						
13									670						
									-, 1						
							Flathead chub								
1*	78ab	79ab	87a	80ab	78ab	72b									
	4, 62	4, 90	10, 35	4, 116	7, 36	7, 22									
2*	136a	137a	132a	133a	126a	112a									
	19, 10	12, 30	14, 23	10, 30	21, 14	-, 1									
3	153	192	166	173	173										
	93, 3	12, 13	12, 15	15, 16	46, 6										
4	172	213	176	198	165										
	-, 1	78, 2	16, 6	39, 5	-, 1										
5			191	210	198										
			33, 3	112, 2	-, 1										
6			203												
			30, 2												
							Freshwater drum								
1*	69ef	69ef	79de	61f	91bcd	86cd		91bcd	91bcd	105ab	118a	106ab	100bc	96bc	93bcd
	1, 128	3, 114	23, 6	17, 7	9, 13	11, 11		45, 7	7, 30	26, 6	11, 20	6, 33	5, 42	5, 47	5, 75
2	126	125	139	121	153	152		139	170	190	183	194	181	162	166
	3, 124	4, 103	38, 6	20, 7	13, 12	14, 11		67, 6	9, 26	28, 5	30, 8	12, 17	8, 26	7, 30	6, 55
3	164	166	188	158	192	203		186	228	255	229	259	231	220	219
	4, 98	3, 89	65, 6	24, 7	16, 6	24, 9		78, 6	11, 24	35, 5	29, 7	24, 10	10, 16	10, 25	8, 41
4*	197d	199d	228cd	196d	229cd	229cd		193d	272abc	303ab	270abc	314a	273abc	249c	256bc
	3, 86	4, 72	78, 6	35, 7	225, 2	43, 4		61, 5	15, 20	42, 5	20, 6	39, 8	25, 7	16, 12	9, 31
5	229	227	263	204	269	265		220	299	348	306	359	312	267	281
	5, 82	6, 61	87, 6	39, 5	219, 2	46, 4		64, 5	26, 10	79, 4	20, 6	62, 6	26, 7	35, 5	15, 20
6	251	248	291	227	299	294		244	316	399	345	418	339	297	303
	6, 61	7, 45	93, 6	41, 5	191, 2	49, 4		66, 5	33, 7	145, 3	29, 5	100, 4	49, 5	35, 5	33, 9
7	269	264	322	233		323		266	325	366	384	435	354	304	327

	Segment														
Age	3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
	10, 33	12, 25	145, 5	16, 4		52, 4		71, 5	31, 5	-, 1	36, 4	183, 2	597, 2	70, 3	40, 6
8	281	274	350	254		353		284	348		416	446	330	323	350
	15, 20	22, 14	164, 5	19, 4		60, 4		73, 5	33, 5		95, 3	-, 1	-, 1	69, 3	38, 6
9	292	273	375	274		379		300	354				346	344	356
	21, 10	21, 8	182, 5	19, 4		63, 4		75, 5	48, 3				-, 1	64, 3	108, 3
10	284	280	327	290		358		314	379					363	350
	22, 4	57, 4	124, 3	17, 4		-, 1		78, 5	-, 1					68, 3	212, 2
11	296	292	333	307		376		327	393					382	348
	23, 4	56, 4	-, 1	21, 3		-, 1		82, 5	-, 1					67, 3	-, 1
12	310	304	346	323		395		339	406					409	
	25, 4	58, 4	-, 1	22, 3		-, 1		84, 5	-, 1					245, 2	
13	322	313	357	340		420		353	419					409	
	28, 4	59, 4	-, 1	23, 3		-, 1		86, 5	-, 1					-, 1	
14	335	325	369	357		437		369	431						
	31, 4	65, 4	-, 1	18, 3		-, 1		91, 5	-, 1						
15	345	331						324							
	66, 3	123, 3						633, 2							
16	356	297						335							
	69, 3	-, 1						638, 2							
17	366							346							
	73,3							638, 2							
18	388							356							
	330, 2							639, 2							
19	400							368							
	340, 2							664, 2							
20	410							377							
	344, 2							674, 2							
21	391							333							
	-, 1							-, 1							
22								343							

Age	Segment														
	3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
								-, 1							
23								350							
								-, 1							
24								358							
								-, 1							
25								364							
								-, 1							
26								373							
								-, 1							
Plains minnow															
1*		70a			48ab					52ab	45b	50ab	40b	41b	48ab
		-, 1			-, 1					4, 13	21, 3	7, 7	9, 10	12, 2	-, 1
River carpsucker															
1*	64c	84a	76abc	66bc	64c	65c	67bc	67bc	73abc	74abc	76abc	76abc	81ab	85a	85a
	13, 10	7, 30	3, 127	4, 63	3, 149	12, 14	6, 33	3, 98	3, 219	5, 59	6, 57	4, 77	7, 40	8, 43	6, 59
2	155	178	165	153	149	158	159	149	157	156	168	159	169	176	166
	21, 10	9, 29	5, 125	7, 56	5, 123	35, 7	8, 33	7,86	4, 202	10, 48	15, 24	8, 51	16, 33	14, 33	10, 49
3	244	267	241	229	223	240	240	224	231	237	233	233	252	261	250
	20, 10	10, 26	5, 124	9, 52	7, 113	51, 6	10, 33	7, 67	5, 178	13, 37	26, 13	12, 34	16, 32	23, 21	13, 40
4*	323ab	335a	302ab	296ab	294b	290b	315ab	291b	291b	293b	299a	287b	313ab	296ab	307ab
	19, 10	11, 25	5, 111	10, 42	9, 78	64, 4	9, 32	8, 51	7, 013	10, 27	36, 8	10, 20	22, 20	36, 10	17, 18
5	368	379	352	340	347	317	378	338	322	333	334	336	353	291	334
	33, 5	14, 12	9, 56	16, 19	10, 39	181, 2	10, 26	11, 22	11, 29	11, 12	90, 3	24, 8	35, 7	298, 2	26, 7
6	400	432	396	383	400	382	416	375	343	362	399	399	376	304	341
	-, 1	65, 4	16, 16	30, 6	19, 12	-, 1	13, 13	15, 11	14, 10	26, 4	-, 1	85, 3	308, 2	-, 1	-, 1
7		455	438	439	428	425	444	401	367					342	
		448, 2	20, 6	16, 5	86, 4	-, 1	94, 4	49, 4	95, 2					-, 1	
8		448	475	474	434	455		401						380	
		-, 1	64, 2	47, 3	236, 2	-, 1		-, 1						-, 1	
9			519		485										
			-, 1		-, 1										

	Segment														
Age	3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
10			553		519										
			-, 1		-, 1										
							Sand shiner								
1*								43a	36a	30a	35a	33a	32a	33a	34a
								-, 1	1, 86	3, 22	-, 1	5, 8	19, 3	4, 7	6, 4
							Sauger								
1*	173cde	175cde	173cde	164de	181cd	171de	147e	205bc	224ab	226ab	230ab	239a	237ab	232ab	
	7, 29	9, 33	12, 12	9, 23	9, 36	8, 33	39, 4	16, 12	10, 25	12, 29	13, 23	23, 14	19, 10	74, 4	
2	244	261	250	240	262	255	229	317	331	344	349	328	321	317	
	15, 16	18, 14	15, 11	13, 18	14, 24	12, 15	34, 3	30, 7	11, 16	24, 14	22, 10	37, 11	23, 8	77, 4	
3	288	320	301	298	317	317	301	384	404	409	421	418	379	354	
	22, 11	31, 10	36, 7	26, 11	18, 19	22, 9	-, 1	31, 6	14, 10	28, 11	30, 9	52, 4	37, 6	338, 2	
4	328	381	350	349	383	363	369	413	450	442	442	481	389	389	
	36, 8	59, 6	50, 5	33, 6	26, 10	28, 7	-, 1	344, 2	20, 7	50, 4	75, 4	30, 3	8, 3	503, 2	
5*	361a	414a	409a	381a	432a	370a	390a	448a	477a	493a	472a				
	59, 6	82, 5	128, 3	45, 5	50, 6	77, 3	-, 1	-, 1	518, 2	-, 1	631, 2				
6	401	439	381	465	510	419		455	448	534	541				
	358, 3	133, 4	-, 1	-, 1	117, 2	-, 1		-, 1	-, 1	-, 1	-, 1				
7	381			491						538					
	-, 1			-, 1						-, 1					
8	400			509						542					
	-, 1			-, 1						-, 1					
9	417									547					
	-, 1									-, 1					
10	435														
	-, 1														
11	451														
	-, 1														
12	471														
	-, 1														

	Segment														
Age	3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
13	489														
	-, 1														
14	506														
	-, 1														
15	523														
	-, 1														
							Shovelnose sturgeon								
1*	103abcd	89d	102bcd	112abcd	110abcd	93cd	128a	117abc	107abcd	106abcd	116abc	109abcd	102bcd	124ab	102bcd
	18, 29	8, 111	10, 84	17, 45	6, 215	11, 56	9, 44	20, 13	9, 59	9, 104	8, 55	6, 171	5, 179	8, 102	10, 52
2	165	160	182	182	182	160	203	188	189	189	195	191	187	209	196
	21, 29	11, 108	12, 83	20, 43	9, 182	16, 43	11, 44	22, 13	15, 59	11, 102	10, 54	8, 165	8, 169	10, 99	17, 45
3	222	215	243	244	240	205	264	241	256	264	266	266	262	286	267
	27, 29	14, 108	13, 83	21, 40	11, 165	21, 41	15, 44	33, 13	19, 59	12, 102	12, 54	10, 163	8, 166	12, 99	19, 41
4	279	266	295	305	293	243	314	294	314	322	333	331	326	354	336
	36, 29	19, 106	14, 82	23, 40	13, 158	24, 40	17, 44	30, 13	21, 59	14, 101	15, 54	10, 156	9, 161	13, 94	25, 36
5	326	310	338	352	336	285	361	338	364	372	384	379	385	406	383
	40, 29	21, 105	16, 81	25, 39	15, 147	27, 40	19, 44	30, 13	21, 59	13, 98	17, 53	10, 139	10, 154	13, 84	25, 31
6	369	343	373	380	374	314	409	388	397	408	426	424	433	447	422
	44, 29	22, 101	16, 79	28, 33	16, 138	29, 39	20, 44	30, 13	21, 53	13, 87	16, 51	10, 121	10, 142	13, 73	25, 26
7*	411bcdef	378fg	400ef	405cdef	401def	341g	440abcde	423abcdef	425abcdef	441abcde	459abcd	460abc	467ab	477a	471a
	46, 29	22, 100	16, 75	28, 31	18, 122	28, 38	19, 41	36, 13	19, 49	13, 75	17, 44	11, 96	10, 110	15, 58	28, 23
8	435	396	427	424	425	363	467	451	450	461	479	489	494	498	504
	46, 27	23, 92	15, 72	33, 26	19, 112	29, 36	19, 36	40, 13	20, 44	14, 60	20, 32	14, 67	11, 79	18, 43	35, 13
9	460	415	452	427	439	383	491	481	470	481	487	509	523	514	521
	45, 26	24, 85	15, 68	34, 21	22, 94	29, 35	20, 30	47, 12	22, 37	16, 43	22, 21	17, 44	15, 50	21, 30	49, 8
10	489	435	470	447	459	398	518	490	485	497	506	531	538	544	520
	45, 25	23, 81	16, 58	36, 19	23, 86	29, 33	20, 28	42, 10	26, 29	18, 30	26, 15	27, 21	18, 31	25, 23	53, 4
11	506	454	495	461	479	421	528	525	477	507	525	530	543	560	562
	44, 23	22, 77	17, 54	39, 17	25, 81	30, 33	24, 18	44, 10	28, 16	30, 15	33, 10	42, 10	26, 14	22, 15	757, 2
12	508	475	515	470	486	436	547	547	491	516	526	547	568	583	598
	34, 20	22, 75	18, 47	42, 15	24, 71	31, 31	28, 15	50, 9	33, 13	42, 9	46, 6	61, 7	44, 8	31, 9	887, 2
13	537	499	533	484	495	454	556	559	489	524	515	554	566	611	548

	Segment														
Age	3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
	37, 20	22, 74	20, 41	44, 14	25, 63	33, 29	34, 10	59, 8	27, 9	87, 5	49, 3	50, 5	91, 4	44, 4	-, 1
14	553	526	548	504	502	476	569	564	501	507	540	544	589	618	
	35, 19	21, 73	24, 33	55, 11	25, 55	34, 29	107, 4	58, 7	33, 7	64, 3	61, 3	-, 1	803, 2	46, 3	
15	574	547	550	492	513	478	581	570	507	510			537	635	
	37, 18	22, 70	30, 22	67, 8	27, 48	34, 25	169, 3	54, 6	92, 2	-, 1			-, 1	-, 1	
16	599	567	556	500	525	480		580	529	546			550		
	36, 18	23, 67	38, 16	71, 7	27, 44	33, 22		178, 3	-, 1	-, 1			-, 1		
17	600	579	564	503	545	477		588	552	581					
	34, 15	23, 59	38, 14	77, 6	28, 41	30, 18		937, 2	-, 1	-, 1					
18	620	599	548	506	558	490		538		605					
	35, 14	25, 50	31, 9	82, 5	31, 35	31, 16		-, 1		-, 1					
19	626	597	564	481	582	502		562							
	35, 12	29, 38	35, 8	61, 3	34, 32	35, 14		-, 1							
20	628	612	573	499	598	502		582							
	34, 10	32, 33	48, 6	78, 3	36, 29	36, 11		-, 1							
21	646	626	586	519	570	504		594							
	41, 9	37, 27	70, 5	102, 3	32, 17	46, 8		-, 1							
22	668	641	583	530	599	515		616							
	49, 8	43, 23	51, 4	579, 2	38, 14	45, 6		-, 1							
23	677	661	590	493	603	529		628							
	49, 7	61, 16	87, 3	-, 1	44, 11	54,5		-, 1							
24	684	671	619	512	623	532									
	75, 5	64, 15	294, 2	-, 1	48, 10	56, 4									
25	704	656	604	555	628	519									
	76, 5	62, 11	-, 1	-, 1	63, 8	200, 2									
26	729	656		607	642	547									
	105, 4	78, 8		-, 1	79, 7	-, 1									
27	749	676			664	572									
	104, 4	96, 7			84, 7	-, 1									
28	746	696			668										

	Segment														
Age	3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
	50, 3	103, 7			96, 6										
29	771	687			650										
	44, 2	160, 5			61, 5										
30	789	702			664										
	27, 2	1128, 2			62, 5										
31	806	716			679										
	-, 1	1160, 2			62, 5										
32	818	734			743										
	-, 1	1257, 2			87, 4										
33	828				755										
	-, 1				174, 3										
34	839				770										
	-, 1				175, 3										
35	977				741										
	-, 1				164, 2										
36	998				737										
	-, 1				-, 1										
37					748										
					-, 1										
							Sicklefin chub								
1*		42a		45a	43a	39a					44a	41a	39a	43a	37a
		1, 76		1, 42	2, 64	1, 49					-, 1	153, 2	48, 2	3, 13	5, 11
2*		72a		79a	73a	72a					83a	73a		75a	
		13, 5		10, 6	4, 23	10, 4					-, 1	-, 1		56, 2	
3		101			87	102									
		-, 1			3, 5	-, 1									
							Smallmouth buffalo								
1*	184ab	181ab	196a	159ab	155ab	132abc	80c	133abc	122bc	134abc	155ab	132abc	125bc	116bc	142abc
	111, 4	60, 8	17, 26	33, 8	23, 16	20, 18	-, 1	17, 16	10, 13	21, 11	26, 10	27, 11	21, 16	10, 23	10, 45
2	262	253	272	242	232	205	150	202	203	217	242	209	201	172	211

	Segment														
Age	3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
	108, 4	67, 8	18, 26	34, 8	27, 16	22, 17	-, 1	20, 16	14, 12	33, 10	31, 7	28, 10	29, 15	10, 20	13, 41
3	326	316	337	314	298	265	239	264	264	294	292	268	271	227	276
	100, 4	66, 8	18, 26	33, 8	30, 16	17, 16	-, 1	21, 16	19, 7	50, 9	43, 4	37, 8	52, 10	11, 16	27, 19
4*	383a	367a	385a	374a	369a	324a	317a	324a	320a	365a	311a	322a	334a	275a	369a
	91, 4	73, 8	18, 24	32, 8	36, 15	15, 16	-, 1	24, 15	41, 5	72, 7	-, 1	48, 8	64, 8	25, 8	62, 7
5	450	419	435	428	432	373	369	374	379	415		380	394	309	420
	59, 4	116, 6	18, 24	46, 5	41, 15	17, 15	-, 1	26, 15	138, 2	96, 6		51, 6	81, 7	91, 3	75, 5
6	514	491	479	472	500	422	410	417		465		396	465	345	442
	32, 4	123, 5	19, 16	71, 4	54, 11	29, 10	-, 1	32, 14		102, 6		7, 3	128, 5	-, 1	30, 3
7	563	533	526	545	582	473	450	436		469		459	468		487
	18, 4	133, 5	34, 9	-, 1	78, 5	46, 5	-, 1	39, 10		153, 4		291, 2	98, 4		46, 3
8	603	510	542	571	621	495	497	460		482			554		506
	20, 3	1145, 2	42, 5	-, 1	304, 2	105, 3	-, 1	43, 8		241, 3			377, 2		-, 1
9	646	547	570		629	603		479		468					
	52, 2	1106, 2	52, 2		-, 1	-, 1		54, 5		30, 2					
10	685	575	619					499		513					
	-, 1	1150, 2	-, 1					144, 2		-, 1					
11			646							563					
			-, 1							-, 1					
12										600					
										-, 1					
							Western silvery minnow								
1*	62ab	66ab	76a	63ab	59ab	62ab					55b				
	2, 77	3, 83	4, 21	7, 13	2, 80	6, 12					-, 1				
2	89	81	84	69											
	-, 1	-, 1	-, 1	-, 1											
3	92														
	-, 1														

Table 5. Summary of contrasts testing for significant differences between groups of segments in length-at-age of fifteen species of benthic fishes in the Missouri and Lower Yellowstone rivers. Contrasts were performed using SAS Proc GLM (SAS Institute 1997). To maintain an experiment-wise alpha of 0.05 for the six contrasts, only contrasts with P<0.008 are considered statistically significant. Dashes (-) indicate insufficient data to evaluate effect.

Age	Contrast	F	P
	Blue sucker		
1	3, 5 vs. 9	-	-
	3, 5 vs. **7**, **8**	-	-
	7, **8** vs. 9	0	0.96
	7, **8**, **10**, **12**, **14** vs. **15**	-	-
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	6.8	0.01
	17, *19*, *22* vs. *23*, *25*, *27*	2.4	0.12
6	3, 5 vs. 9	-	-
	3, 5 vs. **7**, **8**	-	-
	7, **8** vs. 9	0.4	0.57
	7, **8**, **10**, **12**, **14** vs. **15**	-	-
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	-	-
	17, *19*, *22* vs. *23*, *25*, *27*	-	-
	Channel catfish		
1	3, 5 vs. 9	17.3	<0.0001
	3, 5 vs. **7**, **8**	1.5	0.22
	7, **8** vs. 9	6.5	0.01
	7, **8**, **10**, **12**, **14** vs. **15**	1.3	0.26
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	0.8	0.36
	17, *19*, *22* vs. *23*, *25*, *27*	5.2	0.02
4	3, 5 vs. 9	77.6	<0.0001
	3, 5 vs. **7**, **8**	29.2	<0.0001
	7, **8** vs. 9	7.8	0.01
	7, **8**, **10**, **12**, **14** vs. **15**	19.5	<0.0001
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	22.4	<0.0001
	17, *19*, *22* vs. *23*, *25*, *27*	1.0	0.32
	Emerald shiner		
1	3, 5 vs. 9	54.5	<0.0001
	3, 5 vs. **7**, **8**	3.9	0.05
	7, **8** vs. 9	3.6	0.05
	7, **8**, **10**, **12**, **14** vs. **15**	0.01	0.91
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	5.08	0.02
	17, *19*, *22* vs. *23*, *25*, *27*	4.34	0.04
2	3, 5 vs. 9	-	-
	3, 5 vs. **7**, **8**	-	-
	7, **8** vs. 9	-	-
	7, **8**, **10**, **12**, **14** vs. **15**	-	-
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	-	-
	17, *19*, *22* vs. *23*, *25*, *27*	-	-

Age	Contrast	F	P
	Flathead catfish		
1	3, 5 vs. 9	-	-
	3, 5 vs. **7**, **8**	-	-
	7, **8** vs. 9	-	-
	7, **8**, **10**, **12**, **14** vs. **15**	0.1	0.80
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	1.5	0.22
	17, *19*, *22* vs. *23*, *25*, *27*	0.6	0.44
5	3, 5 vs. 9	-	-
	3, 5 vs. **7**, **8**	-	-
	7, **8** vs. 9	-	-
	7, **8**, **10**, **12**, **14** vs. **15**	-	-
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	0.6	0.46
	17, *19*, *22* vs. *23*, *25*, *27*	0.7	0.41
	Flathead chub		
1	3, 5 vs. 9	0.1	0.78
	3, 5 vs. **7**, **8**	4.0	0.05
	7, **8** vs. 9	2.6	0.11
	7, **8**, **10**, **12**, **14** vs. **15**	-	-
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	-	-
	17, *19*, *22* vs. *23*, *25*, *27*	-	-
2	3, 5 vs. 9	1.1	0.30
	3, 5 vs. **7**, **8**	0.4	0.55
	7, **8** vs. 9	0.4	0.51
	7, **8**, **10**, **12**, **14** vs. **15**	-	-
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	-	-
	17, *19*, *22* vs. *23*, *25*, *27*	-	-
	Freshwater drum		
1	3, 5 vs. 9	9.4	0.002
	3, 5 vs. **7**, **8**	8.6	0.004
	7, **8** vs. 9	0.04	0.84
	7, **8**, **10**, **12**, **14** vs. **15**	0.9	0.35
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	2.6	0.11
	17, *19*, *22* vs. *23*, *25*, *27*	25.3	<0.0001
4	3, 5 vs. 9	2.7	0.10
	3, 5 vs. **7**, **8**	3.3	0.07
	7, **8** vs. 9	0.7	0.40
	7, **8**, **10**, **12**, **14** vs. **15**	55.1	<0.0001
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	0.5	0.47
	17, *19*, *22* vs. *23*, *25*, *27*	23.3	<0.0001
	Plains minnow		
1	3, 5 vs. 9	0.6	0.44
	3, 5 vs. **7**, **8**	-	-
	7, **8** vs. 9	-	-

Age	Contrast	F	P
	7, **8**, **10**, **12**, **14** vs. **15**	-	-
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	-	-
	17, *19*, *22* vs. *23*, *25*, *27*	0.9	0.35
	River carpsucker		
1	3, 5 vs. 9	6.1	0.01
	3, 5 vs. **7**, **8**	0.6	0.44
	7, **8** vs. 9	9.1	0.003
	7, **8**, **10**, **12**, **14** vs. **15**	2.9	0.09
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	17.7	<0.0001
	17, *19*, *22* vs. *23*, *25*, *27*	11.4	0.0007
4	3, 5 vs. 9	24.2	<0.0001
	3, 5 vs. **7**, **8**	19.1	<0.0001
	7, **8** vs. 9	1.4	0.25
	7, **8**, **10**, **12**, **14** vs. **15**	2.5	0.12
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	3.1	0.08
	17, *19*, *22* vs. *23*, *25*, *27*	2.9	0.09
	Sand shiner		
1	3, 5 vs. 9	-	-
	3, 5 vs. **7**, **8**	-	-
	7, **8** vs. 9	-	-
	7, **8**, **10**, **12**, **14** vs. **15**	2.3	0.13
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	0.9	0.34
	17, *19*, *22* vs. *23*, *25*, *27*	0.1	0.77
	Sauger		
1	3, 5 vs. 9	0.2	0.65
	3, 5 vs. **7**, **8**	2.8	0.09
	7, **8** vs. 9	3.8	0.05
	7, **8**, **10**, **12**, **14** vs. **15**	71.5	<0.0001
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	0.45	0.50
	17, *19*, *22* vs. *23*, *25*, *27*	-	-
5	3, 5 vs. 9	2.8	0.11
	3, 5 vs. **7**, **8**	0.1	0.76
	7, **8** vs. 9	1.7	0.21
	7, **8**, **10**, **12**, **14** vs. **15**	3.5	0.07
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	0.01	0.91
	17, *19*, *22* vs. *23*, *25*, *27*	-	-
	Shovelnose sturgeon		
1	3, 5 vs. 9	1.7	0.19
	3, 5 vs. **7**, **8**	0.4	0.54
	7, **8** vs. 9	0.6	0.45
	7, **8**, **10**, **12**, **14** vs. **15**	1.3	0.26
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	0.9	0.36
	17, *19*, *22* vs. *23*, *25*, *27*	2.9	0.09

Age	Contrast	F	P
7	3, 5 vs. 9	0.4	0.54
	3, 5 vs. **7**, **8**	0.5	0.50
	7, **8** vs. 9	0.01	0.91
	7, **8**, **10**, **12**, **14** vs. **15**	3.2	0.08
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	9.9	0.002
	17, *19*, *22* vs. *23*, *25*, *27*	4.2	0.04
	Sicklefin chub		
1	3, 5 vs. 9	0.6	0.45
	3, 5 vs. **7**, **8**	9.1	0.003
	7, **8** vs. 9	5.2	0.02
	7, **8**, **10**, **12**, **14** vs. **15**	-	-
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	-	-
	17, *19*, *22* vs. *23*, *25*, *27*	-	-
2	3, 5 vs. 9	0.04	0.84
	3, 5 vs. **7**, **8**	2.1	0.16
	7, **8** vs. 9	2.8	0.11
	7, **8**, **10**, **12**, **14** vs. **15**	-	-
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	-	-
	17, *19*, *22* vs. *23*, *25*, *27*	0.2	0.64
	Smallmouth buffalo		
1	3, 5 vs. 9	5.3	0.02
	3, 5 vs. **7**, **8**	1.0	0.33
	7, **8** vs. 9	3.2	0.08
	7, **8**, **10**, **12**, **14** vs. **15**	2.3	0.13
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	0.8	0.36
	17, *19*, *22* vs. *23*, *25*, *27*	1.4	0.24
4	3, 5 vs. 9	0.1	0.80
	3, 5 vs. **7**, **8**	0.1	0.81
	7, **8** vs. 9	0.3	0.56
	7, **8**, **10**, **12**, **14** vs. **15**	0.9	0.35
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	0.1	0.72
	17, *19*, *22* vs. *23*, *25*, *27*	0.1	0.77
	Western silvery minnow		
1	3, 5 vs. 9	5.0	0.03
	3, 5 vs. **7**, **8**	6.0	0.01
	7, **8** vs. 9	13.5	0.0003
	7, **8**, **10**, **12**, **14** vs. **15**	-	-
	15 vs. *17*, *19*, *22*, *23*, *25*, *27*	-	-
	17, *19*, *22* vs. *23*, *25*, *27*	-	-

shovelnose sturgeon, with the shortest lengths occurring in segment 10 and the greatest lengths occurring in segments 25 and 27. Contrasts for length at age of maturity in shovelnose sturgeon indicated the following significant difference: **15** < *17*, *19*, *22*, *23*, *25*, *27*. There was a significant segment by year interaction for age 1 sicklefin chub. Length at age 1 differed among segments for smallmouth buffalo, with the shortest lengths occurring in segment 12 and the greatest lengths occurring in segment 7. Length at age at maturity differed among segments for smallmouth buffalo, but no pair-wise comparisons or contrasts were significant. Length at age 1 differed among years for western silvery minnow, with the greatest lengths attained after the 1996 growth year.

Hydrological Unit and Zone Comparisons

We tested for significant differences in length at age 1 and length at age of maturity, and expressed the percentages of variance due to main effects, interactions and error in each test (Table 3). We reported length-at-age values for all fifteen species (Table 6), although not all species were collected in all hydrological units or zones and age ranges encountered for a species varied widely among units and zones. Length-at-age values are reported in all six units for blue sucker, channel catfish, emerald shiner, freshwater drum, river carpsucker, sauger, shovelnose sturgeon and smallmouth buffalo, and all three zones for blue sucker, channel catfish, emerald shiner, freshwater drum, river carpsucker, sauger, shovelnose sturgeon, sicklefin chub and smallmouth buffalo. Length-at-age values are reported in only one unit and zone for brassy minnow. Length-at-age values are reported up to age 37 in shovelnose sturgeon, but only to age 1 in brassy minnow, plains minnow and sand shiner. Tukey's tests for pair-wise comparison among units and zones are reported in Table 6.

Length at age of maturity differed among zones for blue sucker, with the shortest lengths occurring in zone LA, and the greatest lengths occurring in zone IR. Length at age of maturity differed among units and zones for channel catfish, with the shortest lengths occurring in units UYS and IR-1 and zones LA and IR, and the greatest lengths occurring in unit LC and zone CH. There was a significant unit by year interaction for age 1 emerald shiner. Length at age 1 differed among years for emerald shiner in the analysis of zones, with the shortest lengths attained after the 1996 growth year and the greatest lengths attained after the 1995 growth year. Length at age 1 differed among years for flathead catfish in both analyses, with the greatest lengths attained after the 1993 growth year and the shortest lengths attained after the 1996 growth year. There was a significant segment by year interaction for age 1 flathead chub in the analysis of units. Both unit and year and zone and year effects were significant for age 1 freshwater drum. Freshwater drum length at age 1 was lowest in unit IR-2 and zone LA, and greatest in units UC and LC and zone CH. Freshwater drum length at age 1 tended to be greater in the early and mid 1990s and lower in the 1980s and 1970s. Length at age of maturity differed among units and zones for freshwater drum, with the shortest lengths occurring in units UU and IR-2 and zone LA, and the greatest lengths occurring in unit UC and zone CH. There was a significant unit by year interaction for age 1 plains minnow. Length at age 1 differed among years for plains minnow in the analysis of zones, with greater lengths attained after the 1996 and 1997 than the 1995 growth year. Length at age 1 differed among units for river carpsucker, with the shortest lengths occurring in unit UYS, and the greatest lengths occurring in

Table 6. Mean length-at-age of fifteen species of benthic fishes in hydrological units and zones of the Missouri and lower Yellowstone rivers. Lengths are means of total body lengths (mm) back-calculated from corresponding annuli on calcified structures for all species except shovelnose sturgeon, which are fork lengths. Numbers below mean lengths are (±) 95% confidence interval and sample size, respectively. Hydrological units and zones defined in text. Asterisks indicate ages tested for significant differences among segments; segment means sharing a letter are not significantly different (Tukey's test, "=0.05). Dashes (-) indicate insufficient data to calculate confidence interval. Empty cells indicate no data.

	Hydrological Unit						Zone		
Age	UU	UYS	IR-1	IR-2	UC	LC	LA	IR	CH
					Blue sucker				
1*	117b	127ab	136ab	119b	176ab	191a	124b	156a	183a
	135, 2	19, 5	24, 5	26, 3	8, 95	17, 28	13, 7	13, 34	8, 97
2	195	211	240	225	322	342	206	289	330
	175, 2	23, 5	35, 5	10, 3	10, 86	41, 15	17, 7	19, 33	11, 76
3	260	300	327	310	431	459	289	382	444
	274, 2	48, 5	44, 5	36, 3	11, 68	54, 11	36, 7	22, 29	14, 58
4	330	391	408	400	497	534	374	452	512
	149, 2	59, 5	63, 5	98, 3	16, 35	67, 7	46, 7	31, 22	18, 28
5	396	414	492	491	566	546	407	498	586
	245, 2	81, 3	119, 4	137, 3	35, 13	369, 2	36, 5	39, 12	24, 10
6*	456a	479a	541a	531a	541a		470b	538a	
	462, 2	58, 3	196, 3	289, 2	708, 2		41, 5	53, 7	
7	518	543	553	582	534		531	556	
	540, 2	95, 2	176, 2	-, 1	-, 1		61, 4	37, 4	
8	582	587		646			585	646	
	490, 2	146, 2		-, 1			53, 4	-, 1	
9	682	626					654		
	-, 1	-, 1					355, 2		
10		668					668		
		-, 1					-, 1		
11		703					703		
		-, 1					-, 1		
					Brassy minnow				
1					44			44	
					1, 10			1, 10	
					Channel catfish				
1*	84a	64c	79ab	77ab	71bc	69bc	73ab	76a	70b
	4, 153	3, 201	5, 82	8, 51	4, 359	4, 230	3, 354	3, 652	3, 444
2	163	126	146	138	171	171	143	155	174
	6, 153	6, 181	8, 82	12, 48	6, 208	9, 147	5, 334	4, 581	7, 237
3	245	191	212	211	254	263	217	227	265
	7, 151	7, 164	8, 82	13, 46	8, 159	10, 131	6, 315	4, 492	8, 199
4*	306b	251c	267c	272c	319ab	332a	280b	281b	335a
	8, 149	9, 133	9, 82	12, 45	11, 117	13, 108	7, 282	5, 403	11, 160
5	362	306	308	314	380	398	336	327	402
	9, 125	10, 105	8, 82	12, 44	14, 89	17, 72	7, 230	6, 359	14, 106
6	422	354	344	349	428	455	387	362	457
	14, 84	9, 88	10, 80	14, 40	24, 44	24, 41	10, 172	6, 299	21, 58

	Hydrological Unit						Zone		
Age	UU	UYS	IR-1	IR-2	UC	LC	LA	IR	CH
7	482	406	371	392	490	478	448	395	487
	18, 61	18, 50	12, 62	17, 31	32, 18	33, 22	15, 111	12, 214	30, 29
8	551	454	402	421	551	492	502	429	506
	27, 29	26, 29	15, 49	23, 16	37, 10	60, 9	22, 58	11, 143	52, 11
9	609	508	431	449	580	531	554	455	576
	35, 14	28, 17	19, 39	30, 10	29, 6	-, 1	28, 31	12, 100	117, 3
10	645	540	452	481	599		591	478	
	41, 13	31, 14	25, 26	38, 9	30, 2		32, 27	16, 66	
11	691	571	462	503	638		615	494	
	43, 8	31, 14	30, 26	57, 7	-, 1		35, 22	21, 42	
12	729	611	462	524	653		654	518	
	66, 3	36, 8	50, 10	879, 2	-, 1		42, 13	35, 22	
13		642	441				680	499	
		93, 4	65, 5				60, 7	75, 8	
14			389					496	
			-, 1					1356, 2	
Emerald shiner									
1*	48a	42c	47ab	44abc	45abc	44bc	47a	47a	45b
	1, 550	1, 151	2, 30	4, 13	1, 614	2, 80	1, 701	1, 766	1, 263
2*	73a	72a		85a	71a		72a	76a	69a
	-, 1	39, 2		-, 1	8, 3		8, 3	3, 16	21, 2
Flathead catfish									
1*					82a	80a		81a	81a
					2, 412	2, 266		4, 92	1, 587
2					175	159		177	168
					4, 156	6, 81		9, 48	4, 190
3					264	259		270	260
					9, 81	18, 37		17, 31	10, 88
4					337	333		352	326
					15, 45	34, 18		22, 25	17, 39
5*					407a	421a		425a	402a
					27, 27	48, 13		37, 17	31, 23
6					468	480		499	450
					50, 19	83, 10		64, 13	55, 16
7					557	443		583	425
					146, 9	135, 4		156, 8	104, 5
8					676	443		754	404
					381, 5	-, 1		464, 4	501, 2
9					796	480		796	480
					490, 4	-, 1		490, 4	-, 1
10					817			817	
					2907, 2			2907, 2	
11					615			615	
					-, 1			-, 1	
12					648			648	
					-, 1			-, 1	
13					670			670	

	Hydrological Unit						Zone		
Age	UU	UYS	IR-1	IR-2	UC	LC	LA	IR	CH
					-, 1			-, 1	
Flathead chub									
1*	78ab	78ab	85a	76b			78a	80a	
	2, 152	7, 36	5, 88	4, 63			2, 188	3, 173	
2*	137a	126a	134a	122a			134a	132a	
	10, 40	21, 14	9, 46	20, 7			9, 54	8, 54	
3	184	173	172	157			181	169	
	14, 16	46, 6	10, 26	29, 5			14, 22	9, 31	
4	199	165	189	180			190	186	
	61, 3	-, 1	25, 8	25, 3			41, 4	17, 11	
5		198	191	210			198	199	
		-, 1	33, 3	112, 2			-, 1	19, 5	
6			203					203	
			30, 2					30, 2	
Freshwater drum									
1*	69cd	91ab	79bc	61d	104a	96a	70c	86b	100a
	2, 242	9, 13	23, 6	17, 7	5, 89	3, 164	2, 255	7, 61	3, 223
2	125	153	139	121	181	169	127	153	173
	2, 227	13, 12	38, 6	20, 7	7, 56	4, 111	3, 239	8, 56	4, 141
3	165	192	188	158	238	222	166	205	227
	3, 187	16, 6	65, 6	24, 7	9, 46	6, 82	3, 193	13, 52	5, 104
4*	198c	229bc	228bc	196c	284a	257ab	199c	240b	268a
	3, 158	225, 2	78, 6	35, 7	12, 39	8, 50	3, 160	17, 42	9, 69
5	228	269	263	204	322	285	228	258	302
	4, 143	219, 2	87, 6	39, 5	19, 26	12, 32	3, 145	22, 30	13, 48
6	250	299	291	227	358	311	251	277	339
	5, 106	191, 2	93, 6	41, 5	28, 19	20, 19	5, 108	24, 27	22, 31
7	267		322	233	367	326	267	295	353
	8, 58		145, 5	16, 4	30, 12	27, 11	8, 58	29, 23	25, 18
8	278		350	254	381	340	278	319	364
	8, 34		164, 5	19, 4	37, 9	23, 10	12, 34	33, 23	29, 14
9	284		375	274	354	350	284	336	350
	14, 18		182, 5	19, 4	48, 3	28, 7	14, 18	39, 21	28, 7
10	282		327	290	379	358	282	318	358
	21, 8		124, 3	17, 4	-, 1	29, 5	21, 8	28, 14	29, 5
11	294		333	307	393	374	294	333	374
	21, 8		-, 1	21, 3	-, 1	45, 4	21, 8	34, 11	45, 4
12	307		346	323	406	409	307	346	409
	22, 8		-, 1	22, 3	-, 1	245, 2	22, 8	34, 11	245, 2
13	318		357	340	419	409	318	362	409
	23, 8		-, 1	23, 3	-, 1	-, 1	23, 8	36, 11	-, 1
14	330		369	357	431		330	377	
	25, 8		-, 1	18, 3	-, 1		25, 8	36, 11	
15	338						338	324	
	38, 6						38, 6	633, 2	
16	342						342	335	
	60, 4						60, 4	638, 2	

	Hydrological Unit						Zone		
Age	UU	UYS	IR-1	IR-2	UC	LC	LA	IR	CH
17	366						366	346	
	73, 3						73, 3	638, 2	
18	388						388	356	
	330, 2						330, 2	639, 2	
19	400						400	368	
	340, 2						340, 2	664, 2	
20	410						410	377	
	344, 2						344, 2	674, 2	
21	391						391	333	
	-, 1						-, 1	-, 1	
22								343	
								-, 1	
23								350	
								-, 1	
24								358	
								-, 1	
25								364	
								-, 1	
26								373	
								-, 1	
Plains minnow									
1*	70a	48b			51ab	41b	59a		47a
	-, 1	-, 1			4, 23	7, 13	139, 2		3, 36
River carpsucker									
1*	79ab	64d	74bc	66cd	74bc	84a	67c	71b	79a
	6, 40	3, 149	3, 160	4, 63	2, 412	4, 142	3, 189	1, 554	2, 335
2	172	149	163	153	158	169	155	157	165
	9, 39	5, 123	3, 158	7, 56	3, 325	6, 115	5, 162	2, 509	5, 238
3	261	223	241	229	232	253	232	233	244
	10, 36	7, 113	5, 157	9, 52	4, 262	9, 93	6, 149	3, 460	6, 177
4*	332a	294b	305b	296b	291b	307b	305a	297a	299a
	10, 35	9, 78	5, 143	10, 42	5, 158	12, 48	7, 113	3, 343	7, 103
5	376	347	360	340	327	337	356	347	335
	12, 17	10, 39	7, 82	16, 19	7, 52	20, 16	9, 56	6, 154	9, 39
6	426	400	405	383	360	349	408	386	370
	48, 5	19, 12	9, 29	30, 6	15, 18	62, 4	18, 17	9, 57	22, 12
7	455	428	441	439	367	342	437	426	342
	448, 2	96, 4	27, 10	16, 5	95, 2	-, 1	52, 6	15, 22	-, 1
8	448	434	475	474		380	439	461	380
	-, 1	236, 2	64, 2	47, 3		-, 1	50, 3	28, 7	-, 1
9		485	519				485	519	
		-, 1	-, 1				-, 1	-, 1	
10		519	553				519	553	
		-, 1	-, 1				-, 1	-, 1	
Sand shiner									
1*					35a	33a		36a	32b
					1, 117	3, 14		1, 87	2, 45

	Hydrological Unit						Zone		
Age	UU	UYS	IR-1	IR-2	UC	LC	LA	IR	CH
					Sauger				
1*	174b	181b	167b	164b	229a	236a	177b	185b	231a
	5, 62	9, 36	13, 16	9, 23	7, 91	19, 14	5, 98	6, 109	7, 80
2	252	262	246	240	338	319	256	273	335
	12, 30	14, 24	13, 14	13, 18	11, 51	21, 12	8, 54	11, 70	12, 47
3	303	317	301	298	412	372	310	338	404
	18, 21	18, 19	30, 8	26, 11	12, 34	28, 8	13, 40	16, 44	15, 32
4	350	383	353	349	452	389	364	383	433
	31, 14	26, 10	39, 6	33, 6	16, 18	35, 5	21, 24	19, 28	24, 16
5*	385b	432ab	404ab	381b	478a		402b	402b	479a
	43, 11	50, 6	68, 4	45, 5	57, 5		32, 17	27, 15	127, 3
6	423	510	381	465	508		442	434	537
	67, 7	117, 2	-, 1	-, 1	129, 3		56, 9	42, 5	49, 2
7	381			491	538		381	491	538
	-, 1			-, 1	-, 1		-, 1	-, 1	-, 1
8	400			509	542		400	509	542
	-, 1			-, 1	-, 1		-, 1	-, 1	-, 1
9	417				547		417		547
	-, 1				-, 1		-, 1		-, 1
10	435						435		
	-, 1						-, 1		
11	451						451		
	-, 1						-, 1		
12	471						471		
	-, 1						-, 1		
13	489						489		
	-, 1						-, 1		
14	506						506		
	-, 1						-, 1		
15	523						523		
	-, 1						-, 1		
					Shovelnose sturgeon				
1*	92b	110a	111a	112a	109a	109a	103a	107a	109a
	7, 140	6, 215	7, 128	17, 45	4, 389	4, 333	4, 355	5, 301	3, 663
2	161	182	189	182	191	195	173	184	193
	9, 137	9, 182	9, 127	20, 43	5, 380	6, 313	7, 319	7, 285	4, 634
3	217	240	250	244	264	270	230	244	268
	13, 137	11, 165	10, 127	21, 40	6, 378	6, 306	9, 302	8, 280	5, 625
4	268	293	302	305	326	336	282	296	332
	16, 135	13, 158	11, 126	23, 40	7, 370	7, 291	10, 293	9, 278	5, 602
5	313	336	346	352	375	391	325	341	384
	18, 134	15, 147	12, 125	25, 39	7, 349	5, 269	12, 281	9, 276	5, 559
6	349	374	386	380	415	436	362	377	427
	20, 130	16, 138	13, 123	28, 33	7, 312	7, 241	13, 268	10, 261	5, 500
7*	386b	401b	414b	405b	448a	471a	393b	404b	462a
	21, 129	18, 122	13, 116	28, 31	7, 264	9, 191	13, 251	9, 247	6, 406
8	405	425	441	424	471	496	415	429	486

	Hydrological Unit						Zone		
Age	UU	UYS	IR-1	IR-2	UC	LC	LA	IR	CH
	20, 119	19, 112	13, 108	33, 26	8, 203	9, 135	14, 251	10, 227	7, 294
9	425	439	464	427	487	520	432	448	505
	20, 111	22, 94	13, 98	34, 21	9, 145	12, 88	15, 205	10, 203	7, 196
10	448	459	486	447	502	539	453	466	523
	21, 106	23, 86	14, 86	36, 19	12, 95	14, 58	15, 192	12, 177	9, 124
11	466	479	503	461	506	553	472	479	535
	20, 100	25, 81	14, 72	39, 17	16, 51	17, 31	16, 181	13, 148	13, 66
12	482	486	523	470	515	578	484	494	551
	19, 95	24, 71	16, 62	42, 15	20, 35	24, 19	15, 166	13, 130	18, 41
13	507	495	537	484	515	584	502	506	554
	19, 94	25, 63	17, 51	44, 14	22, 22	36, 9	15, 157	14, 111	24, 22
14	532	502	550	504	514	606	521	518	560
	19, 92	25, 55	22, 37	55, 11	19, 14	61, 5	15, 147	17, 91	35, 12
15	552	513	554	492	508	586	539	518	560
	19, 88	27, 48	28, 25	67, 8	19, 3	622, 2	16, 136	20, 66	163, 3
16	574	525	556	500	537	550	557	515	548
	20, 85	27, 44	38, 16	71, 7	104, 2	-, 1	16, 129	23, 49	27, 2
17	583	545	564	503	567		569	518	581
	19, 74	28, 41	38, 14	77, 6	187, 2		15, 115	24, 41	-, 1
18	604	558	548	506	605		588	511	605
	21, 64	31, 35	31, 9	82, 5	-, 1		18, 99	21, 31	-, 1
19	604	582	564	481			595	521	
	24, 50	34, 32	35, 8	61, 3			19, 82	24, 26	
20	616	598	573	499			609	526	
	26, 43	36, 29	48, 6	78, 3			21, 72	26, 21	
21	631	570	586	519			611	536	
	29, 36	32, 17	70, 5	102, 3			23, 53	32, 17	
22	648	599	583	530			633	546	
	34, 31	38, 14	51, 4	579, 2			26, 45	32, 13	
23	665	603	590	493			645	554	
	42, 23	44, 11	87, 3	-, 1			32, 34	39, 10	
24	674	623	619	512			657	554	
	48, 20	48, 10	294, 2	-, 1			35, 30	49, 7	
25	671	628	604	555			657	549	
	45, 16	63, 8	-, 1	-, 1			35, 24	67, 4	
26	681	642		607			666	577	
	58, 12	79, 7		-, 1			42, 19	380, 2	
27	703	664					688	572	
	64, 11	184, 7					47, 18	-, 1	
28	711	668					695		
	68, 10	96, 6					50, 16		
29	711	650					686		
	104, 7	61, 5					60, 12		
30	746	664					700		
	141, 4	62, 5					60, 9		
31	746	679					704		
	261, 3	62, 5					63, 8		
32	762	743					751		
	274, 3	87, 4					69, 7		
33	828	755					773		
	-, 1	174, 3					108, 4		
34	839	770					787		
	-, 1	175, 3					107, 4		

	Hydrological Unit						Zone		
Age	UU	UYS	IR-1	IR-2	UC	LC	LA	IR	CH
35	977	741					819		
	-, 1	164, 2					340, 3		
36	998	737					868		
	-, 1	-, 1					1656, 2		
37		748					748		
		-, 1					-, 1		
Sicklefin chub									
1*	42ab	43ab		45a	42ab	40b	42a	42ab	40b
	1, 76	2, 64		1, 42	30, 3	3, 26	1, 140	1, 91	3, 29
2*	72a	73a		79a	78a	75a	72a	76a	76a
	13, 5	4, 23		10, 6	65, 2	56, 2	3, 28	6, 10	9, 4
3	101	87					90	102	
	-, 1	3, 5					7, 6	-, 1	
Smallmouth buffalo									
1*	182a	155ab	192a	159ab	135b	132b	167a	153ab	134b
	43, 12	23, 16	19, 27	33, 8	10,45	8, 84	22, 28	10, 82	6, 116
2	256	232	268	242	215	199	242	229	204
	46, 12	28, 16	20, 27	34, 8	12, 39	10, 76	24, 28	11, 80	8, 103
3	319	298	333	314	279	257	307	295	266
	46, 12	30, 16	19, 27	33, 8	18, 28	16, 45	24, 28	12, 74	14, 66
4*	372a	369a	382a	374a	335a	324a	370a	351ab	331b
	48, 12	36, 15	18, 25	32, 8	26, 21	30, 23	27, 27	12, 69	22, 39
5	431	432	432	428	395	386	432	402	391
	62, 10	41, 15	18, 25	46, 5	39, 14	44, 15	32, 25	13, 62	30, 27
6	501	500	475	472	442	444	500	445	443
	55, 9	54, 11	20, 17	71, 4	66, 9	64, 9	35, 20	16, 45	41, 18
7	546	582	519	545	466	476	559	479	471
	59, 9	78, 5	35, 10	-, 1	80, 6	42, 7	42, 14	24, 26	35, 13
8	566	621	535	571	482	538	582	497	510
	102, 5	304, 2	38, 6	-, 1	241, 3	101, 3	68, 7	28, 18	77, 6
9	597	629	570		468		603	517	468
	146, 4	-, 1	92, 2		30, 2		100, 5	53, 8	30, 2
10	612		619		513		612	539	513
	274, 3		-, 1		-, 1		274, 3	174, 3	-, 1
11			646		563			646	563
			-, 1		-, 1			-, 1	-, 1
12					600				600
					-, 1				-, 1
Western silvery minnow									
1*	64ab	59ab	76a	63ab	55b		63a	69a	55a
	2, 160	2, 80	4, 21	7, 13	-, 1		2, 240	4,4 6	-, 1
2	85		84	69			85	76	
	47, 2		-, 1	-, 1			47, 2	97, 2	
3				92				92	
				-, 1				-, 1	

unit LC. Length at age of maturity differed among units for river carpsucker, with the shortest lengths occurring in units UYS, IR-1, IR-2, UC and LC, and the greatest length occurring in unit UU. There was a significant unit by year interaction for age 1 sand shiner. Length at age 1 differed among zones for sand shiner, with the shortest length occurring in zone CH and the greatest length occurring in zone IR. Length at age 1 differed among units and zones for sauger, with the shortest lengths occurring in units UU, UYS, IR-1 and IR-2 and zones LA and IR, and the greatest lengths occurring in units UC and LC and zone CH. Length at age of maturity differed among units for sauger, with the shortest lengths occurring in units UU and IR-2, and the greatest length occurring in unit UC. Length at age 1 differed among years for shovelnose sturgeon in both the unit and zone analyses, and although there was year-to-year variation, the underlying pattern was of decreasing length with increasing age at capture. Length at age of maturity differed among units and zones for shovelnose sturgeon, with the shortest lengths occurring in unit UU, UYS, IR-1 and IR-2 and zones LA and IR, and the greatest lengths occurring in units UC and LC and zone CH. There was a significant unit by year interaction for age 1 sicklefin chub. Length at age 1 differed among years for sicklefin chub in the analysis of zones, with the shortest lengths attained after the 1995 growth year and the greatest lengths attained after the 1997 growth year. Length at age 1 differed among units for smallmouth buffalo, with the shortest lengths occurring in units UC and LC, and the greatest lengths occurring in units UU and IR-1. Length at age at maturity differed among units for smallmouth buffalo, but no pair-wise comparisons were significant. Length at age 1 differed among units for western silvery minnow, with the shortest length occurring in unit UC, and the greatest length occurring in unit IR-1. Length at age 1 differed among years for western silvery minnow in the analysis of zones, with the greatest lengths attained after the 1996 growth year.

von Bertalanffy Growth Functions

We fit von Bertalanffy growth functions (VBGFs) to describe increases in length-at-age for blue sucker, channel catfish, flathead chub, freshwater drum, river carpsucker, sauger, shovelnose sturgeon and smallmouth buffalo by segment, hydrological unit and zone (Tables 7, 8). We plotted VBGFs to illustrate increases in length-at-age for these species (Figures 2-9).

Age-Specific Growth

Segment Comparisons

We tested for significant differences in annual growth due to segment, age, year and 2-way interactions, and expressed the percentages of variance due to main effects, interactions and error in each test (Table 9). As expected, age differences were significant in every species where multiple ages were present. There was a significant age by year interaction for flathead catfish. Annual growth differed among segments for freshwater drum, with the slowest growth occurring in segments 3, 5, 8 and 9, and the fastest growth occurring in segments 19 and 22. There was a significant segment by year interaction for plains minnow and sand shiner. Annual growth differed among segments for sicklefin chub, with the slowest growth occurring in segments 8, 9 and 22, and the fastest growth occurring in segments 19 and 23.

Hydrological Unit and Zone Comparisons

We tested for significant differences in annual growth due to hydrological unit, zone, age, year and 2-way interactions, and expressed the percentages of variance due to main effects, interactions and error in

Table 7. Von Bertalanffy Growth Functions (VBGFs) for eight species of benthic fishes in segments of the Missouri and Lower Yellowstone rivers. See text for description of the VBGF. Parameters are defined as follows: L_4 = estimated maximum length, K = growth coefficient, **T** = reparameterized growth coefficient (L_4 · K), t_o = time when length is zero, n = number of age classes modeled. Numbers below parameters are (±) 95% confidence interval. Dashes (-) indicate insufficient data to estimate VBGF. Empty cells indicate no data.

	Segment														
Parameter	3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
							Blue sucker								
L_4	-	-	760	-	943		-		592	-	-	1001	-	-	-
	-	-	181	-	424		-		53	-	-	369	-	-	-
K	-	-	0.18	-	0.12		-		0.43	-	-	0.19	-	-	-
	-	-	0.08	-	0.09		-		0.13	-	-	0.12	-	-	-
T	-	-	138	-	110		-		253	-	-	187	-	-	-
	-	-	34	-	35		-		53	-	-	53	-	-	-
t_o	-	-	-0.07	-	-0.23		-		0.24	-	-	-0.14	-	-	-
	-	-	0.61	-	0.64		-		0.24	-	-	0.39	-	-	-
n	-	-	7	-	8		-		6	-	-	5	-	-	-
							Channel catfish								
L_4	1132	-	460	667	1155	1060	558	623	1039	588	895	749	-	677	622
	180	-	32	40	110	151	50	51	317	182	78	144	-	145	81
K	0.08	-	0.24	0.13	0.06	0.06	0.17	0.16	0.09	0.20	0.15	0.20	-	0.19	0.21
	0.02	-	0.06	0.02	0.01	0.01	0.04	0.03	0.04	0.12	0.02	0.08	-	0.08	0.06
T	95	-	112	85	73	68	94	99	93	119	134	153	-	125	129
	11	-	21	6	4	5	15	12	17	36	7	37	-	27	20
t_o	0.20	-	0.33	0.07	0.14	-0.007	0.16	0.06	0.13	0.43	0.44	0.56	-	0.51	0.41
	0.31	-	0.38	0.17	0.14	0.22	0.37	0.3	0.39	0.41	0.06	0.38	-	0.32	0.24
n	13	-	13	12	13	13	13	12	10	7	6	9	-	8	8
							Flathead chub								
L_4	-	-	216	243	-	-									
	-	-	27	40	-	-									
K	-	-	0.43	0.42	-	-									
	-	-	0.21	.21	-	-									
T	-	-	93	102	-	-									

Parameter	Segment 3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
	-	-	35	35	-	-									
t_o	-	-	-.20	0.06	-	-									
	-	-	0.55	0.39	-	-									
n	-	-	6	5	-	-									
Freshwater drum															
L_4	430	332	409	442	492	536		380	371	614	741	620	420	454	383
	48	16	88	98	241	135		20	14	240	238	162	38	74	21
K	0.11	0.21	0.21	0.10	0.14	0.13		0.16	0.34	0.17	0.09	0.17	0.27	0.15	0.27
	0.04	0.04	0.12	0.05	0.12	0.06		0.04	0.05	0.12	0.05	0.08	0.07	0.07	0.05
T	47	71	88	45	71	67		60	124	102	67	108	112	70	104
	11	10	34	12	26	16		11	13	32	14	28	17	20	16
t_o	-1.22	-0.17	0.06	-0.98	-0.47	-0.52		-0.78	0.16	-0.16	-1.00	-0.1	-0.05	-0.81	-0.05
	1.06	0.39	0.78	0.97	0.65	0.56		0.7	0.17	0.49	0.5	0.43	0.24	0.87	0.29
n	20	15	10	14	6	9		20	9	6	8	7	7	12	10
River carpsucker															
L_4	-	594	663	717	565	403	617	537	421	474	491	771	475	-	-
	-	77	47	138	102	131	117	68	40	91	226	484	95	-	-
K	-	0.22	0.16	0.14	0.21	0.36	0.20	0.21	0.31	0.26	0.25	0.12	0.29	-	-
	-	0.06	0.02	0.05	0.08	0.26	0.07	0.05	0.08	0.10	0.21	0.12	0.13	-	-
T	-	132	106	99	118	143	124	114	132	123	121	93	137	-	-
	-	20	7	14	25	59	22	15	22	27	50	31	35	-	-
t_o	-	0.33	0.22	0.28	0.48	0.52	0.46	0.41	0.42	0.37	0.32	0.11	0.38	-	-
	-	0.20	0.11	0.25	0.31	0.37	0.24	0.19	0.20	0.26	0.43	0.23	0.30	-	-
n	-	7	8	8	8	5	7	7	7	6	5	6	6	-	-
Sauger															
L_4	561	530	-	511	-	414	-	-	532	-	490	-	-	-	-
	227	69	-	111	-	106	-	-	24	-	54	-	-	-	-
K	0.17	0.28	-	0.25	-	0.47	-	-	0.44	-	0.63	-	-	-	-
	0.15	0.10	-	0.13	-	0.44	-	-	0.07	-	0.35	-	-	-	-
T	96	147	-	127	-	193	-	-	232	-	307	-	-	-	-
	46	34	-	37	-	135	-	-	28	-	139	-	-	-	-

	Segment														
Parameter	3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
t_o	-1.22	-0.44	-	-0.56	-	-0.13	-	-	-0.25	-	-0.01	-	-	-	-
	1.08	0.40	-	0.48	-	0.9	-	-	0.17	-	0.53	-	-	-	-
n	6	6	-	5	-	5	-	-	5	-	5	-	-	-	-
Shovelnose sturgeon															
L_4	833	772	610	515	793	545	636	647	520	546	559	600	626	664	664
	47	24	12	10	66	10	10	17	10	13	17	15	16	30	53
K	0.07	0.08	0.15	0.21	0.06	0.13	0.16	0.14	0.24	0.24	0.24	0.21	0.20	0.17	0.17
	0.01	0.01	0.01	0.02	0.01	0.01	0.01	0.01	0.02	0.03	0.03	0.01	0.02	0.02	0.03
T	61	59	90	109	48	70	100	92	127	129	132	124	123	116	114
	7	4	6	10	9	4	3	5	9	9	12	8	7	11	16
t_o	-1.37	-1.16	-0.35	-0.13	-3.06	-0.57	-0.42	-0.35	0.11	0.14	0.10	0.09	0.15	-0.22	-0.001
	0.7	0.43	0.25	0.17	1.50	0.23	0.10	0.19	0.16	0.16	0.21	0.14	0.14	0.28	0.33
n	30	32	24	22	35	25	15	17	15	14	14	13	14	14	12
Smallmouth buffalo															
L_4	1208	683	741	750	-	828		580	-	525	-	709	-	-	-
	279	136	76	30	-	185		37	-	61	-	386	-	-	-
K	0.08	0.17	0.15	0.15	-	0.11		0.19	-	0.31	-	0.13	-	-	-
	0.03	0.09	0.04	0.01	-	0.04		0.03	-	0.13	-	0.12	-	-	-
T	92	118	109	113	-	89		111	-	163	-	94	-	-	-
	12	40	15	4	-	14		12	-	49	-	41	-	-	-
t_o	-1.17	-0.71	-1.10	-0.58	-	-0.61		-0.30	-	0.14	-	-0.58	-	-	-
	0.38	0.87	0.37	0.06	-	0.36		0.25	-	0.50	-	0.88	-	-	-
n	9	10	9	6	-	8		10	-	9	-	7	-	-	-

Table 8. Von Bertalanffy Growth Functions (VBGFs) for eight species of benthic fishes in hydrological units and zones of the Missouri and Lower Yellowstone rivers. See text for description of the VBGF. Parameters are defined as follows: L_4 = estimated maximum length, K = growth coefficient, **T** = reparameterized growth coefficient (L_4 · K), t_o = time when length is zero, n = number of age classes modeled. Numbers below parameters are (±) 95% confidence interval. Dashes (-) indicate insufficient data to estimate VBGF. Empty cells indicate no data.

	Hydrological Unit						Zone		
Parameter	UU	UYS	IR-1	IR-2	UC	LC	LA	IR	CH
					Blue sucker				
L_4	2437	943	761	-	607	620	1441	620	763
	1081	424	244	-	132	183	929	17	209
K	0.03	0.12	0.20	-	0.46	0.48	0.06	0.34	0.29
	0.01	0.09	0.13	-	0.35	0.45	0.05	0.03	0.18
T	77	110	151	-	278	299	89	209	222
	6	35	53	-	155	201	23	13	76
t_o	-0.59	-0.23	0.05	-	0.27	0.25	-0.52	0.14	0.05
	0.17	0.64	0.56	-	0.62	0.68	0.62	0.09	0.41
n	8	8	7	-	6	5	9	7	5
					Channel catfish				
L_4	1213	1155	510	667	874	613	1080	559	714
	234	110	36	40	135	80	117	30	115
K	0.08	0.06	0.20	0.13	0.12	0.23	0.08	0.19	0.18
	0.03	0.01	0.04	0.02	0.03	0.07	0.02	0.03	0.06
T	91	73	101	85	107	141	85	105	127
	11	4	15	6	14	24	6	12	23
t_o	0.09	0.14	0.23	0.07	0.27	0.52	0.17	0.25	0.42
	0.35	0.14	0.35	0.18	0.27	0.24	0.20	0.27	0.31
n	13	13	13	12	10	8	13	14	9
					Flathead chub				
L_4	-	-	210	-			-	215	
	-	-	20	-			-	11	
K	-	-	0.56	-			-	0.52	
	-	-	0.26	-			-	0.11	
T	-	-	117	-			-	113	
	-	-	43	-			-	20	
t_o	-	-	0.07	-			-	0.12	
	-	-	0.45	-			-	0.21	
n	-	-	6	-			-	6	
					Freshwater drum				
L_4	433	492	409	442	398	412	434	361	398
	59	241	88	98	43	33	60	13	26
K	0.10	0.14	0.21	0.10	0.34	0.22	0.10	0.25	0.29
	0.04	0.12	0.12	0.05	0.14	0.06	0.04	0.05	0.08
T	44	71	88	45	135	91	44	91	114
	12	26	34	12	41	19	12	17	26
t_o	-1.40	-0.47	0.06	-0.98	0.15	-0.31	-1.46	-0.15	0.01
	1.3	0.65	0.78	0.97	0.49	0.52	1.30	0.52	0.47
n	20	6	10	14	9	12	20	20	12

	Hydrological Unit						Zone		
Parameter	UU	UYS	IR-1	IR-2	UC	LC	LA	IR	CH
River carpsucker									
L_4	603	565	642	717	434	408	556	623	475
	71	102	17	138	52	83	94	42	71
K	0.21	0.21	0.17	0.14	0.30	0.37	0.23	0.17	0.27
	0.05	0.08	0.01	0.05	0.09	0.20	0.09	0.02	0.09
T	129	118	112	99	131	151	125	108	126
	16	25	3	14	25	54	27	7	23
t_o	0.36	0.48	0.30	0.28	0.41	0.42	0.49	0.30	0.33
	0.17	0.31	0.04	0.25	0.22	0.39	0.32	0.11	0.22
n	7	8	8	8	7	6	8	8	6
Sauger									
L_4	553	-	-	511	539	-	612	477	-
	95	-	-	111	32	-	125	46	-
K	0.21	-	-	0.25	0.43	-	0.18	0.37	-
	0.10	-	-	0.13	0.11	-	0.08	0.13	-
T	115	-	-	127	232	-	113	175	-
	30	-	-	37	45	-	27	44	-
t_o	-0.85	-	-	-0.56	-0.29	-	-0.86	-0.33	-
	0.52	-	-	0.48	0.30	-	0.49	0.40	-
n	6	-	-	5	6	-	6	6	-
Shovelnose sturgeon									
L_4	817	793	604	515	548	636	907	553	583
	32	66	10	10	15	15	90	8	11
K	0.07	0.06	0.16	0.21	0.24	0.19	0.05	0.18	0.22
	0.01	0.01	0.01	0.02	0.03	0.01	0.01	0.01	0.01
T	56	48	96	109	131	122	45	100	131
	4	9	6	10	14	7	8	7	8
t_o	-1.42	-3.06	-0.33	-0.13	0.14	0.05	-3.06	-0.24	0.16
	0.52	1.50	0.24	0.17	0.27	0.16	1.44	0.25	0.16
n	32	35	24	22	17	15	36	26	16
Smallmouth buffalo									
L_4	821	-	737	750	553	1325	819	631	597
	151	-	60	30	82	794	175	29	162
K	0.13	-	0.15	0.15	0.24	0.06	0.14	0.18	0.21
	0.05	-	0.03	0.14	0.10	0.05	0.07	0.02	0.15
T	108	-	108	113	133	78	115	116	123
	24	-	12	4	39	17	30	9	54
t_o	-0.83	-	-1.07	-0.58	-0.08	-0.75	-0.51	-0.47	-0.12
	0.60	-	0.31	0.06	0.57	0.50	0.65	0.19	0.87
n	10	-	9	6	9	8	10	10	9

Figures 2-5. Von Bertalanffy Growth Function (VBGF) curves for four species in segments, hydrological units and zones of the Missouri and lower Yellowstone rivers. See text for description of the VBGF. Parameters for VBGF curves are given in Tables 7 and 8.

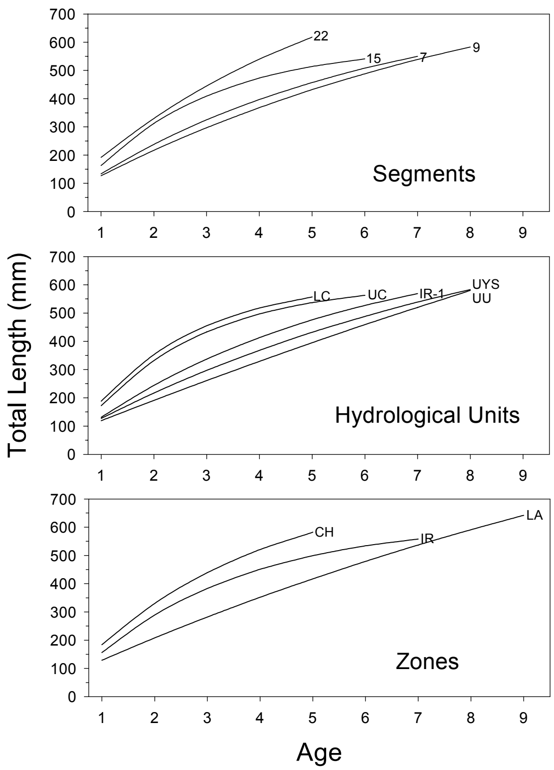

Figure 2. VBGF curves for blue sucker

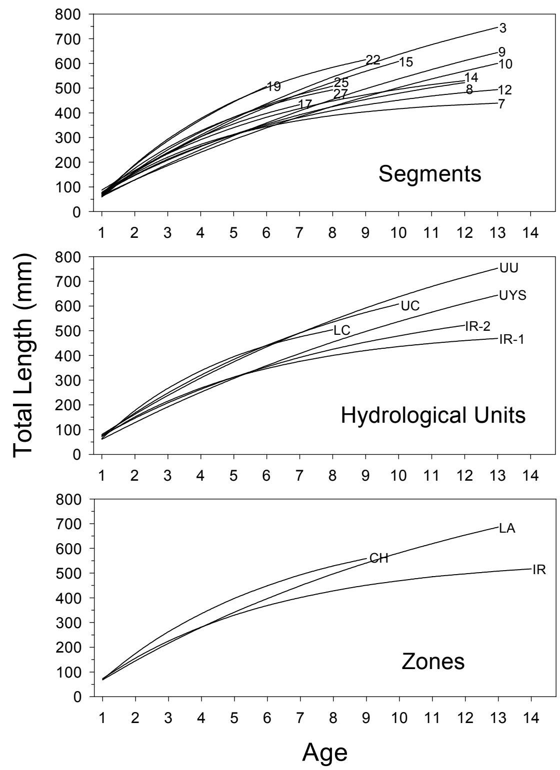

Figure 3. VBGF curves for channel catfish

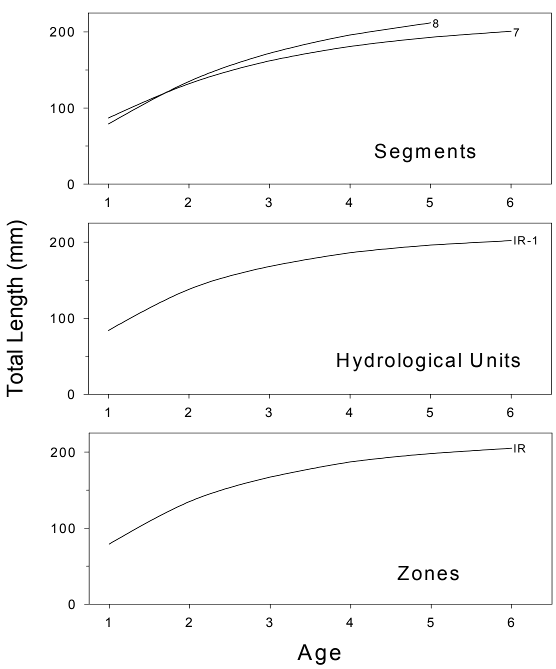

Figure 4. VBGF curves for flathead chub

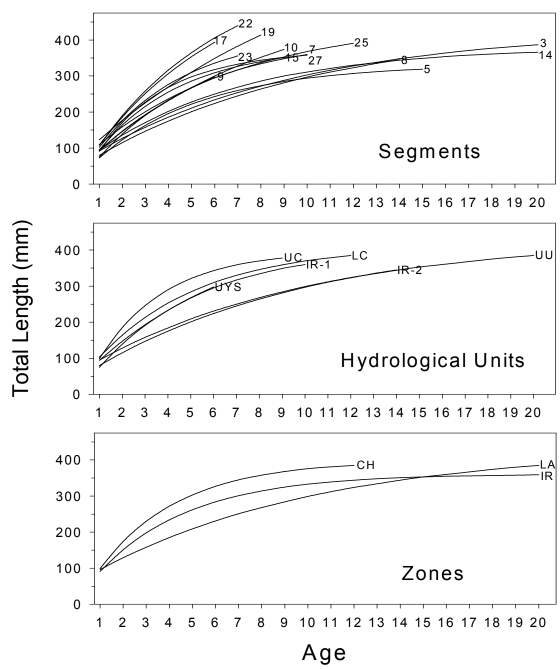

Figure 5. VBGF curves for freshwater drum

Figures 6-9. Von Bertalanffy Growth Function (VBGF) curves for four species in segments, hydrological units and zones of the Missouri and lower Yellowstone rivers. See text for description of the VBGF. Parameters for VBGF curves are given in Tables 7 and 8.

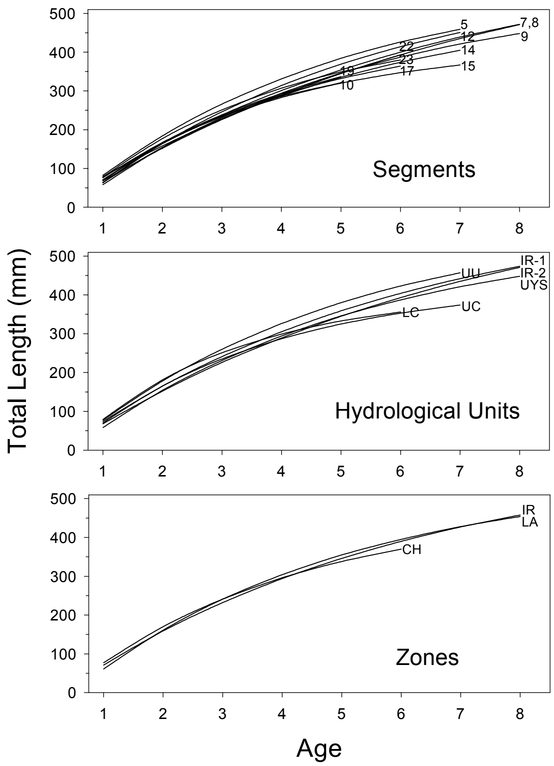

Figure 6. VBGF curves for river carpsucker

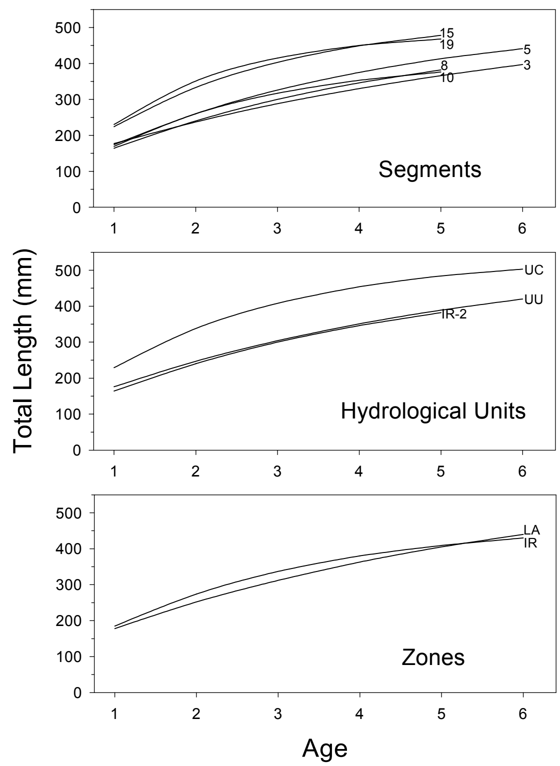

Figure 7. VBGF curves for sauger

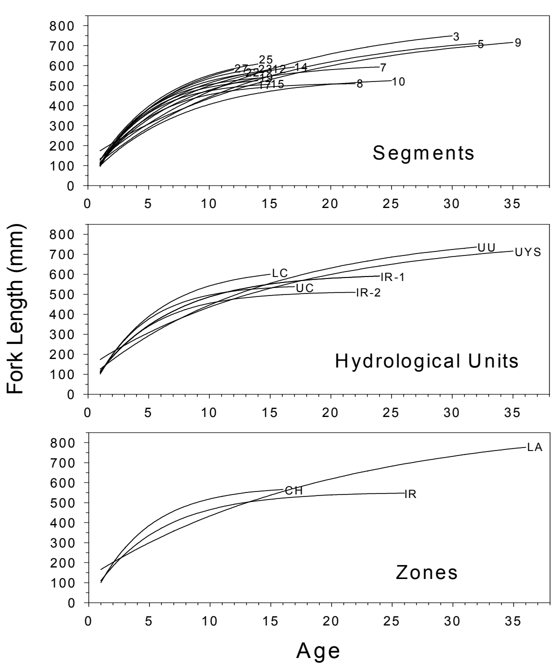

Fig 8. VBGF curves for shovelnose sturgeon

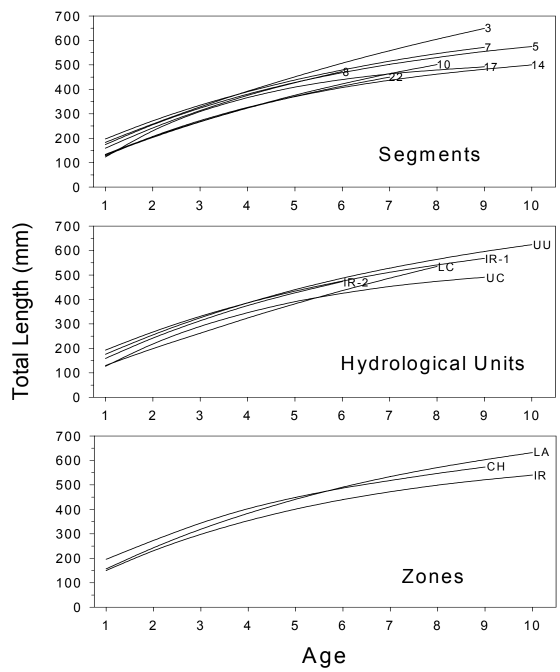

Fig 9. VBGF curves for smallmouth buffalo

each test (Table 9). As expected, age differences were significant in every species where multiple ages were present. There were significant age by year interactions for flathead catfish in the analyses of units and zones. Annual growth differed among units and zones for freshwater drum, with the slowest growth occurring in units UU and IR-2 and zone LA, and the fastest growth occurring in units UC and LC and zone CH. There was a significant unit by year interaction for plains minnow, and a significant zone by year interaction for sand shiner.

Size-Specific Growth

We used locally weighted scatterplot smoothing (LOWESS) regression to fit relationships of annual growth vs. length at the start of the growing season for blue sucker, channel catfish, emerald shiner, flathead catfish, flathead chub, freshwater drum, river carpsucker, sauger, shovelnose sturgeon, sicklefin chub, smallmouth buffalo and western silvery minnow by segment, hydrological unit and zone (Figures 10-21). These regressions illustrate the annual growth expected in different spatial groupings on the river, and how annual growth changes with increasing length. The general pattern for all species was a decline in annual growth as length increased. Growth of channel catfish, flathead catfish and river carpsucker increased initially before declining with increasing length (Figures 11, 13, 16), reflecting more growth in the second year of life than in the first. Size-specific annual growth estimates were obtained at two points on these plots, indicated by vertical arrows on Figures 10-21. The arrows on the right correspond with length at age of maturity, and the positions of curves at this point are estimates of expected annual growth for all spatial groupings at this common size (AG-m). The arrows on the left correspond with length at hatching; here annual growth rate estimates are essentially first-year growth, and we used mean length at age 1 for these estimates (AG-0).

Growth Relationships

To examine relationships of first-year growth with geomorphic and environmental factors, we plotted AG-0 vs. distance from the mouth of the Missouri River, latitude and mean late summer water temperature by species for all segments (Figures 22-24). Plots of first-year growth with distance from the mouth included significant positive, significant negative, and non-significant relationships (Figure 22). First-year growth was positively correlated with distance for smallmouth buffalo, and negatively correlated for blue sucker, freshwater drum, river carpsucker, and sauger. Plots of first-year growth with latitude included significant positive, significant negative, and non-significant relationships (Figure 23). First-year growth was positively correlated with latitude for smallmouth buffalo, and negatively correlated for blue sucker, freshwater drum, river carpsucker, and sauger. Plots of first-year growth with temperature included significant positive, significant negative, and non-significant relationships (Figure 24). First-year growth was positively correlated with temperature for blue sucker, freshwater drum, and sauger, and negatively correlated for smallmouth buffalo and western silvery minnow.

To examine relationships of annual growth at length at maturity with geomorphic and environmental factors, we plotted AG-m vs. distance from the mouth of the Missouri River, latitude and mean late summer water temperature by species for all segments (Figures 25-27). Plots of growth at length at maturity with distance from the mouth included significant positive, significant negative, and non-

Table 9. Summary of ANOVAs testing the effects of spatial units, age and year on annual growth of fifteen species of benthic fishes in the Missouri and Lower Yellowstone rivers. Annual growth increments on calcified structures were used in analyses. Age and year refer to age and calendar year when growth occurred. Separate ANOVAs were used for each of three spatial units: segments, hydrological units and zones. N refers to the number of individual growth increments used in analyses. F-ratios and P-values are based on Type III tests from ANOVAs using Proc MIXED (SAS Institute 1998). Percentages of variance (% Var.) were calculated using Proc VARCOMP (SAS Institute 1988). Error variance percentages are roughly equivalent to $1-R^2$. Dashes (-) indicate insufficient data to evaluate effect.

	Segments				Hydrological Units				Zones			
N	Effect	F	P	% Var.	Effect	F	P	% Var.	Effect	F	P	% Var.
					Blue sucker							
576	Segment (S)	1.6	0.10	10.0	Unit (U)	1.4	0.25	12.6	Zone (Z)	2.3	0.11	8.1
	Age (A)	3.3	0.0005	45.3	Age (A)	2.1	0.02	40.8	Age (A)	5.6	<0.0001	45.6
	Year (Y)	0.3	0.99	1.4	Year (Y)	0.4	0.94	0.6	Year (Y)	0.6	0.85	1.1
	S x A	0.7	0.95	<0.1	U x A	0.2	1.0	2.1	Z x A	0.6	0.79	0.4
	S x Y	1.8	0.002	0.6	U x Y	0.6	0.94	<0.1	Z x Y	1.6	0.09	0.1
	A x Y	0.9	0.60	2.0	A x Y	0.9	0.63	1.6	A x Y	0.9	0.60	1.6
	Error			40.7	Error			42.3	Error			43.1
					Brassy minnow							
10	Segment (S)	-	-	-	Unit (U)	-	-	-	Zone (Z)	-	-	-
	Age (A)	-	-	-	Age (A)	-	-	-	Age (A)	-	-	-
	Year (Y)	-	-	-	Year (Y)	-	-	-	Year (Y)	-	-	-
	S x A	-	-	-	U x A	-	-	-	Z x A	-	-	-
	S x Y	-	-	-	U x Y	-	-	-	Z x Y	-	-	-
	A x Y	-	-	-	A x Y	-	-	-	A x Y	-	-	-
	Error			-	Error			-	Error			-
					Channel catfish							
7846	Segment (S)	4.0	<0.0001	1.5	Unit (U)	7.0	<0.0001	1.5	Zone (Z)	12.7	<0.0001	1.9
	Age (A)	46.9	<0.0001	37.5	Age (A)	43.3	<0.0001	37.9	Age (A)	46.4	<0.0001	38.0
	Year (Y)	1.9	0.018	0.7	Year (Y)	1.2	0.26	<0.1	Year (Y)	2.1	0.009	<0.1
	S x A	2.1	<0.0001	1.5	U x A	2.4	<0.0001	1.5	Z x A	5.6	<0.0001	1.2
	S x Y	5.1	<0.0001	5.6	U x Y	6.2	<0.0001	3.8	Z x Y	13.6	<0.0001	4.4
	A x Y	3.6	<0.0001	3.2	A x Y	3.2	<0.0001	3.5	A x Y	4.5	<0.0001	3.3
	Error			50.1	Error			51.8	Error			51.2
					Emerald shiner							
1955	Segment (S)	2.9	0.0003	4.1	Unit (U)	1.1	0.35	<0.1	Zone (Z)	1.2	0.30	0.3

	Segments				Hydrological Units				Zones			
N	Effect	F	P	% Var.	Effect	F	P	% Var.	Effect	F	P	% Var.
	Age (A)	29.9	<0.0001	44.7	Age (A)	14.9	<0.0001	32.9	Age (A)	58.6	<0.0001	45.0
	Year (Y)	1.2	0.30	0.3	Year (Y)	3.1	0.03	1.1	Year (Y)	4.9	0.003	0.5
	S x A	3.0	0.0003	2.0	U x A	1.5	0.19	4.4	Z x A	0.8	0.55	<0.1
	S x Y	3.9	<0.0001	4.0	U x Y	4.8	<0.0001	9.2	Z x Y	4.6	0.0002	1.0
	A x Y	1.6	0.18	0.7	A x Y	4.1	0.009	2.1	A x Y	3.3	0.02	1.7
	Error			44.1	Error			50.3	Error			51.4
					Flathead catfish							
1628	Segment (S)	1.0	0.44	0.4	Unit (U)	0.1	0.82	<0.1	Zone (Z)	1.5	0.22	2.5
	Age (A)	4.8	<0.0001	29.0	Age (A)	4.1	<0.0001	26.5	Age (A)	4.9	<0.0001	33.4
	Year (Y)	3.1	0.0002	1.4	Year (Y)	2.7	0.001	1.6	Year (Y)	2.4	0.004	0.6
	S x A	3.4	<0.0001	3.7	U x A	6.3	<0.0001	2.8	Z x A	4.6	<0.0001	1.7
	S x Y	1.6	0.009	1.1	U x Y	1.0	0.45	0.2	Z x Y	2.0	0.05	0.4
	A x Y	5.2	<0.0001	19.9	A x Y	4.6	<0.0001	20.8	A x Y	4.5	<0.0001	17.4
	Error			44.6	Error			48.1	Error			44.0
					Flathead chub							
581	Segment (S)	0.6	0.71	0.2	Unit (U)	0.5	0.72	<0.1	Zone (Z)	0.15	0.70	0.3
	Age (A)	23.7	<0.0001	53.2	Age (A)	25.6	<0.0001	52.8	Age (A)	26.8	<0.0001	51.7
	Year (Y)	2.2	0.03	4.2	Year (Y)	1.5	0.14	4.1	Year (Y)	1.9	0.05	4.5
	S x A	0.7	0.81	<0.1	U x A	1.0	0.44	0.6	Z x A	0.3	0.93	<0.1
	S x Y	1.8	0.009	0.8	U x Y	2.0	0.01	1.0	Z x Y	1.4	0.22	0.1
	A x Y	1.5	0.06	0.2	A x Y	1.2	0.25	<0.1	A x Y	1.1	0.39	<0.1
	Error			41.4	Error			41.5	Error			43.4
					Freshwater drum							
2836	Segment (S)	12.2	<0.0001	13.7	Unit (U)	5.7	<0.0001	10.7	Zone (Z)	11.7	<0.0001	12.9
	Age (A)	38.1	<0.0001	60.7	Age (A)	21.9	<0.0001	61.6	Age (A)	54.5	<0.0001	60.6
	Year (Y)	2.4	<0.0001	0.3	Year (Y)	0.6	0.94	<0.1	Year (Y)	1.2	0.26	<0.1
	S x A	4.3	<0.0001	4.8	U x A	7.5	<0.0001	5.8	Z x A	10.2	<0.0001	4.0
	S x Y	3.1	<0.0001	2.0	U x Y	3.3	<0.0001	2.4	Z x Y	5.1	<0.0001	2.1
	A x Y	2.4	<0.0001	2.0	A x Y	2.3	<0.0001	2.9	A x Y	2.1	<0.0001	2.2
	Error			16.6	Error			16.5	Error			18.2
					Plains minnow							
38	Segment (S)	1.3	0.27	<0.1	Unit (U)	2.0	0.13	<0.1	Zone (Z)	1.0	0.32	<0.1
	Age (A)	-	-	-	Age (A)	-	-	-	Age (A)	-	-	-

	Segments				Hydrological Units				Zones			
N	Effect	F	P	% Var.	Effect	F	P	% Var.	Effect	F	P	% Var.
	Year (Y)	11.0	0.0004	49.3	Year (Y)	19.4	<0.0001	49.8	Year (Y)	7.8	0.002	52.4
	S x A	-	-	-	U x A	-	-	-	Z x A	-	-	-
	S x Y	4.2	0.02	17.9	U x Y	8.3	0.001	23.1	Z x Y	0.5	0.50	<0.1
	A x Y	-	-	-	A x Y	-	-	-	A x Y	-	-	-
	Error			32.8	Error			27.2	Error			47.6
					River carpsucker							
4687	Segment (S)	1.4	0.13	1.3	Unit (U)	0.5	0.74	1.5	Zone (Z)	0.4	0.65	0.6
	Age (A)	18.2	<0.0001	50.4	Age (A)	20.8	<0.0001	49.6	Age (A)	23.4	<0.0001	49.0
	Year (Y)	1.2	0.28	0.4	Year (Y)	1.0	0.45	0.7	Year (Y)	1.2	0.31	<0.1
	S x A	1.5	0.0008	1.2	U x A	2.0	0.0004	1.1	Z x A	3.7	<0.0001	1.0
	S x Y	1.3	0.04	0.5	U x Y	1.2	0.15	0.2	Z x Y	1.4	0.11	<0.1
	A x Y	1.3	0.06	0.5	A x Y	1.1	0.26	0.2	A x Y	1.5	0.01	0.6
	Error			45.5	Error			46.8	Error			48.8
					Sand shiner							
177	Segment (S)	0.7	0.69	<0.1	Unit (U)	0.9	0.34	<0.1	Zone (Z)	0	0.95	<0.1
	Age (A)	29.4	<0.0001	27.4	Age (A)	15.4	0.0003	21.7	Age (A)	19.3	<0.0001	22.9
	Year (Y)	6.9	0.001	6.0	Year (Y)	4.5	0.008	6.3	Year (Y)	4.9	0.006	<0.1
	S x A	3.5	0.03	<0.1	U x A	4.6	0.04	<0.1	Z x A	0.8	0.39	<0.1
	S x Y	5.6	0.0002	13.6	U x Y	2.7	0.08	<0.1	Z x Y	12.2	<0.0001	15.3
	A x Y	-	-	-	A x Y	-	-	-	A x Y	-	-	-
	Error			53.0	Error			72.1	Error			61.8
					Sauger							
930	Segment (S)	2.6	0.002	0.1	Unit (U)	3.4	0.006	0.3	Zone (Z)	0.7	0.49	0.2
	Age (A)	194.5	<0.0001	84.0	Age (A)	145.7	<0.0001	82.5	Age (A)	226.6	<0.0001	83.4
	Year (Y)	0.8	0.69	0.1	Year (Y)	0.5	0.92	<0.1	Year (Y)	0.6	0.90	<0.1
	S x A	2.9	<0.0001	4.2	U x A	4.3	<0.0001	4.8	Z x A	7.1	<0.0001	2.6
	S x Y	2.3	<0.0001	1.0	U x Y	1.7	0.02	0.7	Z x Y	2.0	0.02	0.5
	A x Y	1.4	0.09	0.6	A x Y	1.1	0.37	0.5	A x Y	1.8	0.005	1.0
	Error			9.9	Error			11.1	Error			12.4
					Shovelnose sturgeon							
13595	Segment (S)	1.8	0.04	1.6	Unit (U)	2.1	0.07	1.2	Zone (Z)	4.7	0.009	0.9
	Age (A)	25.7	<0.0001	34.3	Age (A)	26.4	<0.0001	33.1	Age (A)	29.8	<0.0001	34.2
	Year (Y)	1.2	0.16	4.4	Year (Y)	1.4	0.04	3.7	Year (Y)	1.6	0.01	4.5
	S x A	2.1	<0.0001	0.6	U x A	1.2	0.12	0.6	Z x A	1.3	0.13	0.6

	Segments				Hydrological Units				Zones			
N	Effect	F	P	% Var.	Effect	F	P	% Var.	Effect	F	P	% Var.
	S x Y	1.3	0.0003	0.3	U x Y	1.4	0.002	0.3	Z x Y	1.6	0.007	0.4
	A x Y	0.9	0.93	1.4	A x Y	0.9	0.96	1.1	A x Y	0.9	0.98	1.0
	Error			57.5	Error			60.0	Error			58.4
					Sicklefin chub							
538	Segment (S)	5.1	<0.0001	10.9	Unit (U)	5.0	0.0007	2.4	Zone (Z)	9.9	<0.0001	3.1
	Age (A)	67.8	<0.0001	62.8	Age (A)	50.7	<0.0001	66.2	Age (A)	56.7	<0.0001	67.7
	Year (Y)	1.4	0.24	<0.1	Year (Y)	3.1	0.02	<0.1	Year (Y)	2.1	0.08	<0.1
	S x A	7.0	<0.0001	4.2	U x A	8.7	<0.0001	5.0	Z x A	4.3	0.0008	2.5
	S x Y	4.1	<0.0001	3.2	U x Y	5.6	<0.0001	5.5	Z x Y	2.5	0.01	0.3
	A x Y	0.8	0.56	<0.1	A x Y	2.3	0.05	0.9	A x Y	1.2	0.31	0.2
	Error			18.9	Error			20.0	Error			26.2
					Smallmouth buffalo							
1267	Segment (S)	1.6	0.09	1.0	Unit (U)	0.6	0.73	<0.1	Zone (Z)	2.2	0.11	0.1
	Age (A)	37.8	<0.0001	65.0	Age (A)	45.1	<0.0001	66.9	Age (A)	54.1	<0.0001	65.4
	Year (Y)	2.2	0.008	3.0	Year (Y)	1.9	0.0234	0.7	Year (Y)	1.2	0.25	3.8
	S x A	1.6	0.0006	2.7	U x A	3.0	<0.0001	2.3	Z x A	1.1	0.31	0.1
	S x Y	1.0	0.58	<0.1	U x Y	1.7	0.006	0.6	Z x Y	1.1	0.35	0.2
	A x Y	0.9	0.73	0.4	A x Y	1.2	0.13	0.6	A x Y	0.9	0.78	0.3
	Error			27.8	Error			28.9	Error			30.1
370					**Western silvery minnow**							
	Segment (S)	1.3	0.26	<0.1	Unit (U)	0.4	0.83	<0.1	Zone (Z)	0.1	0.91	<0.1
	Age (A)	27.7	<0.0001	56.5	Age (A)	20.1	<0.0001	52.2	Age (A)	25.3	<0.0001	53.1
	Year (Y)	3.0	0.02	1.5	Year (Y)	3.1	0.02	3.5	Year (Y)	2.1	0.07	4.9
	S x A	1.3	0.27	1.8	U x A	2.0	0.13	3.5	Z x A	3.5	0.07	0.7
	S x Y	6.5	<0.0001	9.4	U x Y	3.1	0.008	2.9	Z x Y	0.3	0.78	<0.1
	A x Y	1.4	0.24	4.2	A x Y	4.0	0.01	6.4	A x Y	2.3	0.09	4.6
	Error			26.3	Error			31.5	Error			36.7

Figures 10-11. Size-specific growth curves for several species in segments, hydrological units and zones of the Missouri and lower Yellowstone rivers. Arrows indicate lengths used for growth comparisons; left arrow indicates age-0 growth, right arrow indicates growth at length at maturity. Curves were fit by LOWESS regression; see text for details.

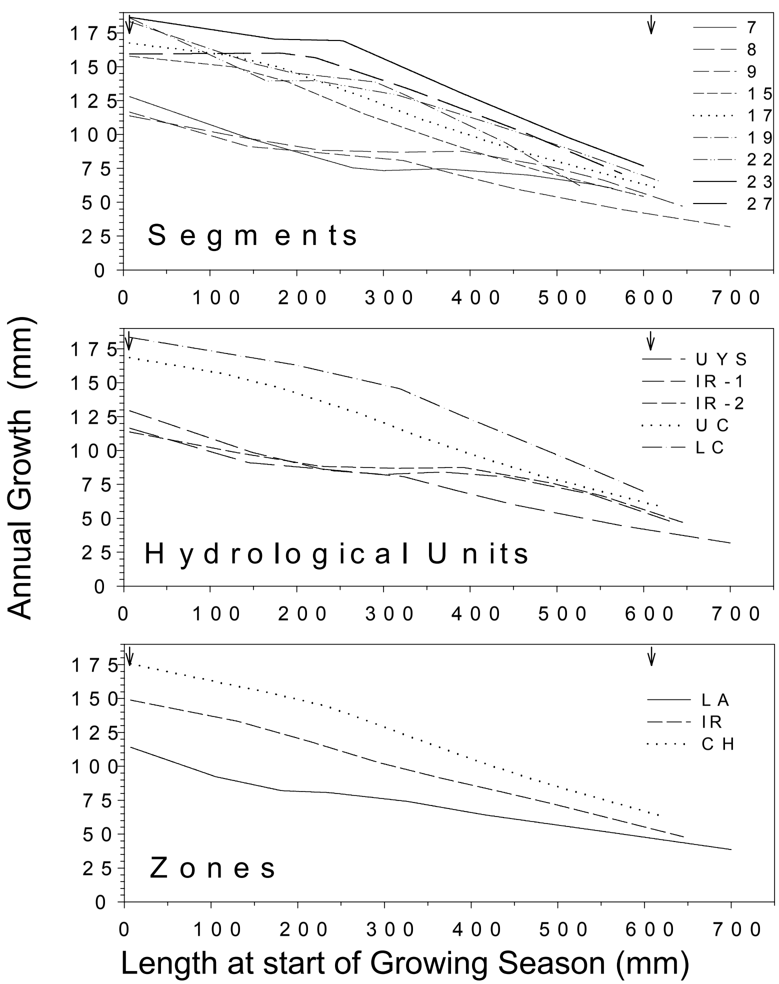

Figure 10. Blue sucker

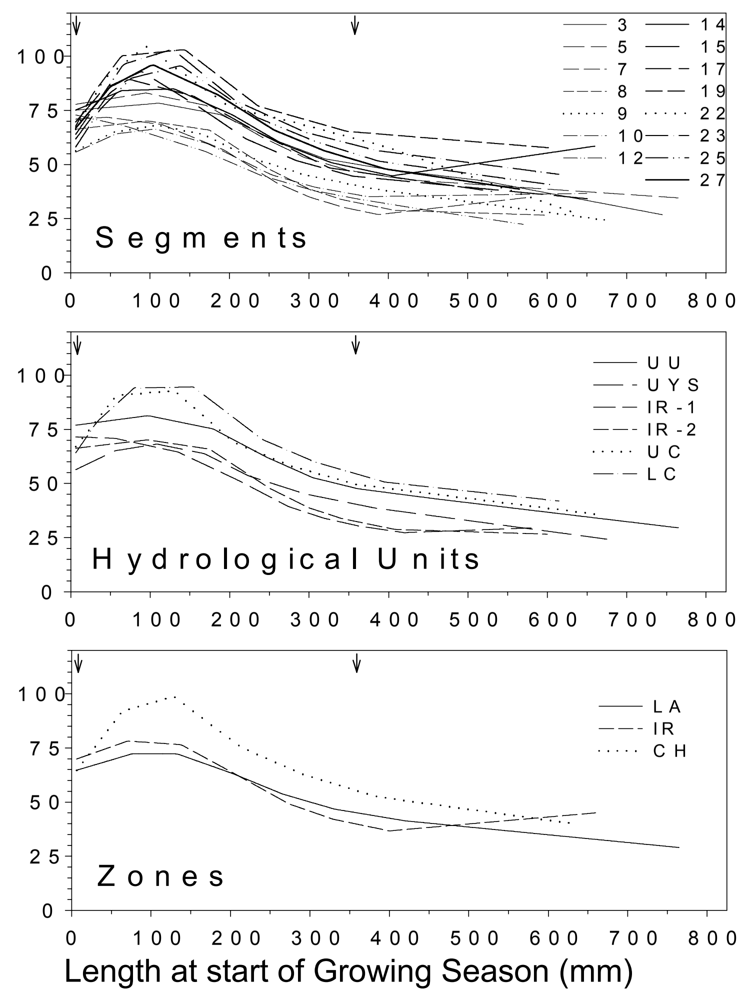

Figure 11. Channel catfish

Figures 12-13. Size-specific growth curves for several species in segments, hydrological units and zones of the Missouri and lower Yellowstone rivers. Arrows indicate lengths used for growth comparisons; left arrow indicates age-0 growth, right arrow indicates growth at length at maturity. Curves were fit by LOWESS regression; see text for details.

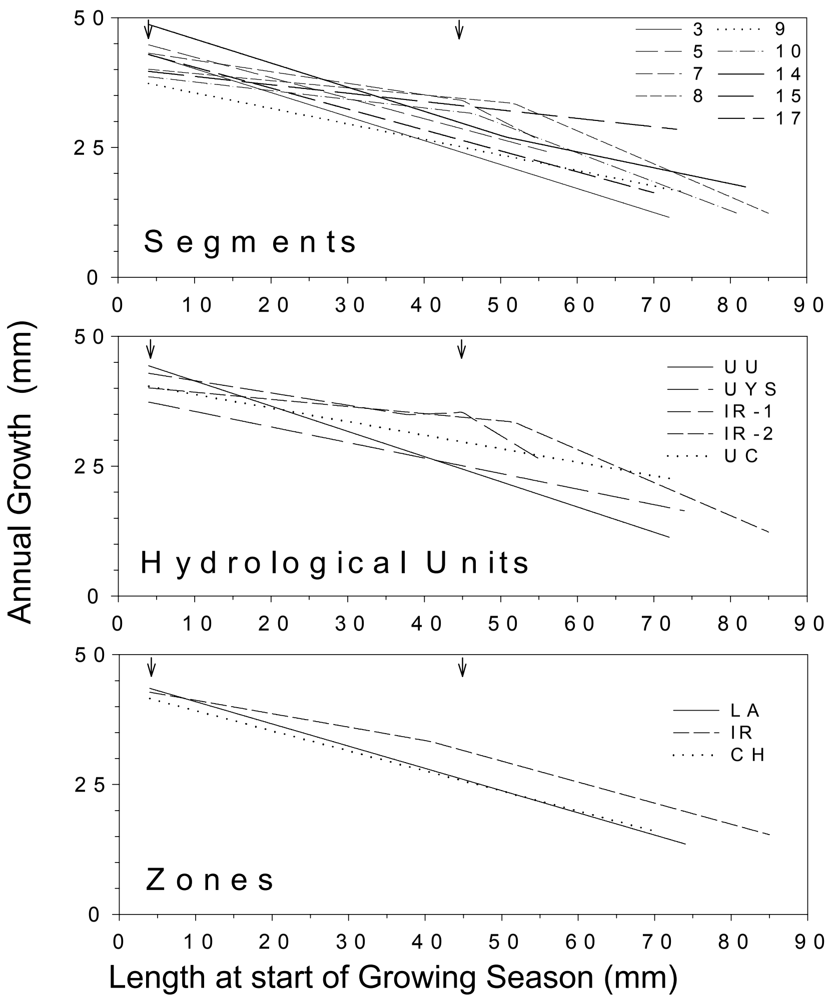

Figure 12. Emerald shiner

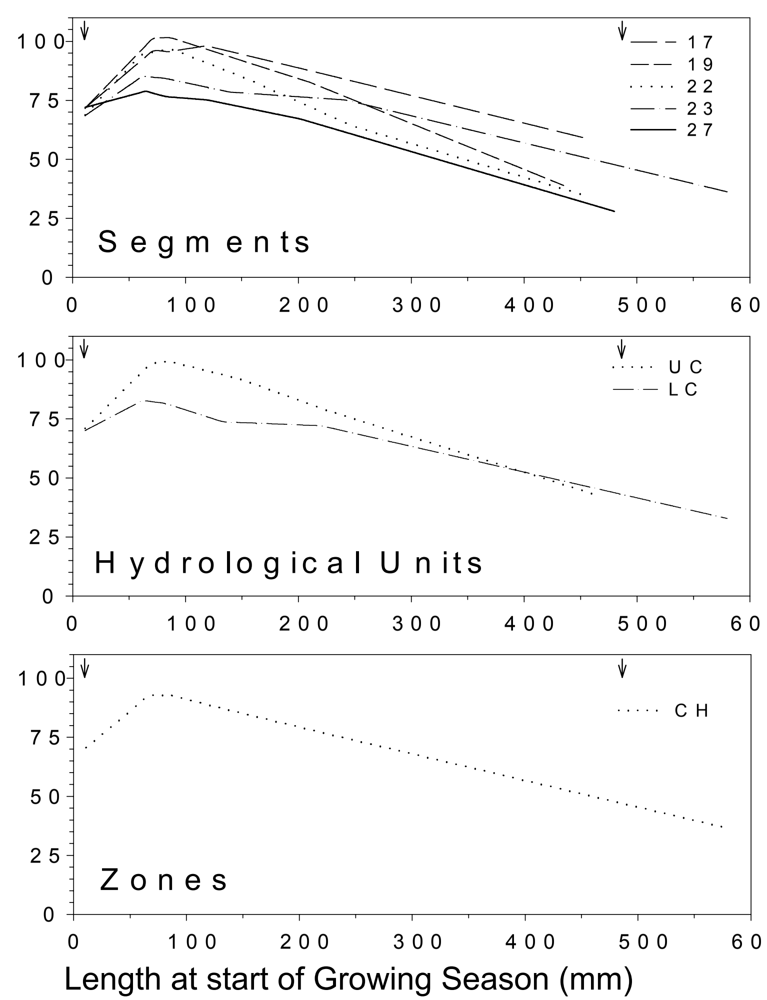

Figure 13. Flathead catfish

Figures 14-15. Size-specific growth curves for several species in segments, hydrological units and zones of the Missouri and lower Yellowstone rivers. Arrows indicate lengths used for growth comparisons; left arrow indicates age-0 growth, right arrow indicates growth at length at maturity. Curves were fit by LOWESS regression; see text for details.

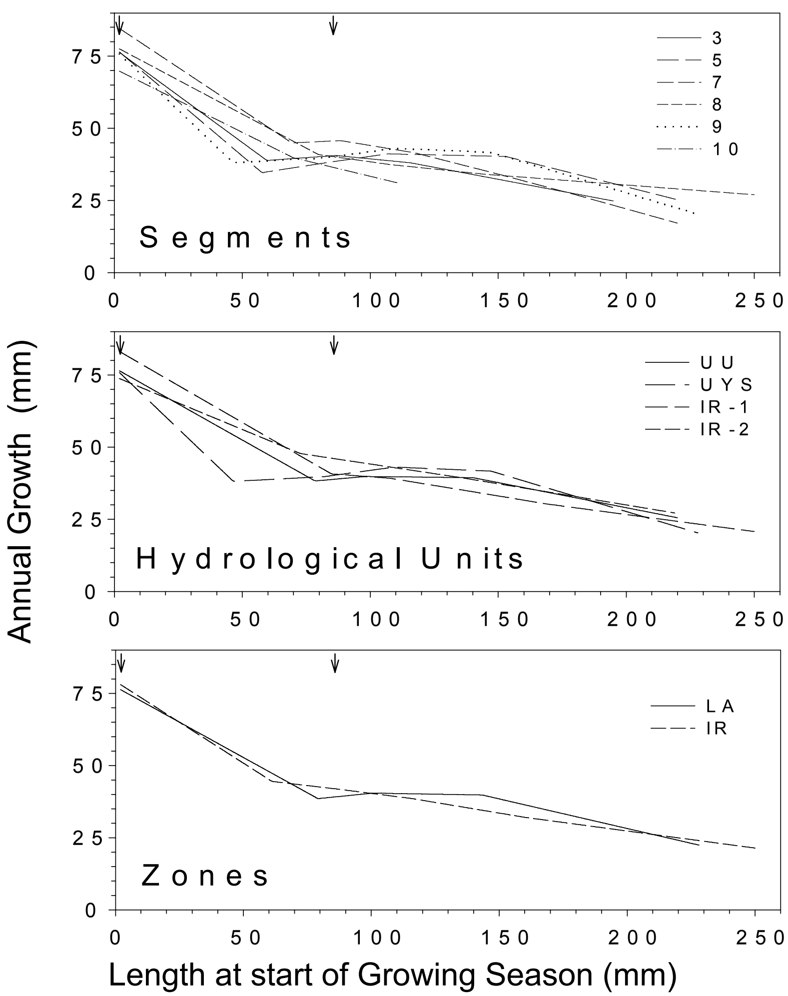

Figure 14. Flathead chub

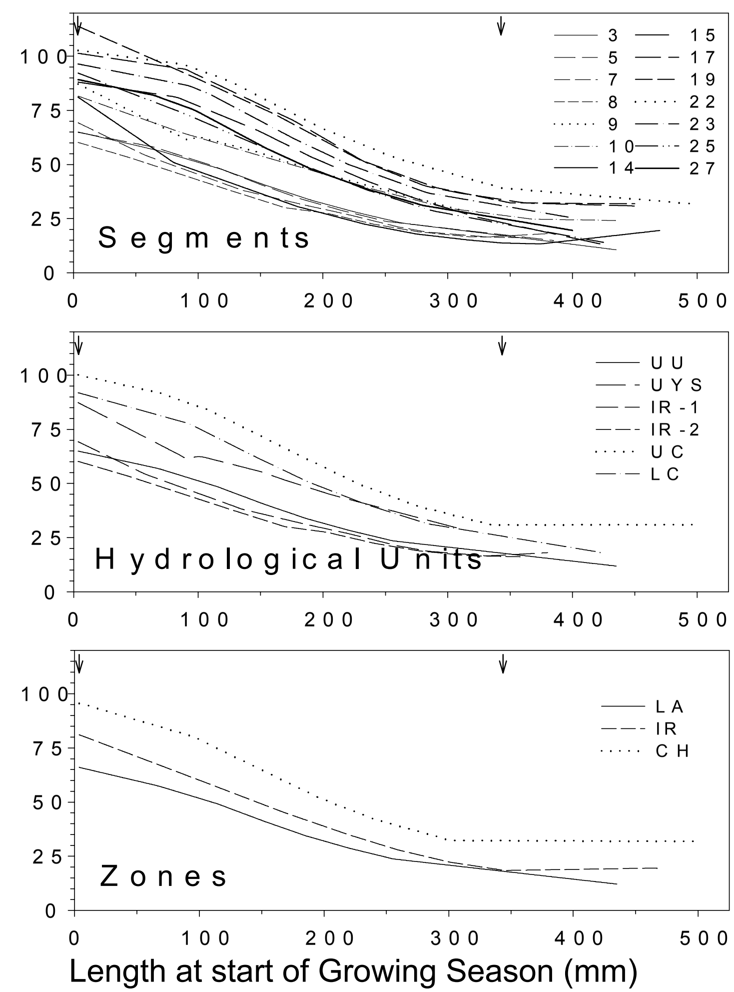

Figure 15. Freshwater drum

Figures 16-17. Size-specific growth curves for several species in segments, hydrological units and zones of the Missouri and lower Yellowstone rivers. Arrows indicate lengths used for growth comparisons; left arrow indicates age-0 growth, right arrow indicates growth at length at maturity. Curves were fit by LOWESS regression; see text for details.

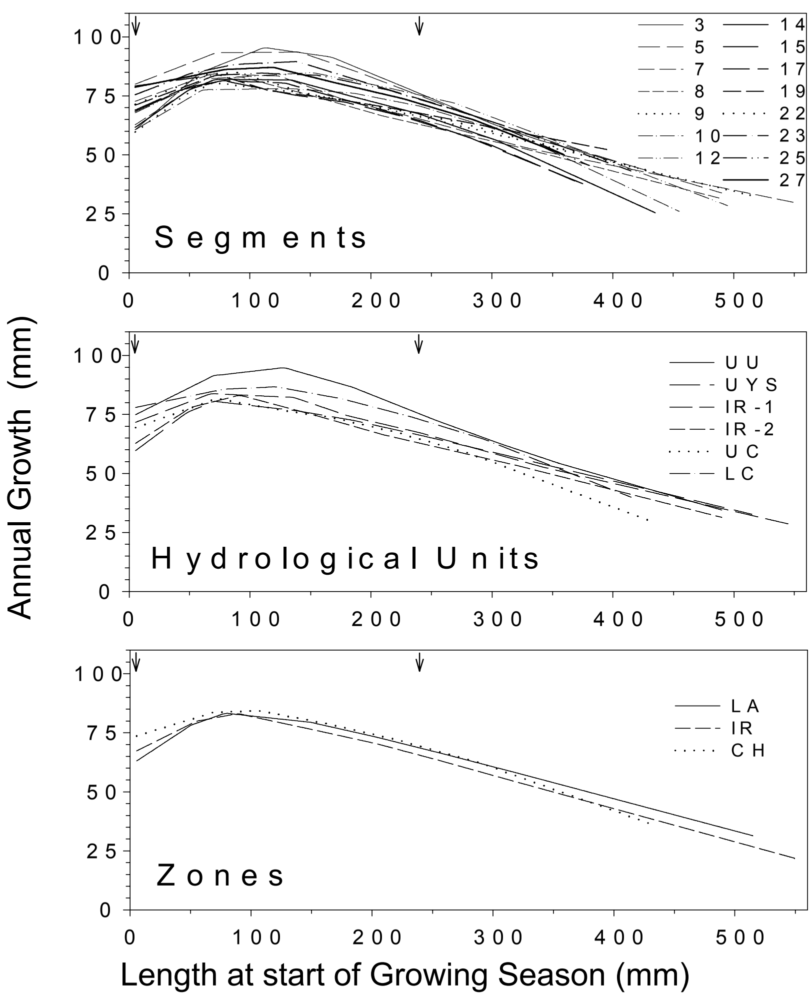

Figure 16. River carpsucker

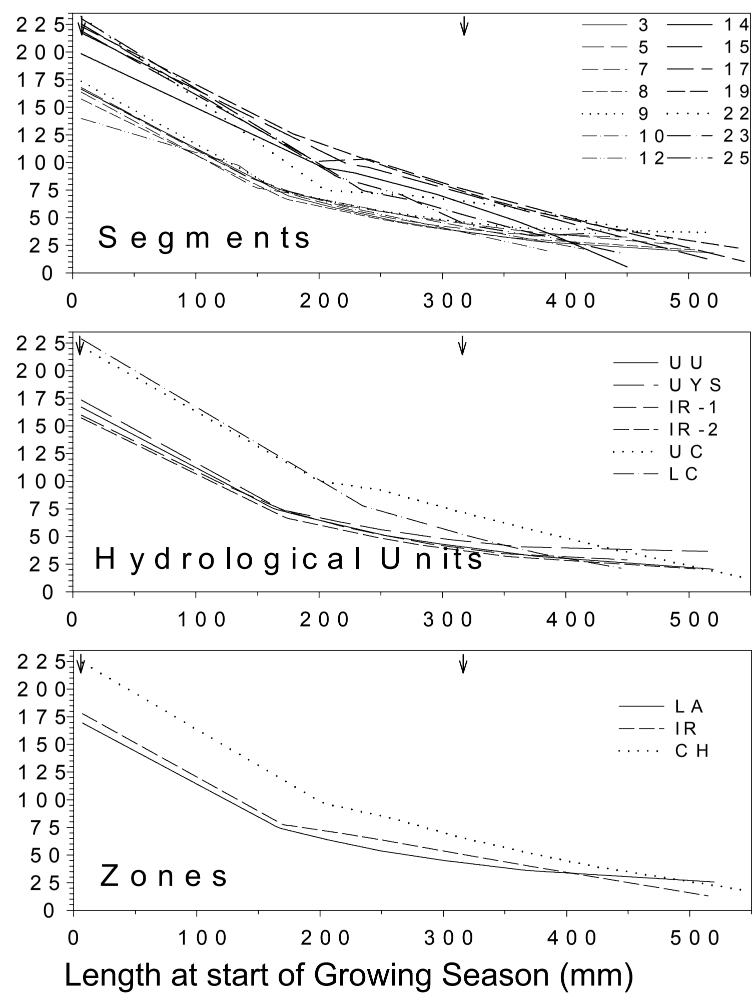

Figure 17. Sauger

Figures 18-19. Size-specific growth curves for several species in segments, hydrological units and zones of the Missouri and lower Yellowstone rivers. Arrows indicate lengths used for growth comparisons; left arrow indicates age-0 growth, right arrow indicates growth at length at maturity. Curves were fit by LOWESS regression; see text for details.

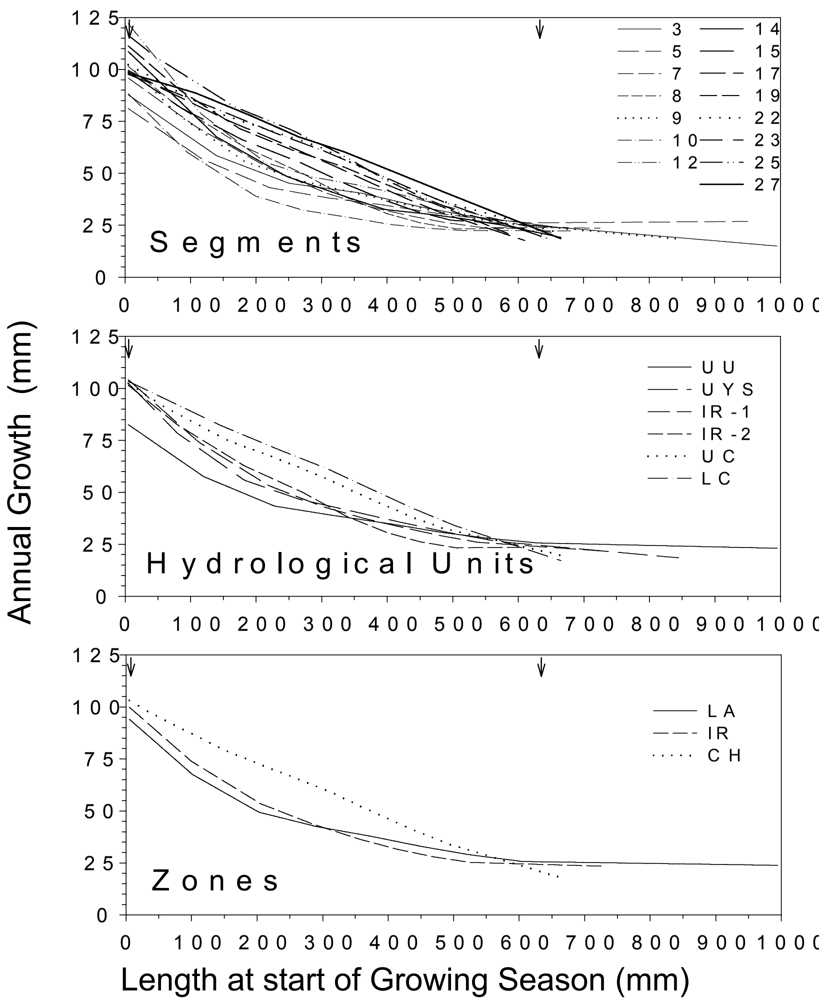

Figure 18. Shovelnose sturgeon

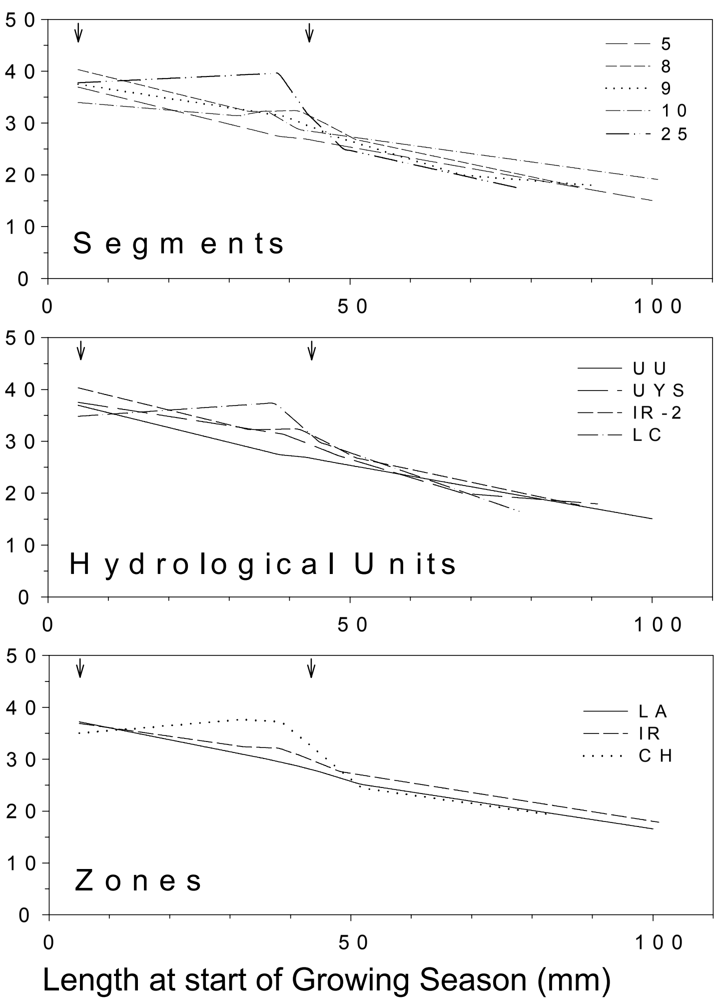

Figure 19. Sicklefin chub

Figures 20-21. Size-specific growth curves for several species in segments, hydrological units and zones of the Missouri and lower Yellowstone rivers. Arrows indicate lengths used for growth comparisons; left arrow indicates age-0 growth, right arrow indicates growth at length at maturity. Curves were fit by LOWESS regression; see text for details.

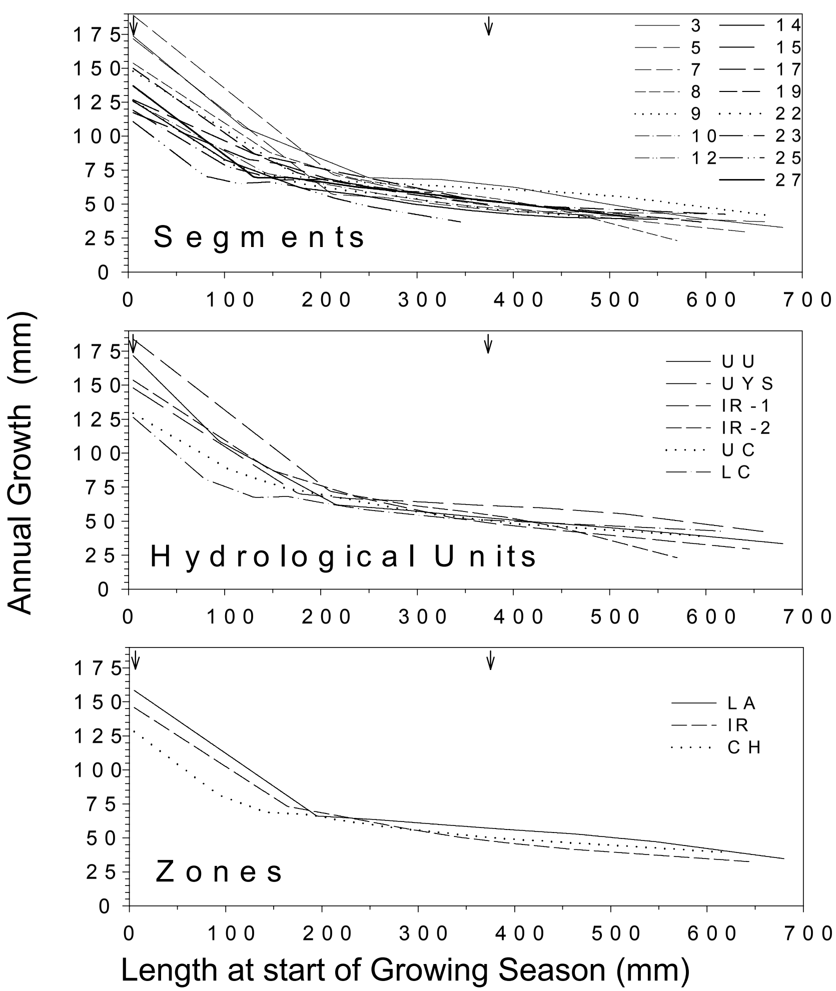

Figure 20. Smallmouth buffalo

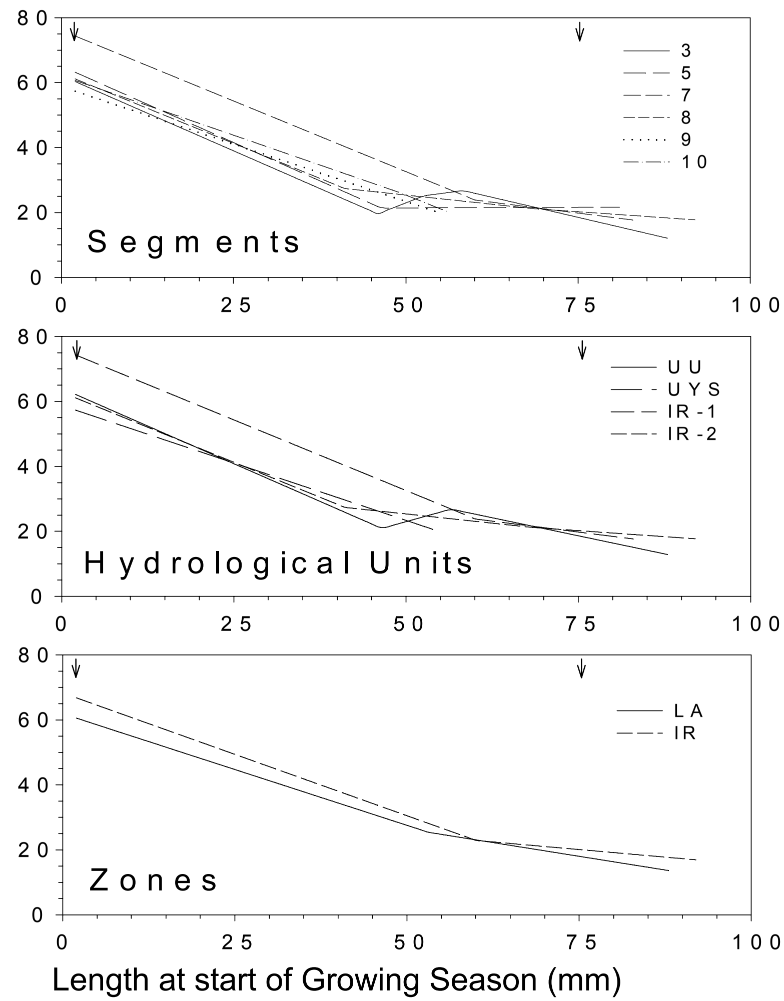

Figure 21. Western silvery minnow

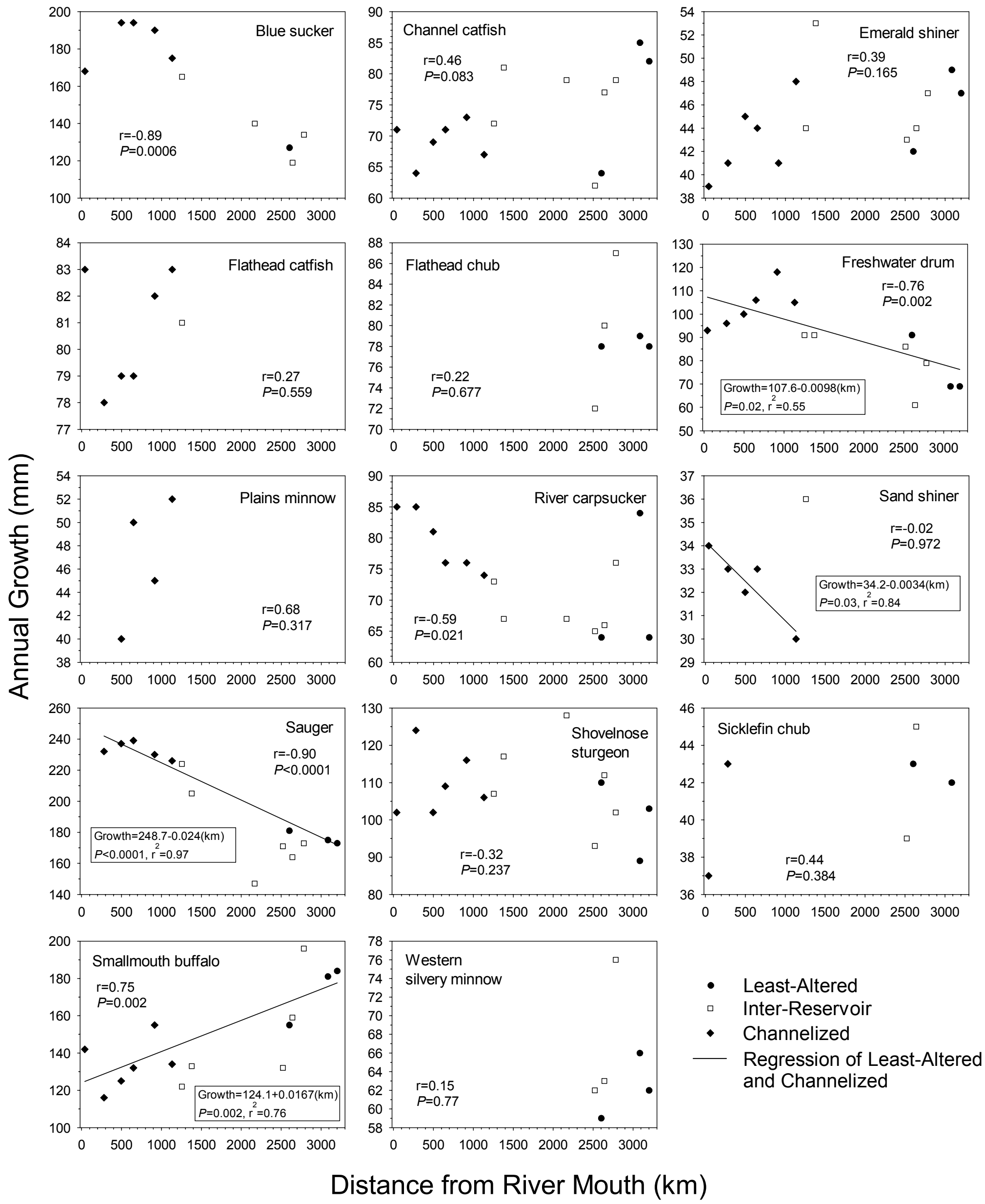

Figure 22. Annual growth of age-0 fishes in the Missouri and lower Yellowstone rivers in relation to distance from the mouth of the Missouri River. Annual growth is estimated as the mean back-calculated length at age 1. Distance from river mouth is the channel distance from the midpoints of segments to the mouth of the Missouri River. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points. Regression lines indicate significant regressions of growth vs. distance using data from the least-altered and channelized zones only; regression equations and statistics are in boxes.

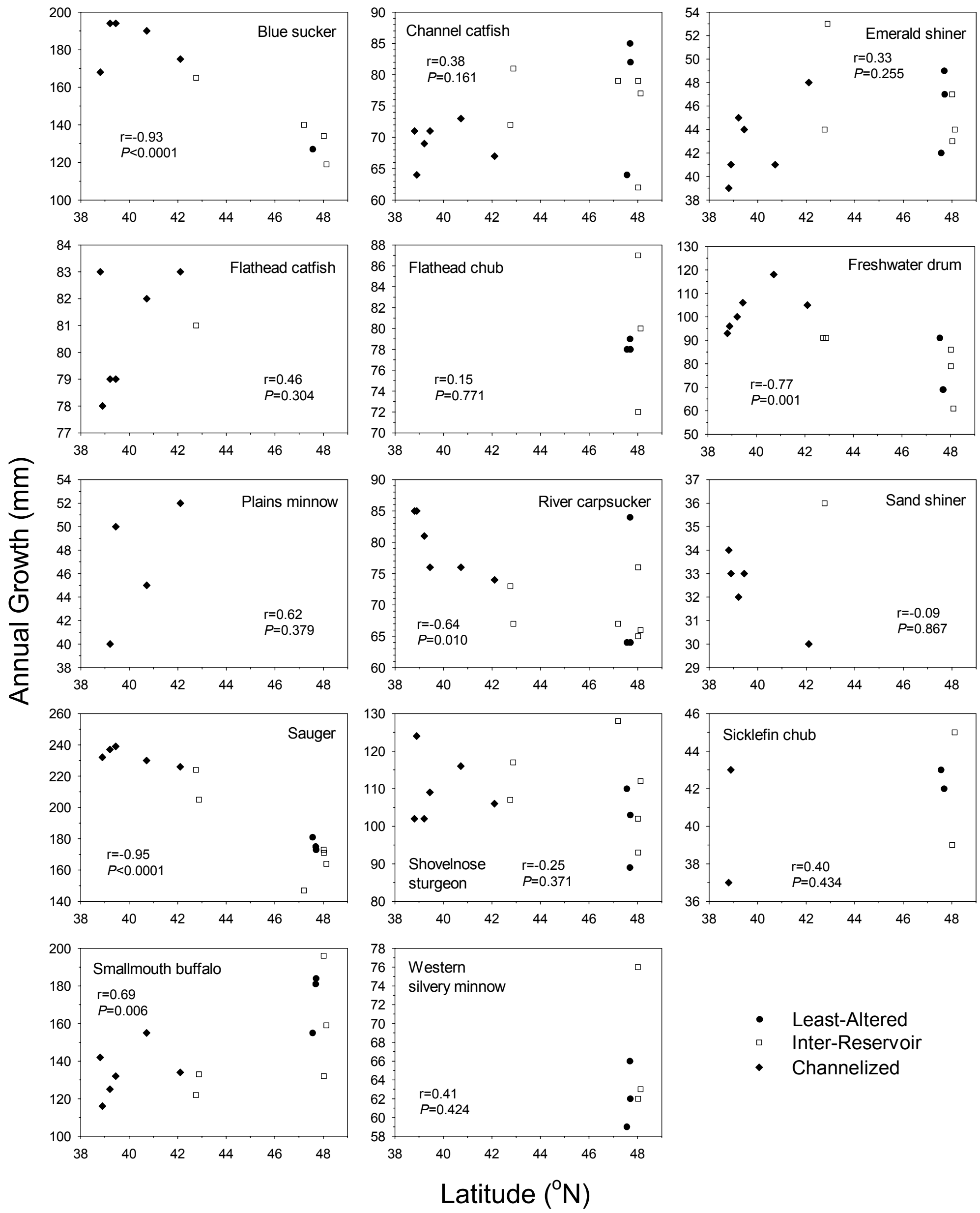

Figure 23. Annual growth of age-0 fishes in the Missouri and lower Yellowstone rivers in relation to latitude. Annual growth is estimated as the mean back-calculated length at age 1. Latitude is measured at the midpoints of segments. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points.

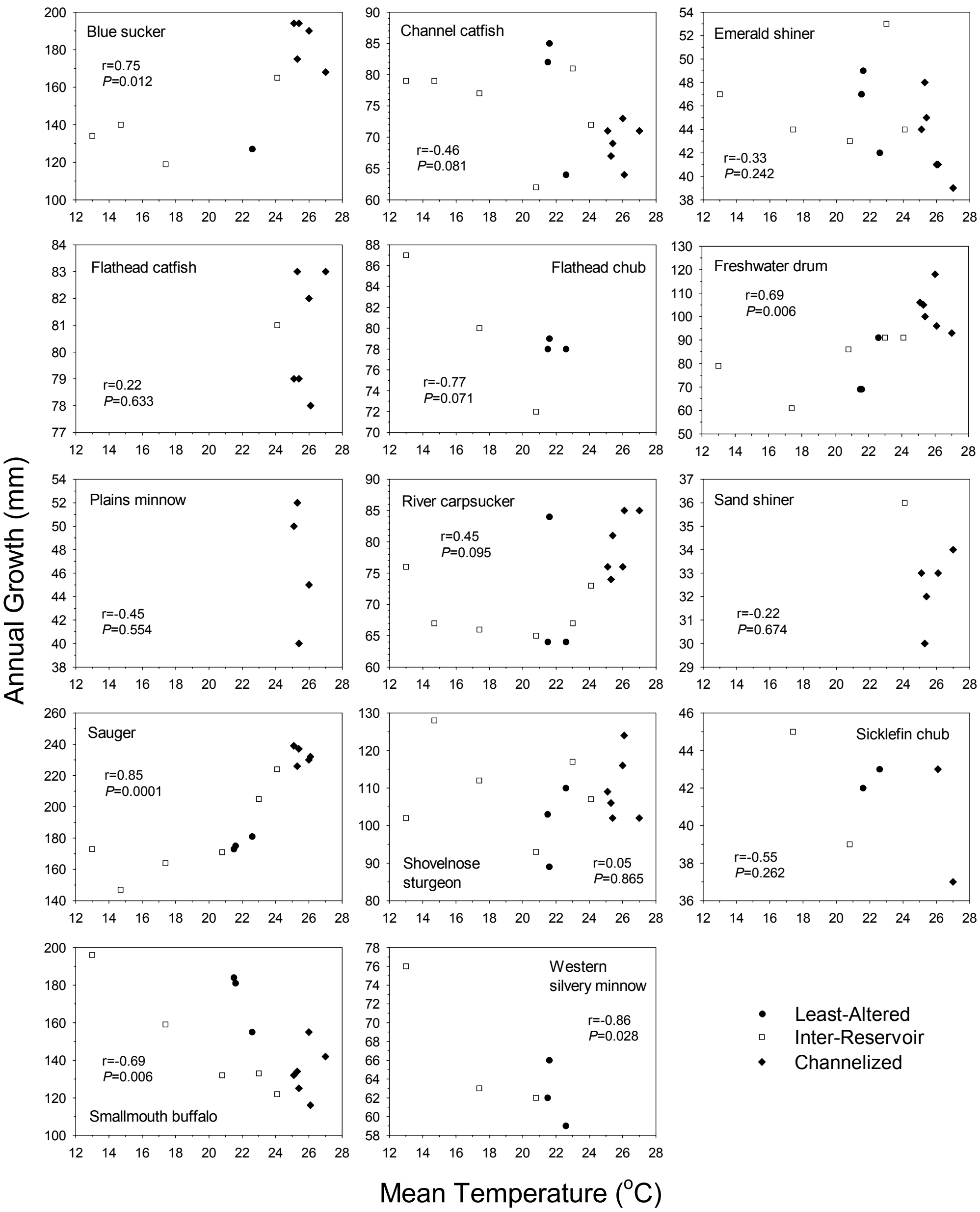

Figure 24. Annual growth of age-0 fishes in the Missouri and lower Yellowstone rivers in relation to mean late summer water temperature. Annual growth is estimated as the mean back-calculated length at age 1. Temperatures were averaged from all measurements taken in bends as described by Galat et al. 2001. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points.

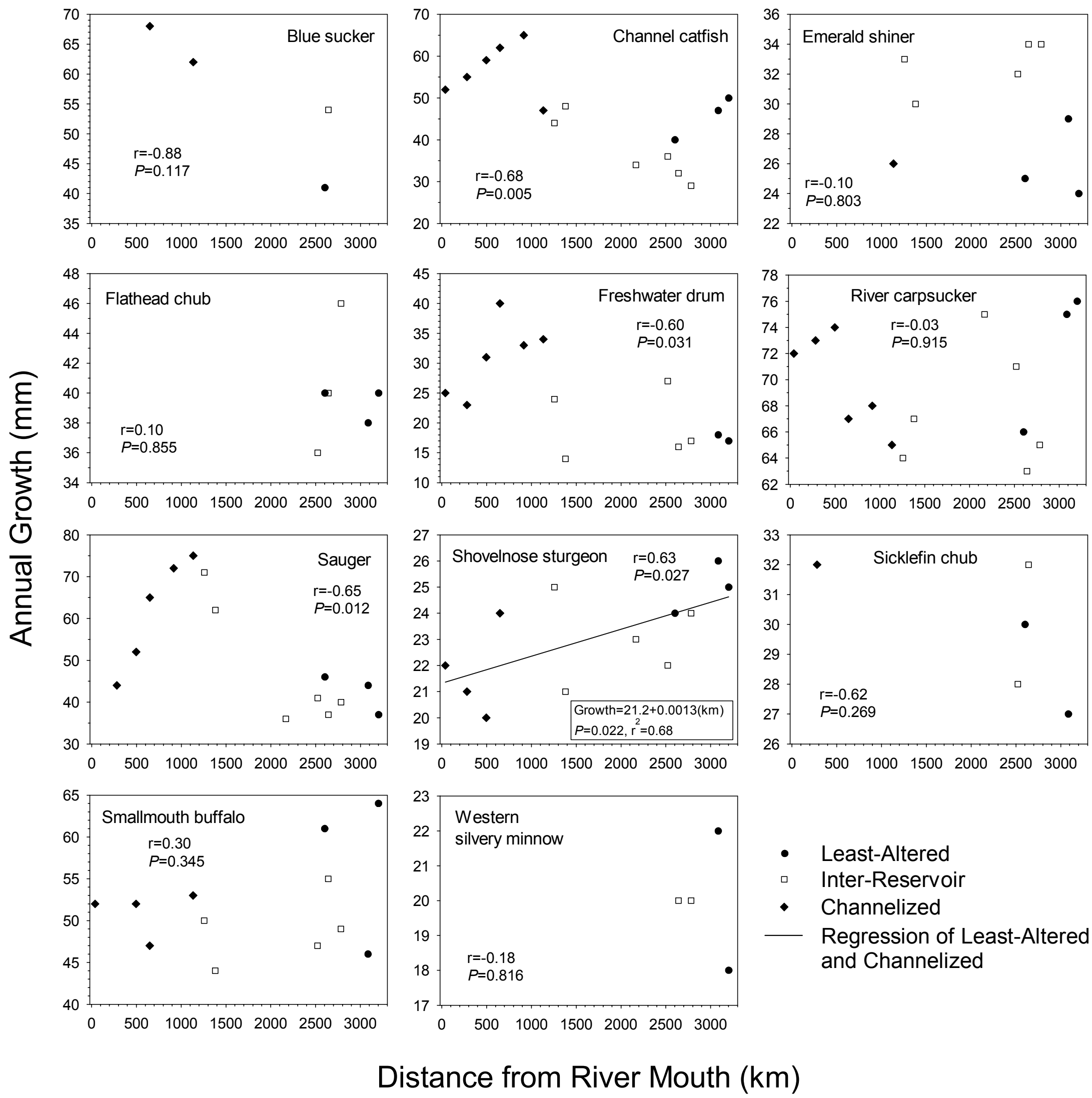

Figure 25. Annual growth of fishes at length-at-maturity in the Missouri and lower Yellowstone rivers in relation to distance from the mouth of the Missouri River. Annual growth is estimated from size-specific regressions of annual growth, using species-specific estimates of size-at maturity compiled by Pegg and Pierce 2002. Distance from river mouth is the channel distance from the midpoints of segments to the mouth of the Missouri River. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points. Regression lines indicate significant regressions of growth vs. distance using data from the least-altered and channelized zones only; regression equations and statistics are in boxes.

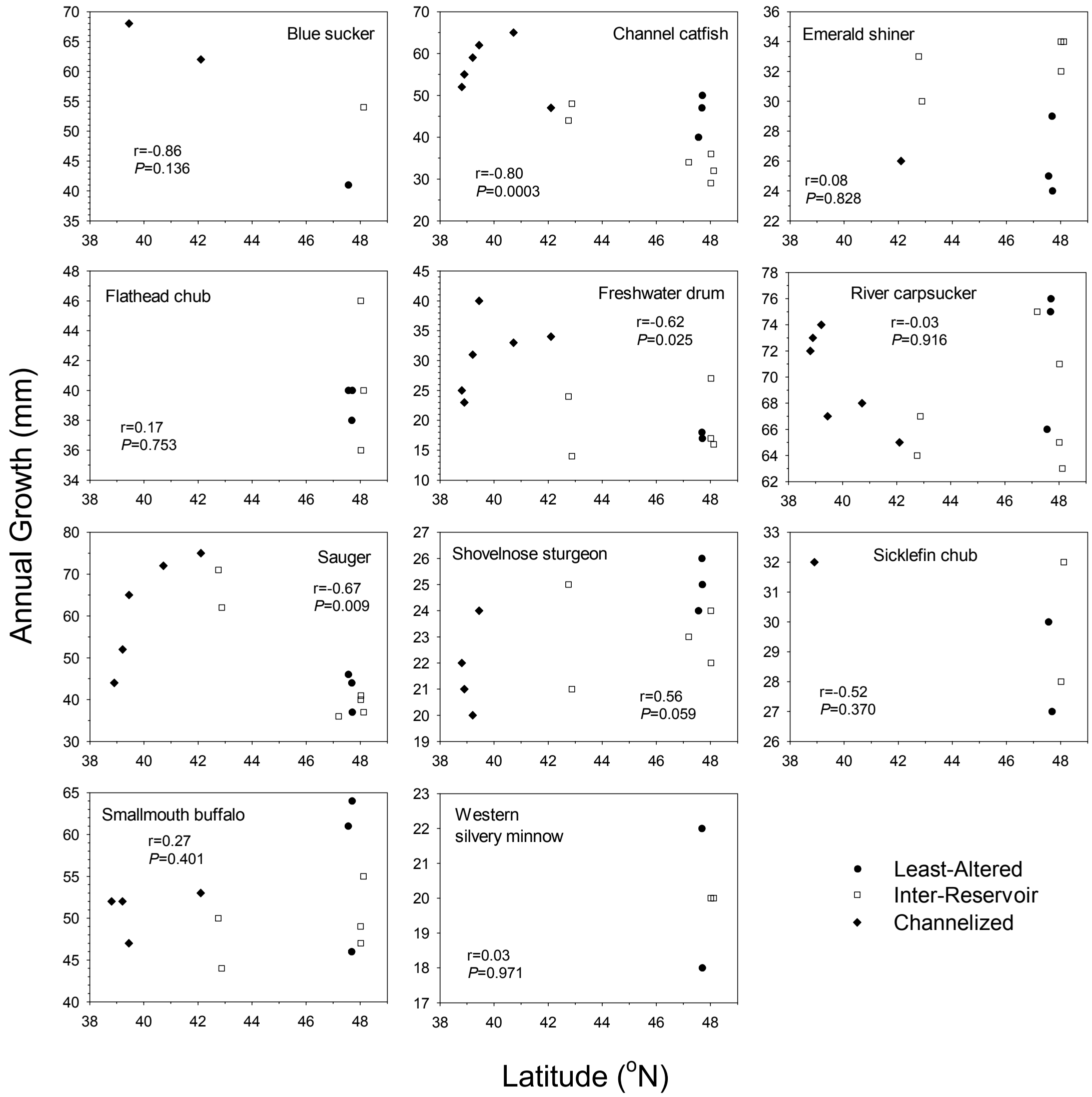

Figure 26. Annual growth of fishes at length-at-maturity in the Missouri and lower Yellowstone rivers in relation to latitude. Annual growth is estimated from size-specific regressions of annual growth, using species-specific estimates of size-at maturity compiled by Pegg and Pierce 2002. Latitude is measured at the midpoints of segments. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points.

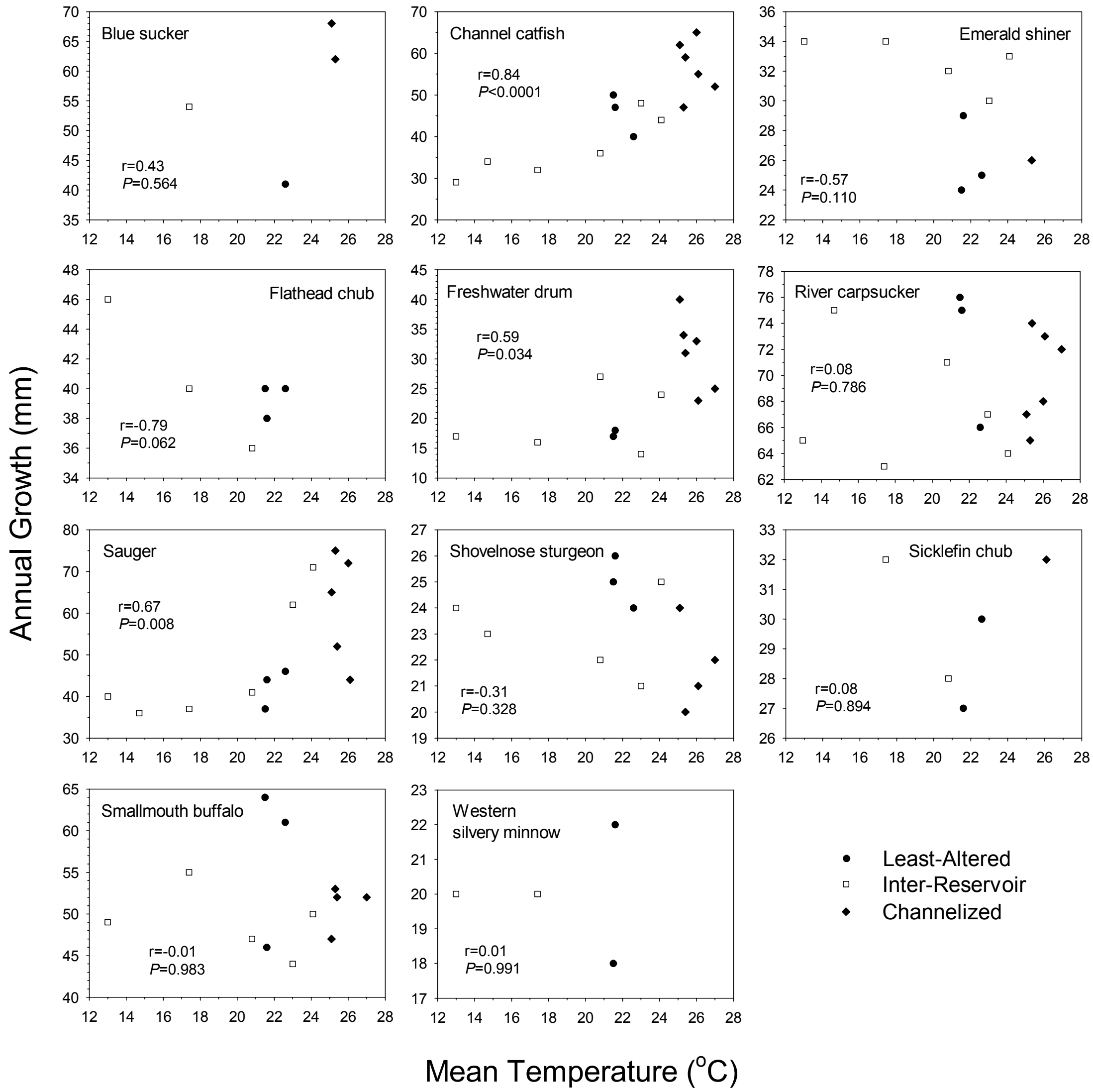

Figure 27. Annual growth of fishes at length-at-maturity in the Missouri and lower Yellowstone rivers in relation to mean late summer water temperature. Annual growth is estimated from size-specific regressions of annual growth, using species-specific estimates of size-at maturity compiled by Pegg and Pierce 2002. Temperatures were averaged from all measurements taken in bends as described by Galat at al. 2001. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points.

significant relationships (Figure 25). Growth at length at maturity was positively correlated with distance for shovelnose sturgeon, and negatively correlated for channel catfish, freshwater drum and sauger. Plots of growth at length at maturity with latitude included significant negative and non-significant relationships (Figure 26). Growth at length at maturity was negatively correlated for channel catfish, freshwater drum and sauger. Plots of growth at length at maturity with temperature included significant positive and non-significant relationships (Figure 27). Growth at length at maturity was negatively correlated for channel catfish, freshwater drum and sauger.

To examine relationships of length at age of maturity with geomorphic and environmental factors, we plotted L-m vs. distance from the mouth of the Missouri River, latitude and mean late summer water temperature by species for all segments (Figures 28-30). Plots of length at age of maturity with distance from the mouth included significant positive, significant negative, and non-significant relationships (Figure 28). Length at age of maturity was positively correlated with distance for smallmouth buffalo, and negatively correlated for channel catfish, freshwater drum and shovelnose sturgeon. Plots of length at age of maturity with latitude included significant positive, significant negative, and non-significant relationships (Figure 29). Length at age of maturity was positively correlated with latitude for smallmouth buffalo, and negatively correlated for channel catfish, freshwater drum and shovelnose sturgeon. Plots of length at age of maturity with temperature included significant positive and non-significant relationships (Figure 30). Length at age of maturity was positively correlated with temperature for channel catfish, freshwater drum and shovelnose sturgeon.

To examine relationships of growth among species, we calculated all pair-wise Pearson correlation coefficients in three groups: AG-0, AG-m and L-m (Tables 10-12). Significant correlations of AG-0 and AG-m included both positive and negative relationships, whereas all significant correlations of L-m were positive. For AG-0, blue sucker was positively correlated with freshwater drum, river carpsucker and sauger, channel catfish was positively correlated with emerald shiner and smallmouth buffalo, flathead chub was positively correlated with smallmouth buffalo, and freshwater drum was positively correlated with sauger (Figure 31). For AG-0, channel catfish was negatively correlated with freshwater drum, and sauger was negatively correlated with smallmouth buffalo (Figure 31). For AG-m, channel catfish was positively correlated with freshwater drum and sauger, freshwater drum was positively correlated with sauger, and channel catfish was negatively correlated with emerald shiner (Figure 32). For L-m, channel catfish was positively correlated with flathead chub, freshwater drum and shovelnose sturgeon, and freshwater drum was positively correlated with shovelnose sturgeon (Figure 33).

Condition

Segment Comparisons

Relative weight differed significantly among segments for all species and length categories, except Q-P sauger and shovelnose sturgeon (Table 13). Shovelnose sturgeon and sauger exhibited clear longitudinal patterns in W_r. In general, shovelnose sturgeon W_r values decreased from upstream to downstream for the Q-P and P-M length categories. Conversely, W_r values for P-M sauger increased from upstream to downstream. Longitudinal patterns by segment for common carp, channel catfish, freshwater drum, and river carpsuckers

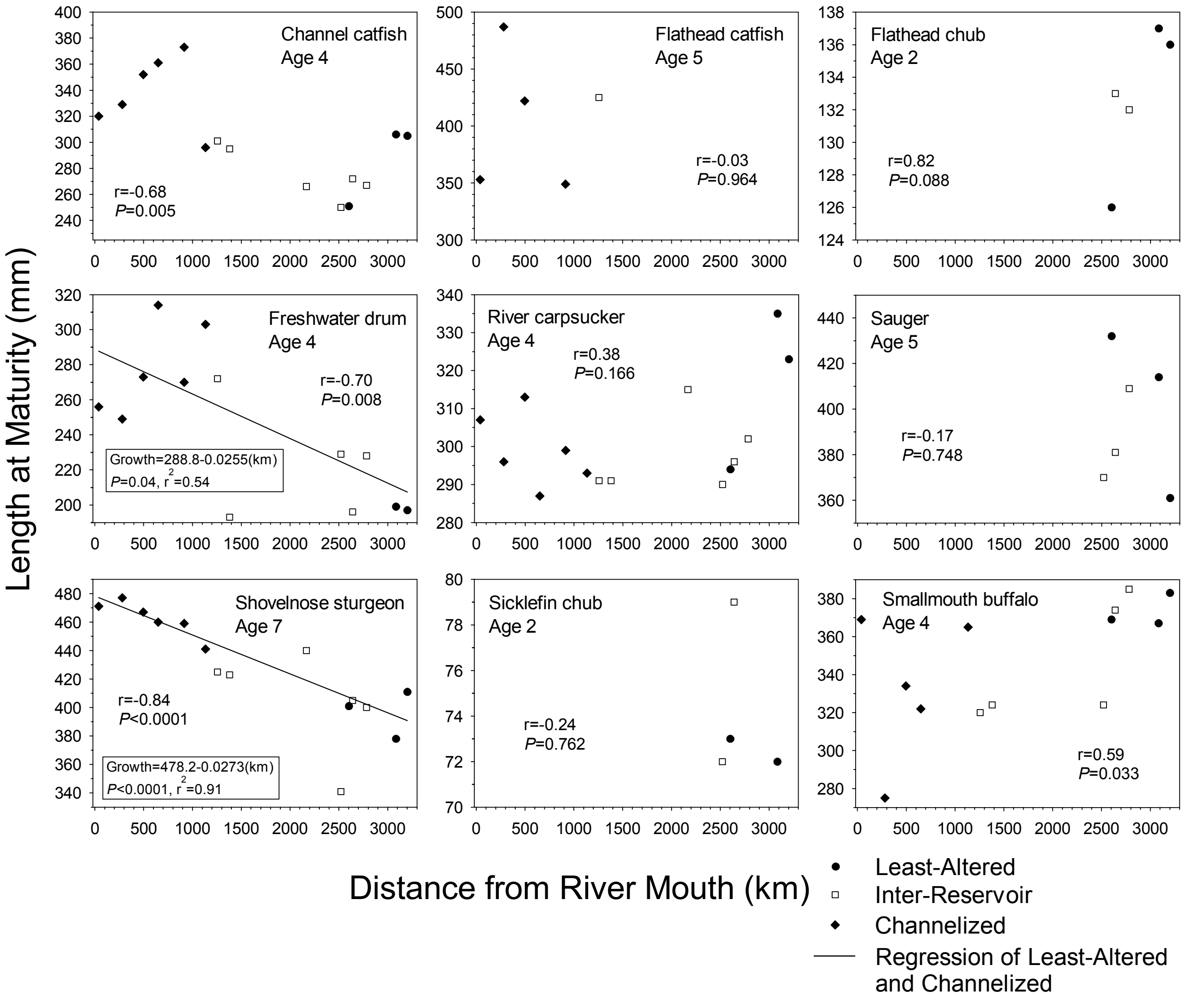

Figure 28. Mean length of fishes at age of maturity in the Missouri and lower Yellowstone rivers in relation to distance from the mouth of the Missouri River. Lengths are mean back-calculated lengths at species-specific age-at-maturity estimates compiled by Pegg and Pierce 2002. Age of maturity estimates are shown below species names. Distance from river mouth is the channel distance from the midpoints of segments to the mouth of the Missouri River. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points. Regression lines indicate significant regressions of growth vs. distance using data from the least-altered and channelized zones only; regression equations and statistics are in boxes.

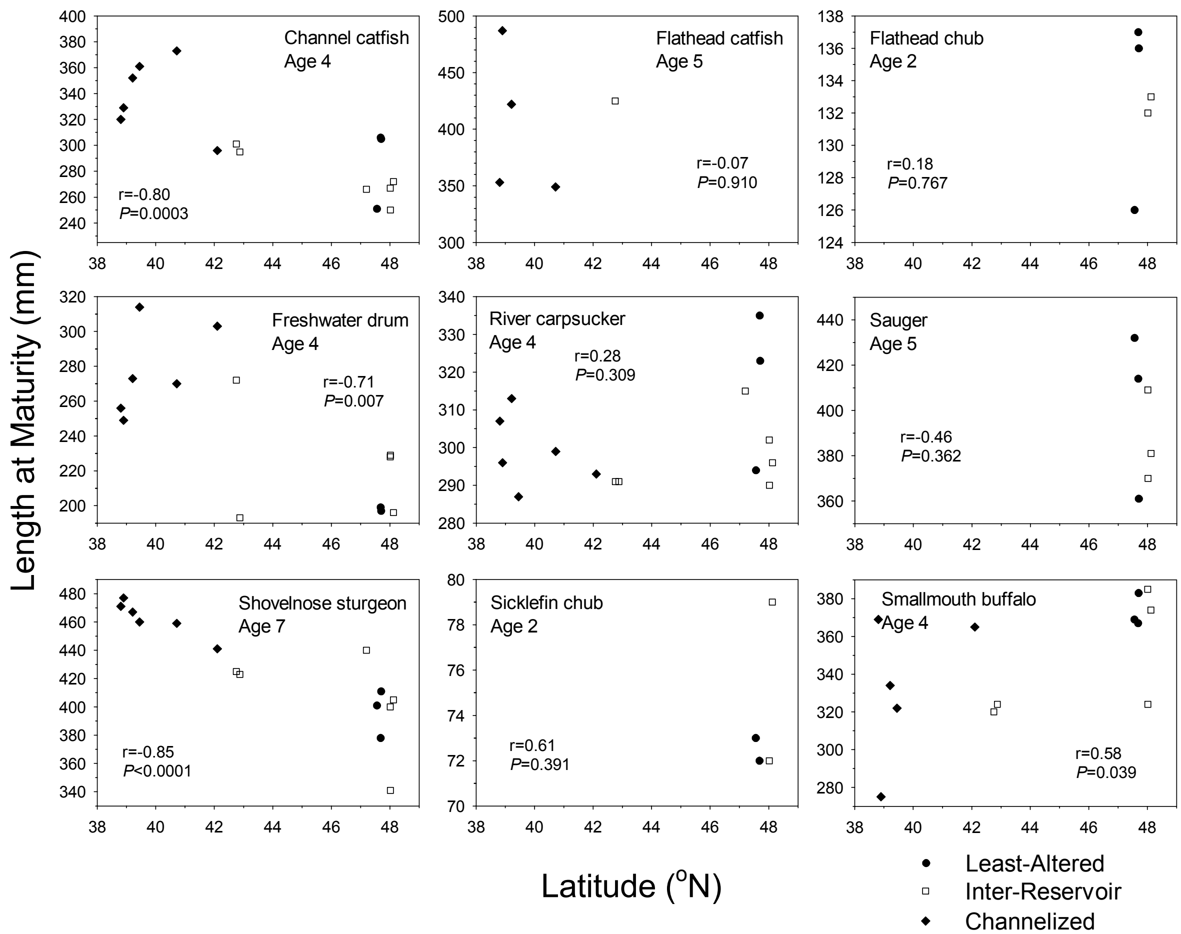

Figure 29. Mean length of fishes at age of maturity in the Missouri and lower Yellowstone rivers in relation to latitude. Lengths are mean back-calculated lengths at species-specific age-at-maturity estimates compiled by Pegg and Pierce 2002. Age of maturity estimates are shown below species names. Latitude is measured at the midpoints of segments. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points.

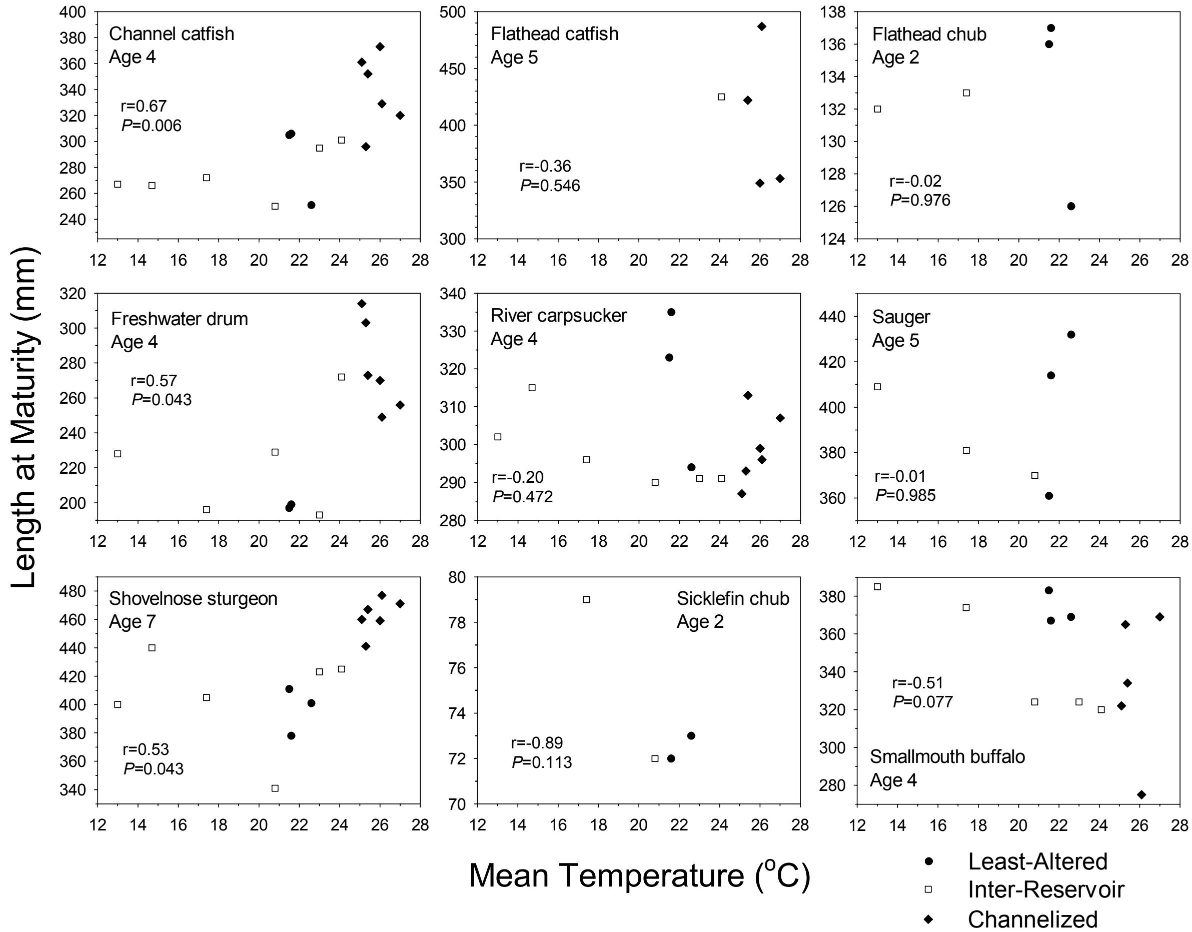

Figure 30. Mean length of fishes at age of maturity in the Missouri and lower Yellowstone rivers in relation to mean late summer water temperature. Lengths are mean back-calculated lengths at species-specific age of maturity estimates compiled by Pegg and Pierce 2002. Age-at-maturity estimates are shown below species names. Temperatures were averaged from all measurements taken in bends as described by Galat at al. 2001. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points.

Table 10. Pair-wise Pearson correlations of annual growth at age-0 (AG-0) among fourteen species of benthic fishes in segments of the Missouri and lower Yellowstone rivers. Species are abbreviated as follows: busk=blue sucker, cncf=channel catfish, ersn=emerald shiner, fhcf=flathead catfish, fhcb=flathead chub, fwdm=freshwater drum, rvcs=river carpsucker, snsn=sand shiner, sger=sauger, snsg=shovelnose sturgeon, sfcb=sicklefin chub, smbf=smallmouth buffalo, wsmw=western silvery minnow. Numbers below correlation coefficients are sample size (n). Asterisks indicate *P*-value levels as follows: * 0.01<=*P*<0.05, ** 0.001<=*P*<0.01, *** 0.0001<=*P*<0.001, **** *P*<0.0001. Dashes indicate n<5.

	Species											
Species	cncf	ersn	fhcf	fhcb	fwdm	rvcs	snsn	sger	snsg	sfcb	smbf	wsmw
busk	-0.35 10	-0.06 9	-0.66 6	-	0.85** 9	0.70* 10	-0.44 5	0.91*** 9	-0.24 10	-	-0.63 9	-
cncf		0.62* 14	0.41 7	0.56 6	-0.54* 14	-0.06 15	0.56 6	-0.43 14	-0.05 15	0.22 6	0.67** 14	0.47 6
ersn			0.01 7	0.46 6	-0.30 14	-0.25 14	-0.57 6	-0.21 13	-0.17 14	0.40 6	0.26 14	0.57 6
fhcf				-	0.14 7	-0.29 7	-0.09 6	-0.70 6	-0.44 7	-	0.67 7	-
fhcb					-0.25 6	0.46 6	-	-0.02 6	0.29 6	-	0.82* 6	0.80 6
fwdm						0.30 14	-0.79 6	0.85*** 13	0.39 14	-0.50 6	-0.58 14	-0.13 6
rvsc							0.02 6	0.56 14	-0.16 15	-0.30 6	-0.16 14	0.63 6
snsn								-0.20 5	0.04 6	-	-0.20 6	-
sger									0.11 14	0.10 5	-0.70** 13	-0.13 6
snsg										0.50 6	-0.39 14	-0.21 6
sfcb											0.25 6	-
smbf												0.68 6

Table 11. Pair-wise Pearson correlations of annual growth at length of maturity (AG-m) among 9 species of benthic fishes in segments of the Missouri and lower Yellowstone rivers. Species are abbreviated as follows: cncf=channel catfish, ersn=emerald shiner, fhcb=flathead chub, fwdm=freshwater drum, rvcs=river carpsucker, sger=sauger, snsg=shovelnose sturgeon, sfcb=sicklefin chub, smbf=smallmouth buffalo. Numbers below correlation coefficients are sample size (n). Asterisks indicate *P*-value levels as follows: * 0.01<=*P*<0.05, ** 0.001<=*P*<0.01, *** 0.0001<=*P*<0.001, **** *P*<0.0001. Dashes indicate n<5.

	Species							
Species	ersn	fhcb	fwdm	rvcs	sger	snsg	sfcb	smbf
cncf	-0.69*	-0.46	0.61*	0.26	0.57*	-0.27	0.04	-
	9	6	13	15	14	12	12	
ersn		0.24	-0.22	-0.47	-0.09	-0.23	-	-0.61
		6	8	9	9	7		9
fhcb			-0.61	-0.48	-0.2	0.18	-	0.11
			5	6	6	5		6
fwdm				-0.07	0.61*	-0.18	-	-0.12
				13	12	10		11
rvsc					-0.46	-0.14	-0.56	0.12
					14	12	5	12
sger						-0.03	-0.3	-0.34
						11	5	11
snsg							-	0.23
								10
sfcb								-

Table 12. Pair-wise Pearson correlations of length at age of maturity (L-m) among eight species of benthic fishes in segments of the Missouri and lower Yellowstone rivers. Species are abbreviated as follows: cncf=channel catfish, fhcf=flathead catfish, fhcb=flathead chub, fwdm=freshwater drum, rvcs=river carpsucker, sger=sauger, snsg=shovelnose sturgeon, smbf=smallmouth buffalo. Numbers below correlation coefficients are sample size (n). Asterisks indicate *P*-value levels as follows: * 0.01<=*P*<0.05, ** 0.001<=*P*<0.01, *** 0.0001<=*P*<0.001, **** *P*<0.0001. Dashes indicate n<5.

	Species						
Species	fhcf	fhcb	fwdm	rvcs	sger	snsg	smbf
cncf	-0.35	0.94*	0.56*	0.06	-0.22	0.73*	-0.4
						*	
	5	5	13	15	6	15	13
fhcf		-	-0.34	-0.3	-	0.06	-
			5	5		5	
fhcb			-	0.83	-0.6	-0.29	0.18
				5	5	5	5
fwdm				-0.43	0.12	0.59*	-0.31
				13	5	13	12
rvsc					0.01	-0.09	0.44
					6	15	13
sger						0.17	0.24
						6	6
snsg							-0.34
							13

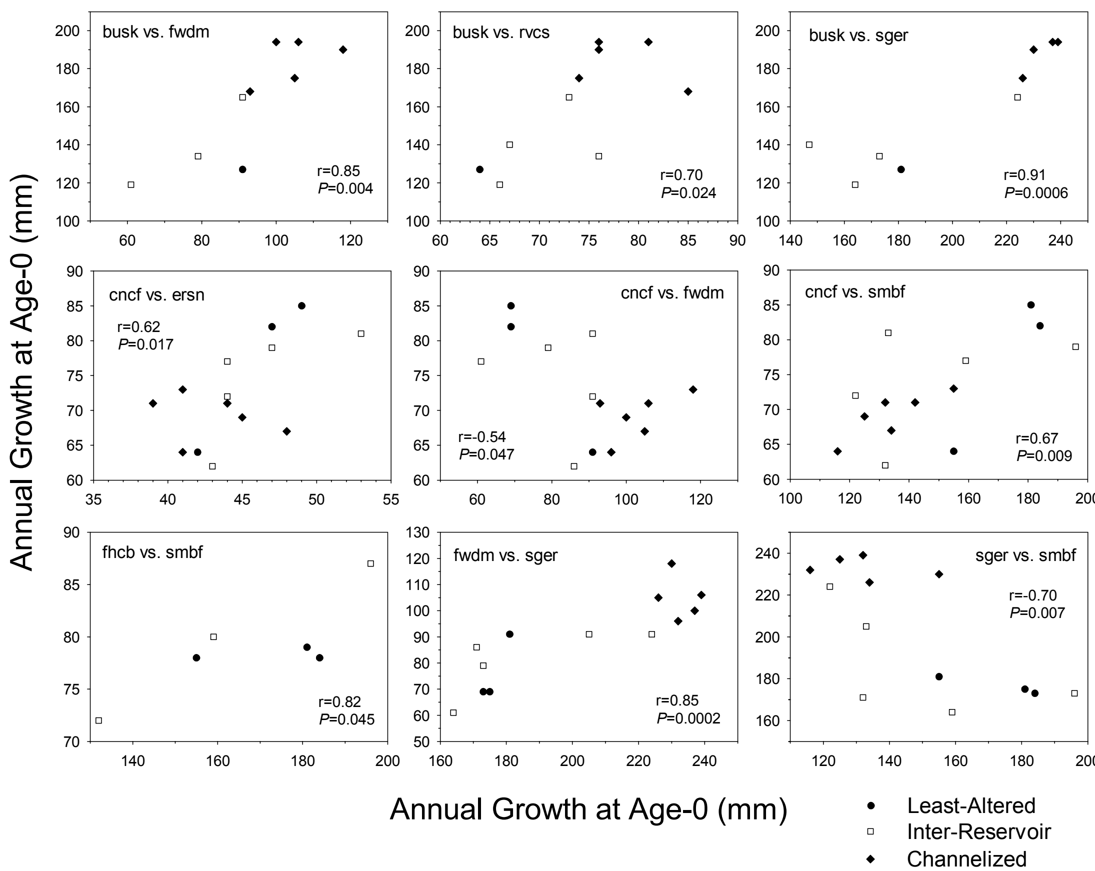

Figure 31. Scatterplots of significant ($\alpha<0.05$) correlations of annual growth at age-0 (AG-0) in the Missouri and lower Yellowstone rivers. Annual growth is estimated as the mean back-calculated length at age 1. Species are abbreviated as follows: busk=blue sucker, cncf=channel catfish, ersn=emerald shiner, fhcb=flathead chub, fwdm=freshwater drum, rvcs=river carp-sucker, sger=sauger, smbf=smallmouth buffalo. In each graph, growth of the first species listed is shown on the Y-axis. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points.

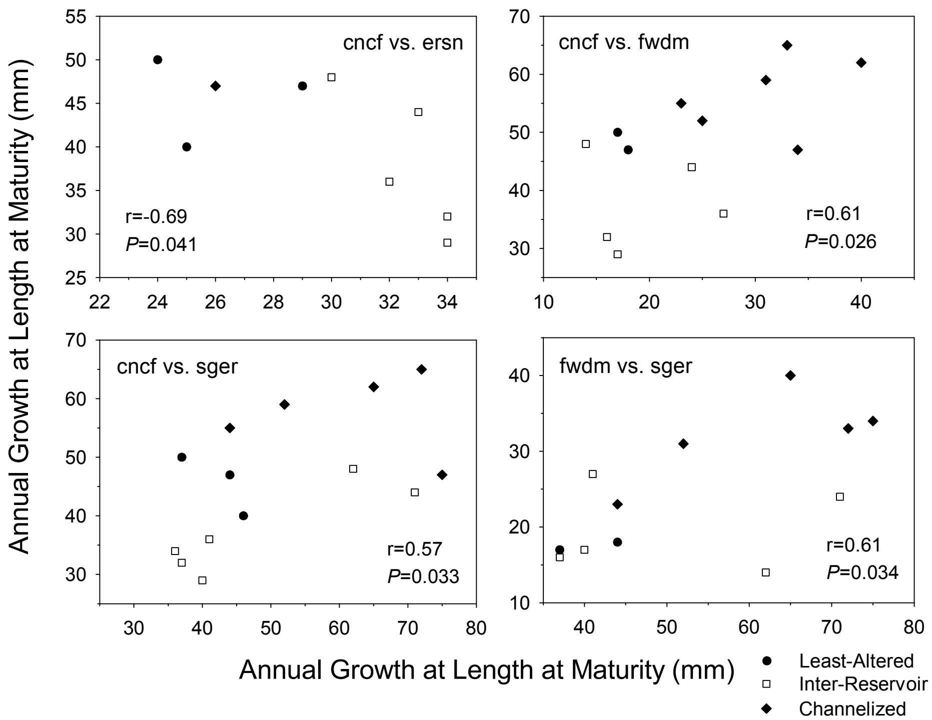

Figure 32. Scatterplots of significant (α<0.05) correlations of annual growth at length at maturity (AG-m) in the Missouri and lower Yellowstone rivers. Annual growth is estimated from size-specific regressions of annual growth, using species-specific estimates of size-at maturity compiled by Pegg and Pierce 2002. Species are abbreviated as follows: cncf=channel catfish, ersn=emerald shiner, fwdm=freshwater drum, sger=sauger. In each graph, growth of the first species listed is shown on the Y-axis. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points.

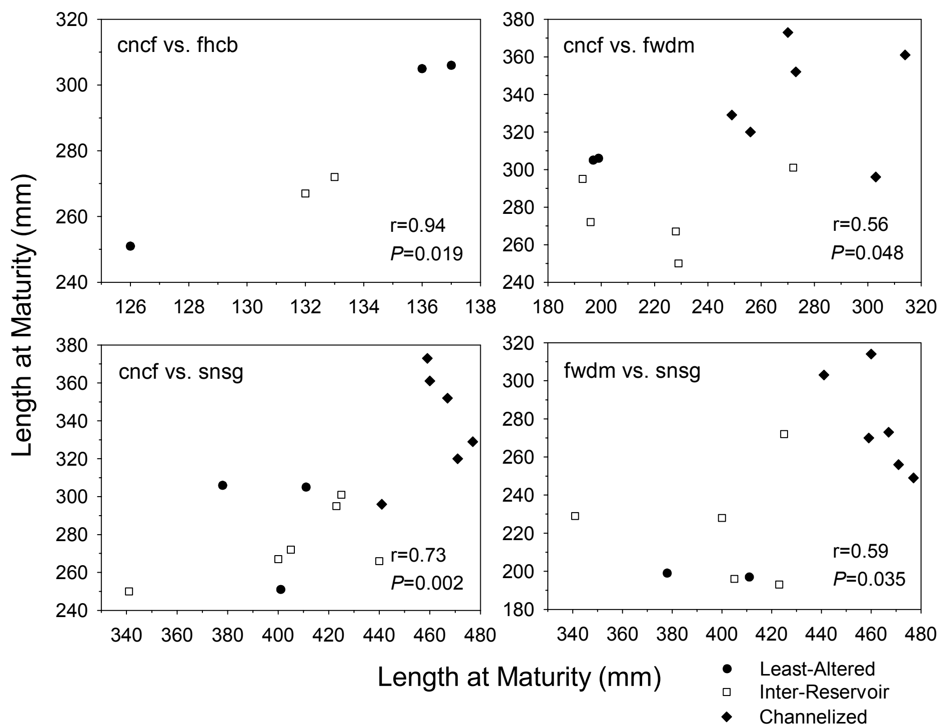

Figure 33. Scatterplots of significant (α<0.05) correlations of mean length at age of maturity (L-m) in the Missouri and lower Yellowstone rivers. Lengths are mean back-calculated lengths at species-specific age of maturity estimates compiled by Pegg and Pierce 2002. Species are abbreviated as follows: cncf=channel catfish, fhcb=flathead chub, fwdm=freshwater drum, snsg=shovelnose sturgeon. In each graph, length of the first species listed is shown on the Y-axis. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points.

Table 13. Mean relative weight (W_r) by species and length category (Lcat=stock to quality [S-Q], quality to preferred [Q-P], preferred to memorable [P-M], and memorable to trophy [M-T]), and segment (see methods for segment definitions) for fish sampled from the Missouri and Yellowstone rivers during 1996-1998. Numbers in parentheses are one standard error and sample size, respectively. Mean relative weight was not calculated when less than five fish were sampled by year, length category, and segment. Means with the same letter are not significantly different at "=0.05.

			Segment														
Species	P	Lcat.	3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
CARP	<0.0001	S-Q		101z (3,12)		93x (2,5)	94yx (2,25)	87x (2,18)		102z (2,31)	92x (2,64)	100zy (5,8)	93x (1,25)	91x (1,29)	89x (1,41)	92x (1,75)	92x (1,127)
	<0.0001	Q-P	97zyxw (2,51)	95wv (1,70)	101z (2,34)	92vut (1,41)	90t (1,68)	90ut (2,22)	92vut (1,65)	100zy (1,113)	91vut (1,214)	92vut (1,59)	99zyx (1,66)	96xw (1,78)	94wvu (1,70)	94wvut (1,87)	96yxw (1,103)
	<0.0001	P-M	92wvu (1,68)	92wvu (1,67)	100zyx (1,40)	91vu (2,17)	92wvu (1,34)	94wvu (2,16)	92wvu (2,26)	100z (1,69)	89u (1,82)	94wv (2,37)	101z (2,44)	96zyxw (2,34)	95xwv (2,32)	96xywv (2,28)	100zy (2,35)
CNCF	<0.0001	S-Q	96zy (2,18)	92zyxw (3,32)	76t (1,21)	80ut (2,24)	93zyx (1,83)	85wvu (1,29)		91yxw (1,112)	85wvu (1,67)	89yxwv (3,16)	99z (5,9)	91yxw (5,15)	83uvt (2,19)	90yxwv (5,7)	88xwv (3,26)
	<0.0001	Q-P	96y (2,26)	91xvyw (1,61)	85w (2,37)	88xvw (2,35)	87vw (1,65)	87vw (2,32)	88xvw (2,24)	95y (1,128)	93yxw (3,25)	94yx (3,10)	111z (6,8)	87vw (2,16)	86w (2,21)	95y (3,21)	87xvw (2,45)
	0.0005	P-M	119z (6,7)	107zy (4,8)			90x (3,10)			99yx (4,10)							99yx (5,5)
FHCF	0.002	S-Q									96z (3,27)	95z (2,17)	91zy (2,41)	87yx (2,16)	84yx (2,17)	91zx (3,12)	90zyx (2,15)
FWDM	<0.0001	S-Q	101zyx (1,79)	106zy (1,71)			99yx (3,11)	108z (7,5)			94xw (1,8)		101zyx (3,6)	95xw (3,10)	89w (2,19)	95xw (1,20)	97xw (3,29)
	0.0004	Q-P	98z (1,47)	98z (1,39)							87x (3,14)			93zy (2,10)	92yx (1,15)	94zy (2,15)	93zy (2,29)
	0.003	P-M								99y (6,6)	91y (5,8)		114z (3,6)	96y (2,5)			93y (2,8)
RVCS	0.039	S-Q					98z (3,13)			89yx (1,10)	94zy (4,13)	95zy (3,11)	97zy (4,18)	90zyx (1,24)		84x (3,6)	90zyx (2,14)
	<0.0001	Q-P			97z (3,16)	95zy (2,12)	97z (1,53)			87w (2,39)	90yxw (1,100)	95zyx (4,15)	94zyx (2,11)	89xw (2,17)		93zyx (2,16)	90yxw (3,20)
	<0.0001	P-M	92yxw (4,14)	95y (3,22)	92yxw (1,141)	87wv (1,57)	93yx (1,80)	100z (2,10)	90xw (2,24)	88wv (1,104)	83v (1,200)	94yx (1,36)	95zy (3,16)	87wv (1,33)	88wv (1,36)	90yxw (2,25)	87wv (2,48)
SGER	0.038	S-Q	77zy (2,17)	76zyx (1,28)	70x (2,5)	74zyx (1,16)	79z (2,21)	80z (2,16)			72yx (2,6)	75zyx (2,7)					
	0.102	Q-P	74 (2,14)	74 (2,17)	72 (3,10)	73 (2,11)	74 (1,15)	75 (2,11)		79 (6,9)		80 (5,5)	78 (1,9)	88 (10,5)		75 (4,5)	
	<0.0001	P-M	77ywx (3,5)	75w (2,9)	76w (3,7)	71w (2,9)	70w (2,10)	75w (3,8)		72w (1,7)	75w (2,16)	84zy (2,12)	89z (3,6)	76wx (1,6)	76w (2,6)	83zyx (5,6)	
SNSG	<0.0001	S-Q					96z (1,44)							79x (2,10)	85y (2,14)		85y (3,9)
	0.103	Q-P			92 (2,11)	88 (1,14)	91 (1,39)					81 (2,11)	89 (3,5)	88 (2,52)	86 (2,48)	87 (2,26)	86 (2,12)
	<0.0001	P-M		112z (3,34)	94vu (1,68)	95wv (3,28)	99xw (1,92)	105y (3,38)	95wv (3,39)	103xy (5,10)	84sr (1,54)	84sr (1,90)	88srut (2,56)	85srt (1,100)	83r (1,123)	89sut (2,64)	90ut (4,19)
	<0.0001	M-T	106yzx (3,25)	108z (2,65)	94wx (3,20)	95ywx (7,5)	104yzx (1,58)	108yz (5,6)	97ywzx (9,8)	104yzx (6,7)				77v (2,12)	79v (3,9)	80v (2,14)	86wv (8,5)

were less clear (Table 13).

The effects of reservoirs on condition were more pronounced in the upper portion of the Missouri River. For example, W_r declined between segments 5 and 7 (above Ft. Peck Lake and below, respectively) for channel catfish, river carpsucker, sauger (except P-M), and shovelnose sturgeon, but only significantly for P-M and M-T shovelnose sturgeon (Table 13). However, W_r values increased significantly from segment 5 to 7 for common carp. Similar to comparisons between above Fort Peck Lake and below, W_r significantly declined from above Lake Sakakawea to below (segments 10 and 12, respectively) for P-M river carpsucker and shovelnose sturgeon. Relative weight was significantly lower below Gavins Point Dam than Lewis and Clark headwaters (segments 14 and 15) for S-Q, Q-P, and P-M common carp; and P-M shovelnose sturgeon (Table 13). Despite the lack of significant differences, segment 15 typically had lower W_r values than segments 14 and 17.

Zone, Group, and Hydrological Unit Comparisons

Variation in condition among size categories by species was best illustrated by zone, group, and hydrological unit comparisons. Relative weight values for common carp varied among zones and patterns differed among size categories. For example, W_r was highest in the least-altered zone for S-Q fish, but W_r was highest in the channelized zone for P-M fish (Figure 34). Interestingly, W_r was similar between the inter-reservoir and least-altered groups for the S-Q and Q-P length categories. Common carp from the Lewis and Clark group had some of the lowest W_r values and fish in the P-M length category were similar to the least-altered group (Figure 34).

Channel catfish had significantly higher W_r values in the least-altered zone than the inter-reservoir and channelized zones for the S-Q length category (Figure 35). Relative weight values of P-M channel catfish were significantly higher for the least-altered group and hydrological unit than all other groups or hydrological units (Figure 35). Relatively few P-M channel catfish were sampled throughout the study; thus, the P-M data are highly influenced by a few fish captured in segments 3 and 5. Relative weight values were lowest in the inter-reservoir and Lewis and Clark groups and the inter-reservoir hydrological units for S-Q channel catfish (Figure 35).

Flathead catfish were only sampled below Gavins Point Dam and analyses were only performed on S-Q fish because sample size was limited for the other length categories. Flathead catfish had higher W_r values in the inter-reservoir zone, Lewis and Clark group, and upper channelized hydrological unit (Figure 36). The high W_r values observed in the upper channelized river were primarily a function of fish sampled in segments 15 and 17 (Table 13).

Relative weight values for freshwater drum differed significantly among zones. Stock- to quality length and Q-P freshwater drum had higher W_r values in the least-altered than the channelized zone (Figure 37). In the hydrological unit analysis, P-M freshwater drum in the upper channelized unit was significantly higher than the least-altered unit (Figure 37). Similar to other species, W_r values for the Lewis and Clark group (i.e., segment 15) were typically lower than other groups (Figure 37).

River carpsucker had significantly higher W_r values in the least-altered than the inter-reservoir or channelized zone for Q-P and P-M length categories (Figure 38). Preferred- to memorable-length river carpsuckers had the lowest W_r values in the inter-reservoir zone. The lower W_r values for P-M river carpsucker below Lewis and Clark Reservoir (i.e., segment 15) are well represented in the group analysis (Figure

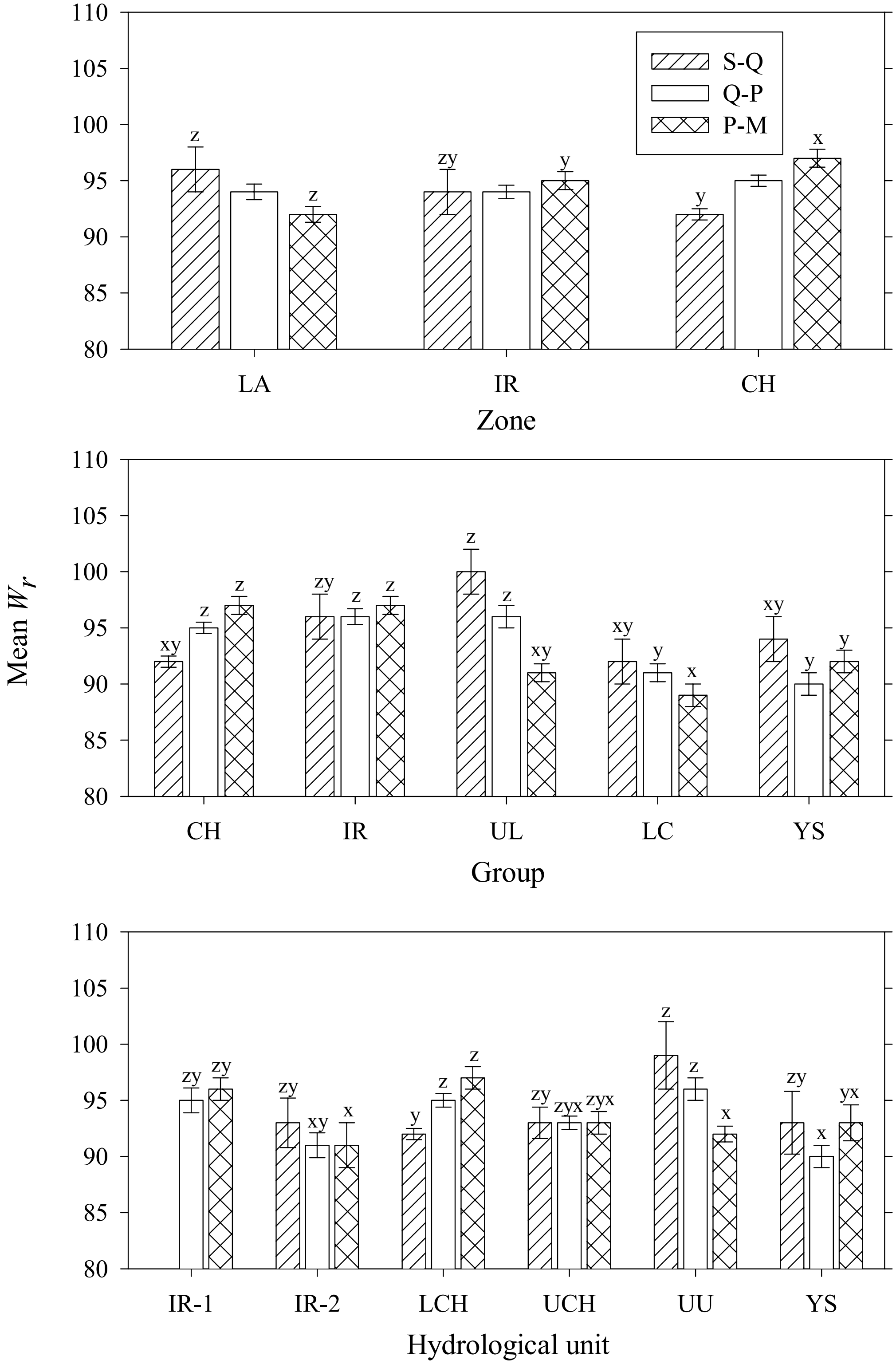

Figure 34. Mean relative weight (W_r) for common carp sampled in the Missouri and Yellowstone rivers from 1996-1998 by zone (top panel), group (middle panel), and hydrological unit (bottom panel) for stock to quality, quality to preferred, and preferred to memorable length categories (see text for acronym definitions). Error bars delineate one standard error.

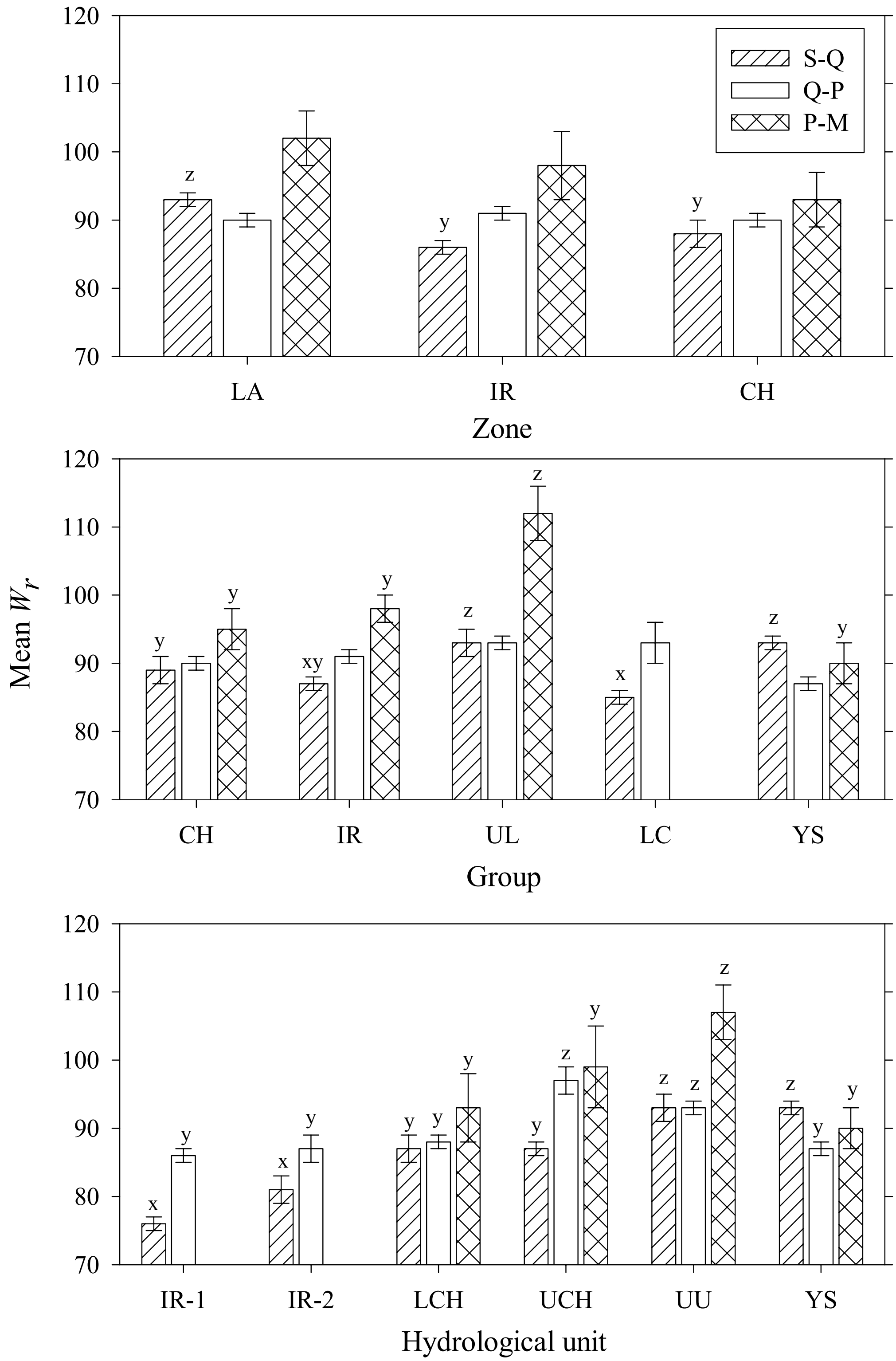

Figure 35. Mean relative weight (W_r) for channel catfish sampled in the Missouri and Yellowstone rivers from 1996-1998 by zone (top panel), group (middle panel), and hydrological unit (bottom panel) for stock to quality, quality to preferred, and preferred to memorable (see text for acronym definitions). Error bars delineate one standard error.

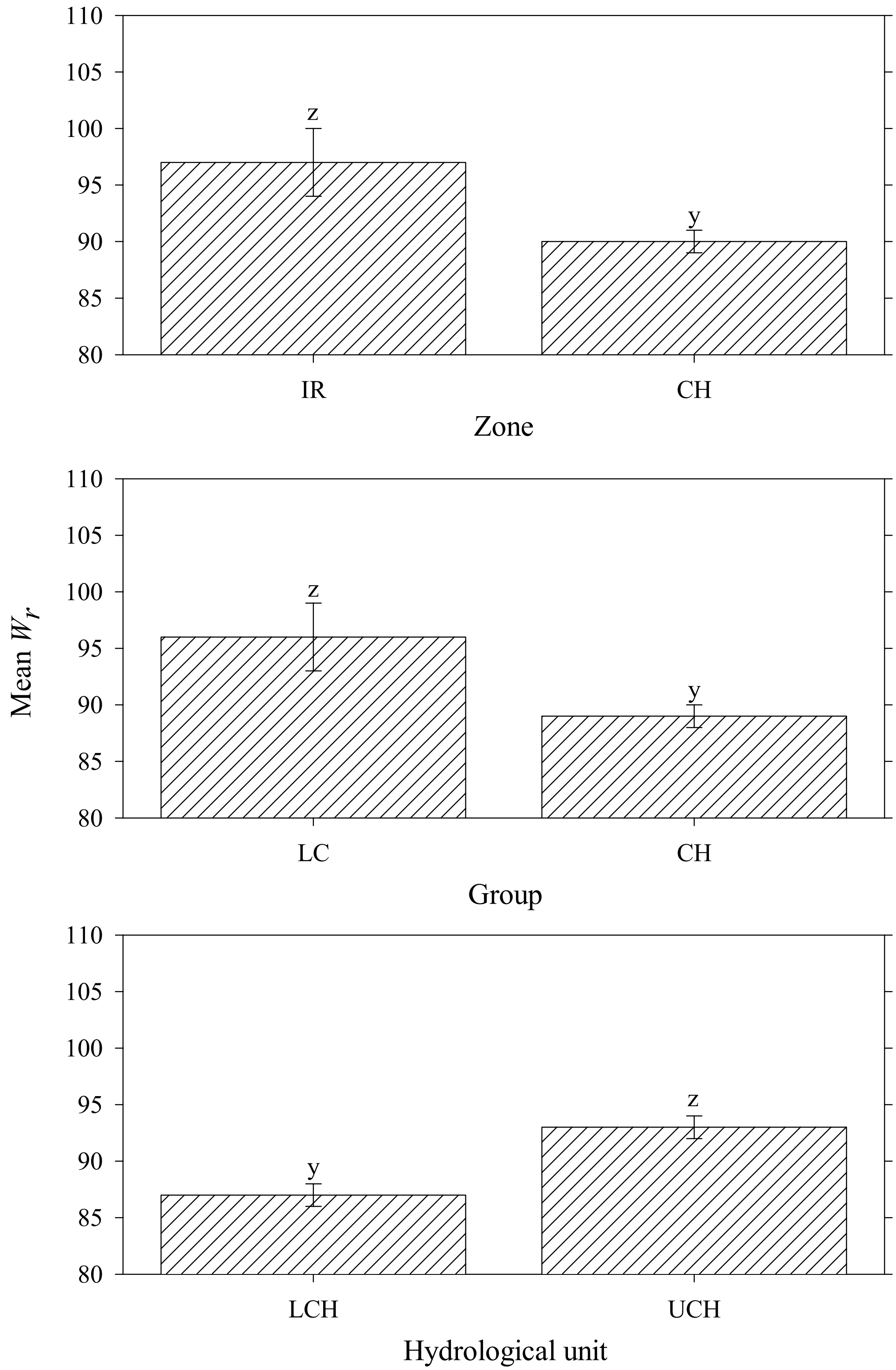

Figure 36. Mean relative weight (W_r) for flathead catfish sampled in the Missouri and Yellowstone rivers during 1996-1998 by zone (top panel), group (middle panel), and hydrological unit (bottom panel) for the stock to quality length category (see text for acronym definitions). Error bars delineate one standard error.

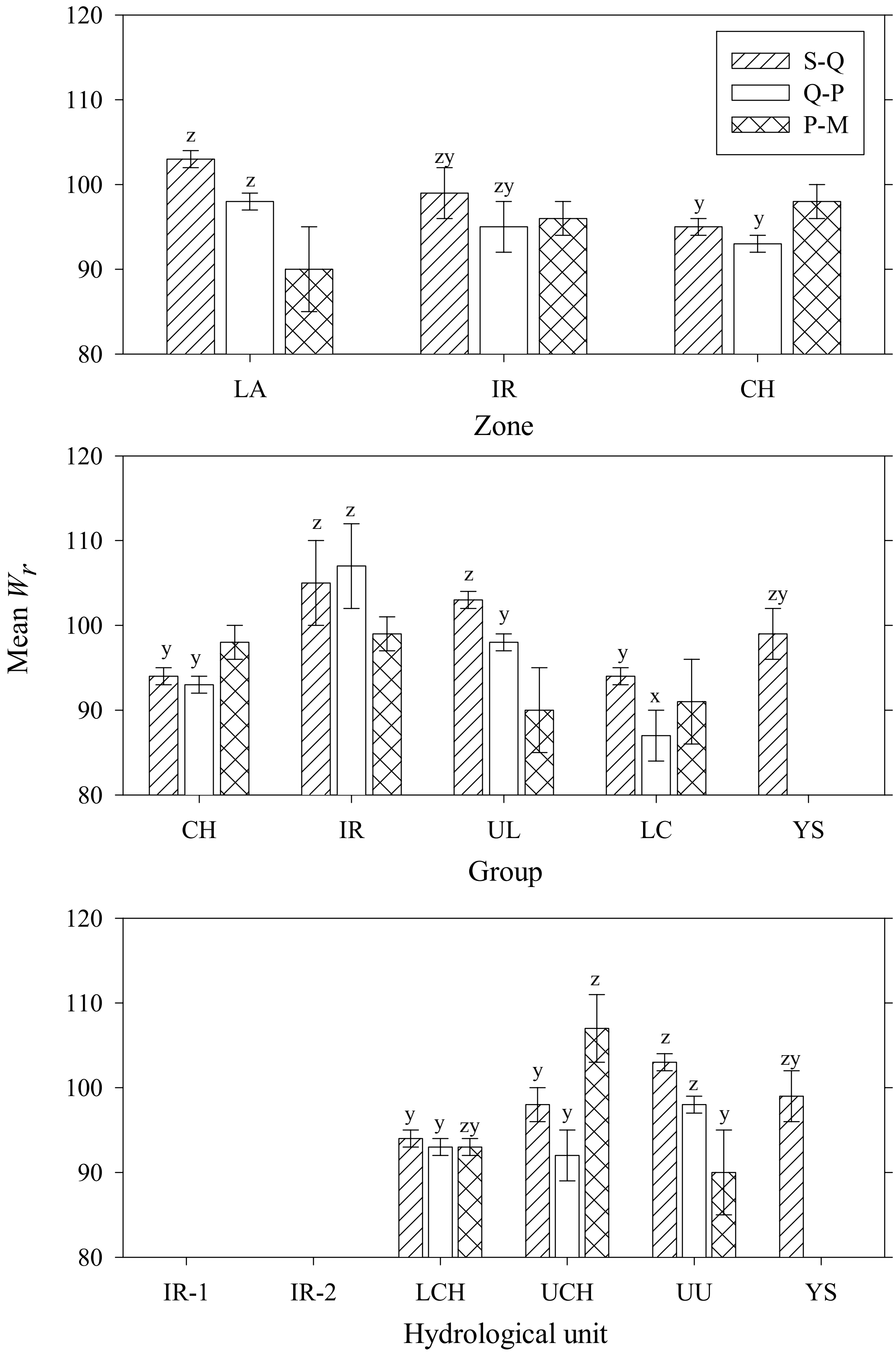

Figure 37. Mean relative weight (W_r) for freshwater drum sampled in the Missouri and Yellowstone rivers from 1996-1998 by zone (top panel), group (middle panel), and hydrological unit (bottom panel) for stock to quality, quality to preferred, and preferred to memorable (see text for acronym definitions). Error bars delineate one standard error.

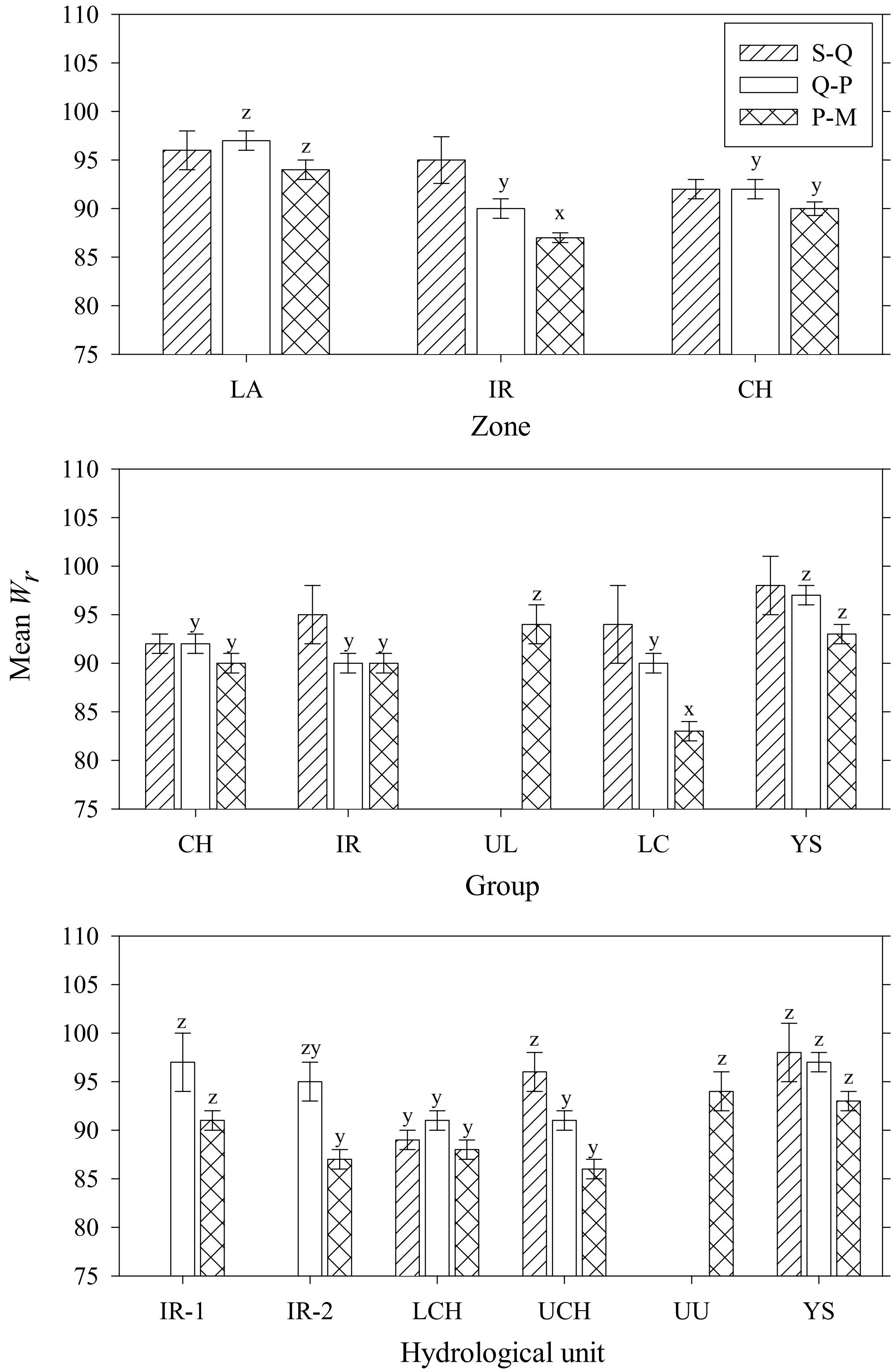

Figure 38. Mean relative weight (W_r) for river carpsucker sampled in the Missouri and Yellowstone rivers from 1996-1998 by zone (top panel), group (middle panel), and hydrological unit (bottom panel) for stock to quality, quality to preferred, and preferred to memorable length categories (see text for acronym definitions). Error bars delineate one standard error.

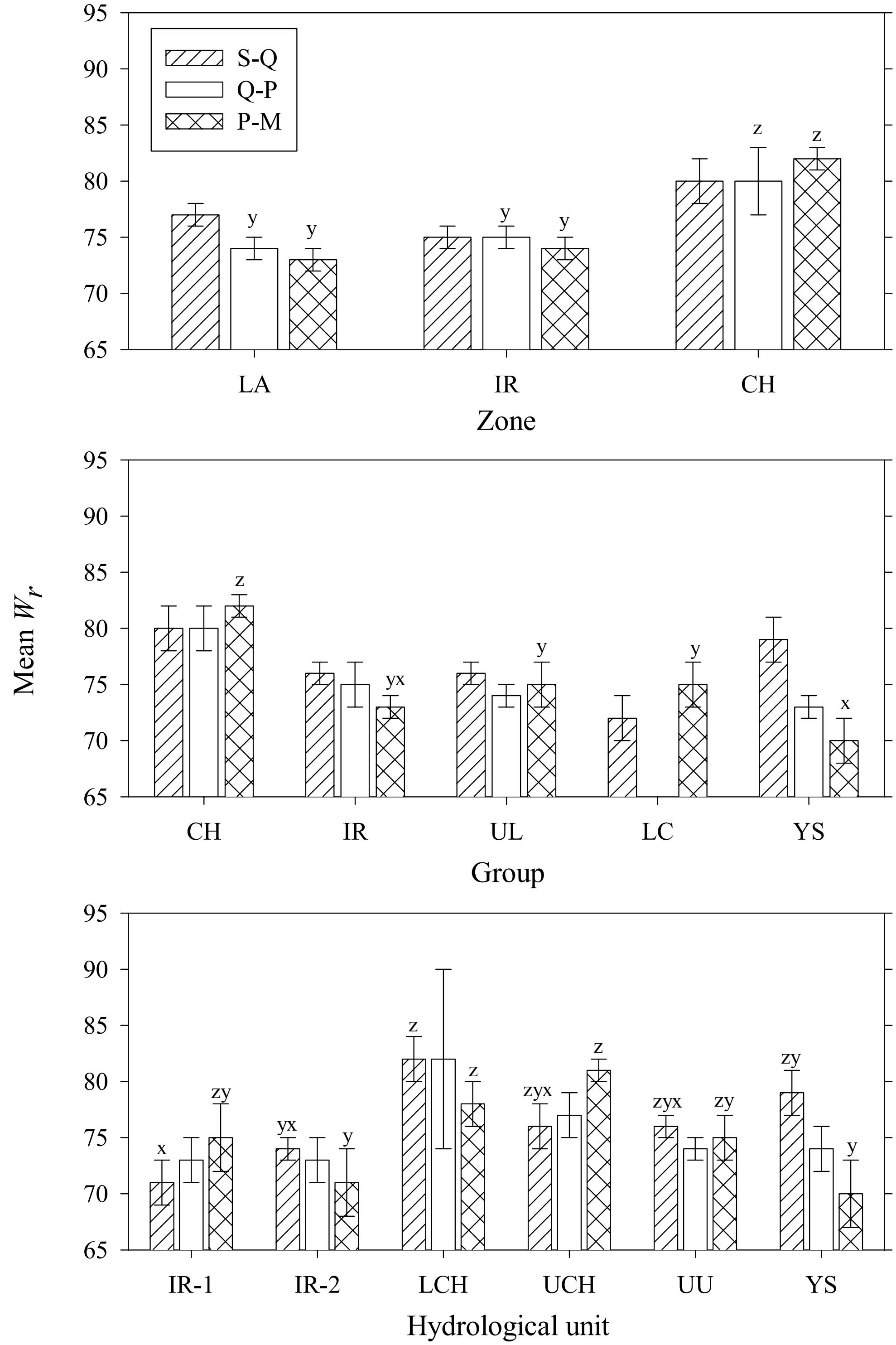

Figure 39. Mean relative weight (W_r) for sauger sampled in the Missouri and Yellowstone rivers from 1996-1998 by zone (top panel), group (middle panel), and hydrological unit (bottom panel) for stock to quality, quality to preferred, and preferred to memorable (see text for acronym definitions). Error bars delineate one standard error.

38). Conversely, W_r values were high for all length categories in the Yellowstone River. Analysis by hydrological unit illustrated the difference in S-Q W_r values between the lower and upper channelized hydrological units. The difference between channelized hydrological units was primarily a function of higher W_r values in segment 19 (Table 13).

Sauger had significantly higher W_r values in the channelized zone than the least-altered or inter-reservoir zones for Q-P and P-M length categories (Figure 39). Relative weight of P-M sauger in the Yellowstone River was the lowest W_r value in the study. Relative weight of S-Q sauger did not differ significantly among zones or groups. Similarly, W_r of Q-P sauger did not differ among groups or hydrological units. The comparison of W_r among hydrological units further illustrated the low W_r values for the inter-reservoir and Yellowstone River hydrological units (Figure 39). Mean W_r of stock-length sauger (i.e., $ 200 mm) was weakly correlated with river kilometer (Figure 40). Mean W_r decreased as river kilometer increased and longitudinal position of the segments explained 38% of the variation in mean W_r.

Relative weight of shovelnose sturgeon was significantly higher in the least-altered zone than the channelized zone for all length categories (Figure 41). Relative weight for the S-Q and Q-P length categories were more similar among the least-altered zone and the inter-reservoir zone

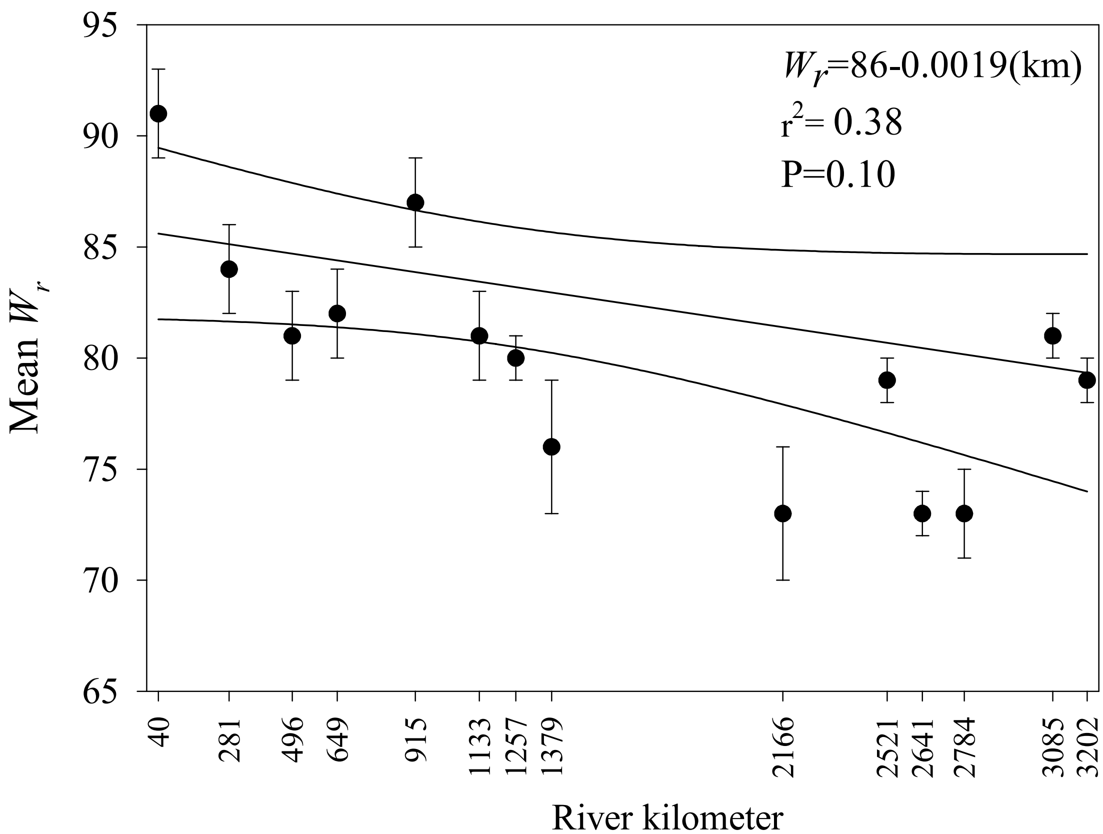

Figure 40. Mean relative weight (W_r) for sauger by segment and liner regression line with 95% confidence bands for upper river kilometers (3202 and 3085) and lower river kilometers (1133-40) of the Missouri River sampled from 1996-1998.

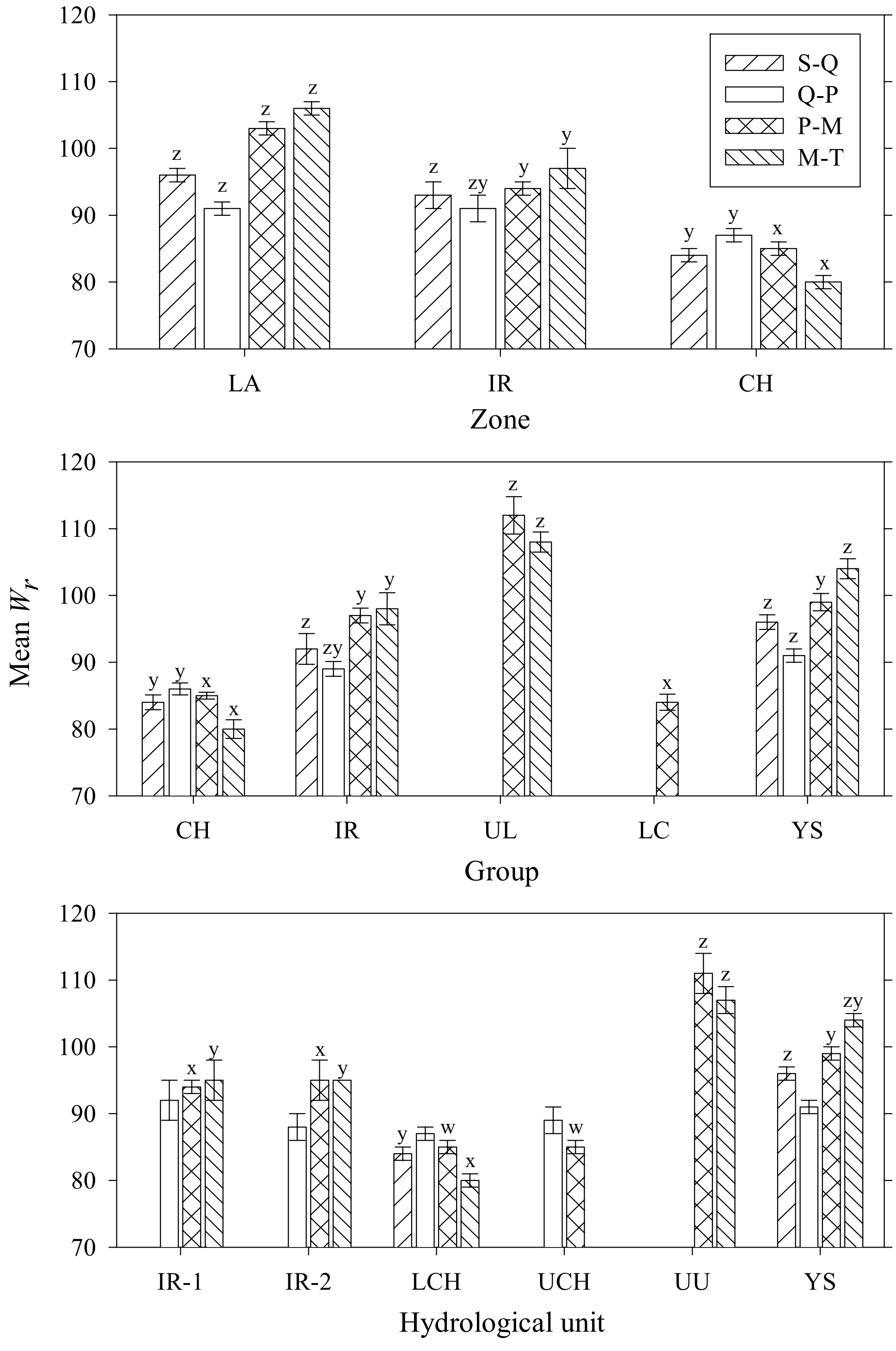

Figure 41. Mean relative weight (W_r) for shovelnose sturgeon sampled in the Missouri and Yellowstone rivers from 1996-1998 by zone (top panel), group (middle panel), and hydrological unit (bottom panel) for stock to quality, quality to preferred, preferred to memorable and memorable to trophy length categories (see text for acronym definitions). Error bars delineate one standard error.

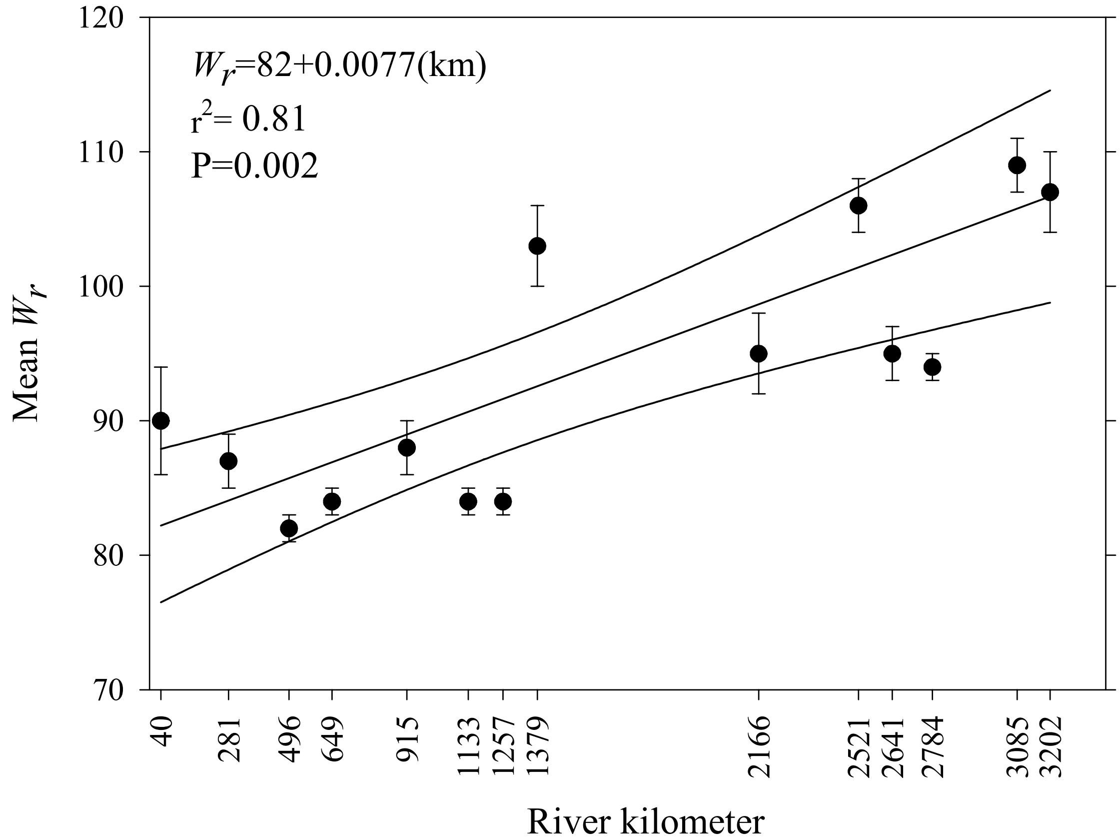

Figure 42. Mean relative weight (W_r)for shovelnose sturgeon by segment and liner regression line with 95% confidence bands for upper river kilometers (3202 and 3085) and lower river kilometers (1133-40) of the Missouri River sampled from 1996-1998.

than W_r for the P-M and M-T length categories. Condition of shovelnose sturgeon in the Yellowstone River was more similar to the least-altered group than the inter-reservoir and channelized groups (Figure 41). Relative weight of P-M shovelnose sturgeon in the Lewis and Clark group (LW, segment 15) were not significantly different than the channelized group (Table 13 and Figure 41). Comparison by hydrological unit exhibited similar patterns to zone and group comparisons, but better illustrated the lack of significant difference in W_r among inter-reservoir and channelized units for shovelnose sturgeon. Mean W_r for preferred-length shovelnose sturgeon (i.e., $510 mm) was significantly correlated with river kilometer (Figure 42). Mean W_r increased as river kilometer increased and longitudinal position of the segments explained 81% of the variation in mean W_r.

Size Structure

Segment Comparisons

Size structure was variable among segments for all species (Table 14). Spatial variation in size structure values was most discernable among segments for the preferred- and memorable-length categories. In general, RSD-P and RSD-M values decreased from upstream to downstream for common carp, river carpsucker, and shovelnose sturgeon. Size structure analy-

Table 14. Size structure values by species, year, and segment (see methods for segment definitions) for fish sampled from the Missouri and Yellowstone rivers during 1996-1998. Size structure was not calculated when less than ten stock-length fish were sampled by year and segment. Size structure values were only calculated for fish sampled in the gear that captured the most stock-length fish (boat electrofishing-CARP, FWDM, RVCS, and SGER; stationary gill net-CNCF; drifting trammel net-SNSG). See methods for acronym and gear definitions.

		Segment														
Species	Variable	3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
CARP	No. of stock-length fish	122	132	50	56	103	35	92	150	355	99	121	122	129	186	249
	PSD	98	95	96	93	84	69	100	90	80	93	83	81	69	60	52
	RSD-P	57	42	58	36	28	23	29	29	22	31	36	26	20	17	12
	RSD-M	5	2	12	11	2			1	1	1	5	4	1	2	
CNCF	No. of stock-length fish		36	58	59	98	57	25	201	63	22	11	21	22	11	22
	PSD		64	64	59	66	56	100	55	33	45	55	57	59	91	77
	RSD-P				7	11	7	8	5	2	5	9	19	32	27	5
	RSD-M					1	2							5		
FHCF	No. of stock-length fish									36	18	32	15	18	13	15
	PSD									25	11	3	7	17	23	27
	RSD-P									6					8	7
	RSD-M									6						

Species	Variable	Segment														
		3	5	**7**	**8**	9	**10**	**12**	**14**	**15**	*17*	*19*	*22*	*23*	*25*	*27*
FWDM	No. of stock-length fish	129	109			9				20		7	13	21	30	52
	PSD	37	34			11				80		57	38	43	43	60
	RSD-P	2	2							35		43	23	14	10	13
	RSD-M														3	
RVCS	No. of stock-length fish	23	31	103	24	71		31	109	286	52	20	27	17	27	46
	PSD	100	100	99	96	90		100	94	96	77	50	37	82	81	80
	RSD-P	100	94	90	79	59		100	80	61	52	30	30	76	56	54
	RSD-M	35	48	6	4	8		32	8		2			18	4	2
SGER	No. of stock-length fish	33	45	11	17	18	19	5	6	13	11	7	10	2	10	
	PSD	52	47	64	47	50	58	60	67	69	55	57	80	50	80	
	RSD-P	21	27	9	12	28	21	40	17	54	27	29	40		20	
	RSD-M	6	9		6	6										
SNSG	No. of stock-length fish	30	114	95	41	222	45	41	15	50	14	7	101	145	8	17
	PSD	100	98	100	93	84	93	100	100	100	93	86	92	91	100	82
	RSD-P	100	96	89	68	67	89	100	100	92	79	71	58	61	88	65
	RSD-M	97	68	20	10	25	16	20	47	6			12	5		1

sis by segment for other species was problematic because of low sample size.

The effects of reservoirs on size structure was most more pronounced in the upper portion of the Missouri River. For example, RSD-M for river carpsucker decreased from 48 above Ft. Peck Reservoir (Segment 5) to 6 below the reservoir (Segment 7) and shovelnose sturgeon decreased from 68 to 20 for the same comparison (Table 14). Similarly, RSD-P of sauger decreased from 27 above Ft. Peck Reservoir (Segment 5) to 9 below the reservoir (Segment 7).

Zone, Group, and Hydrological Unit Comparisons

Similar to the W_r data, variation in size structure was best illustrated by zone, group, and hydrological unit comparisons. Proportional stock density did not differ significantly among zones or groups for common carp (Figure 43). However, PSD did differ significantly among hydrological units with lowest mean PSD value for the lower-channelized hydrological unit. Relative stock density for preferred-length and RSD-M did not differ significantly among zones, groups, or hydrological units for common carp (Figure 43).

Proportional stock density, RSD-P and RSD-M did not differ significantly among zones, groups, or hydrological units for channel catfish (Figure 44).

Proportional stock density differed significantly among zones and groups for flathead catfish. Proportional stock density of flathead catfish was highest for the inter-reservoir zone and group (Figure 45).

Size structure values were highly variable for freshwater drum (Figure 46). For example, RSD-P was significantly higher in the inter-reservoir zone than the least-altered zone. Proportional stock density and RSD-P were highest in the inter-reservoir-two hydrological unit and differed significantly from the lower channelized, least-altered, and Yellowstone River hydrological units (Figure 46). Freshwater drum populations in the least-altered zone and Yellowstone River group had the lowest size structure values.

Proportional stock density values were near 100 for river carpsucker in the least-altered and inter-reservoir zones. Similarly, RSD-P was greater than 80 for the least-altered and inter-reservoir groups. The lowest size structure values were for the channelized area. For example, the channelized zone had significantly lower PSD and RSD-P values than the least-altered and inter-reservoir zones. Similarly, the channelized group, lower channelized hydrological unit, and upper channelized hydrological unit had lower size structure values (Figure 47).

Size structure for sauger did not differ significantly among zones, groups, and hydrological units (Figure 48). Despite the lack of significant differences, PSD and RSD-M appeared to increase from upstream to downstream. For example, mean PSD for the channelized zone was 63 and 45 for the least-altered zone. Memorable-length sauger were not sampled in the channelized section of the Missouri River.

Relative stock density of preferred-length shovelnose sturgeon differed significantly among groups and RSD-M differed significantly among zones, groups, and hydrological units (Figure 49). The least-altered zone and group had the highest RSD-M values for shovelnose sturgeon. Conversely, the channelized zone and the Lewis and Clark group had the lowest RSD-M values for shovelnose sturgeon. Interestingly, RSD-M values for the Yellowstone River group and hydrological unit only differed significantly from the least-altered group, and least-altered hydrological unit (Figure 49). Thus, RSD-M values for shovelnose sturgeon in the Yellowstone River were similar to all other areas in the

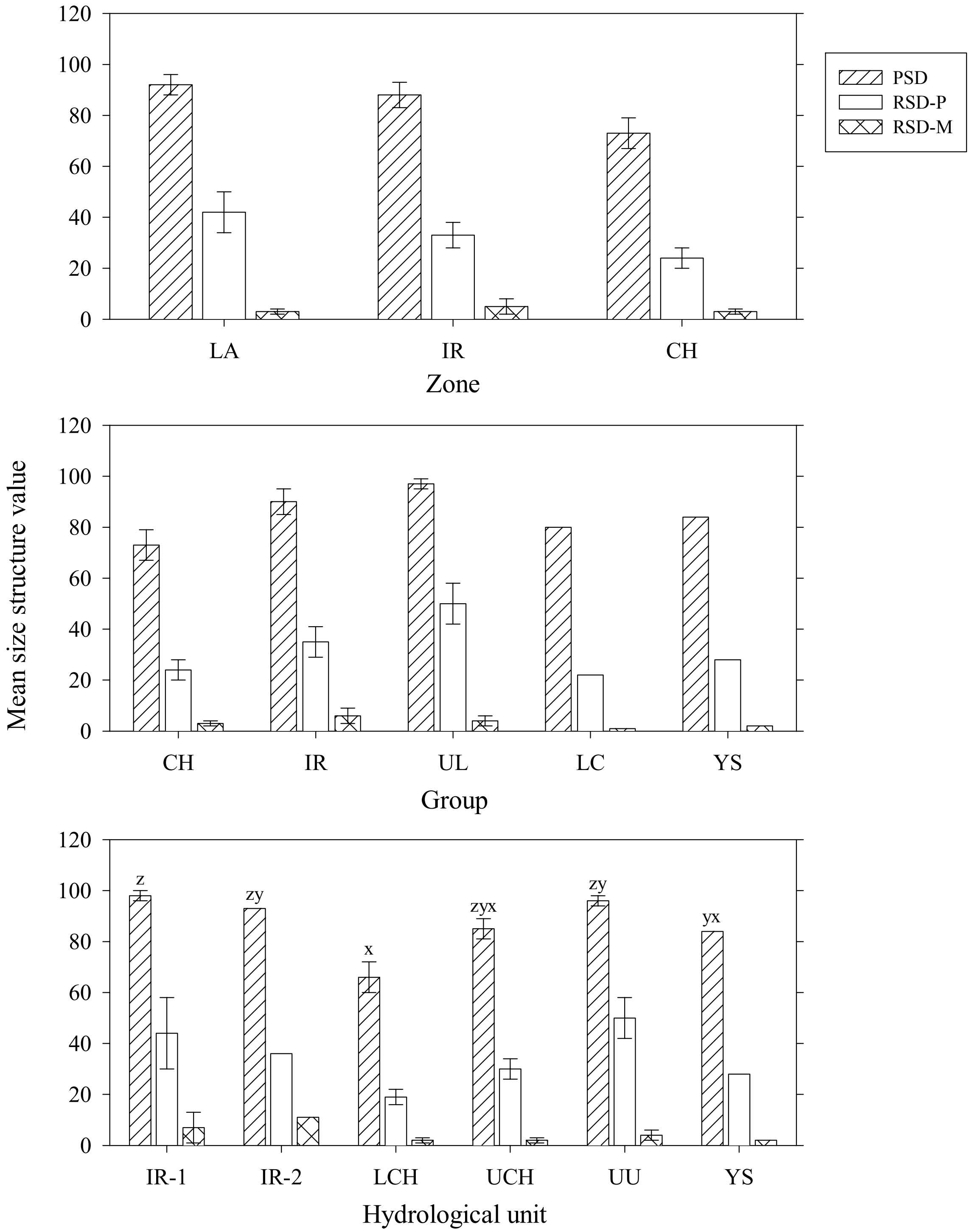

Figure 43. Mean size structure values for proportional stock density (PSD), relative stock density preferred (RSD-P), and relative stock density memorable (RSD-M) for common carp sampled in the Missouri and Yellowstone rivers by boat electrofishing from 1996-1998 by zone (top panel), group (middle panel), and hydrological unit (bottom panel). Error bars delineate one standard error. See text for acronym definitions.

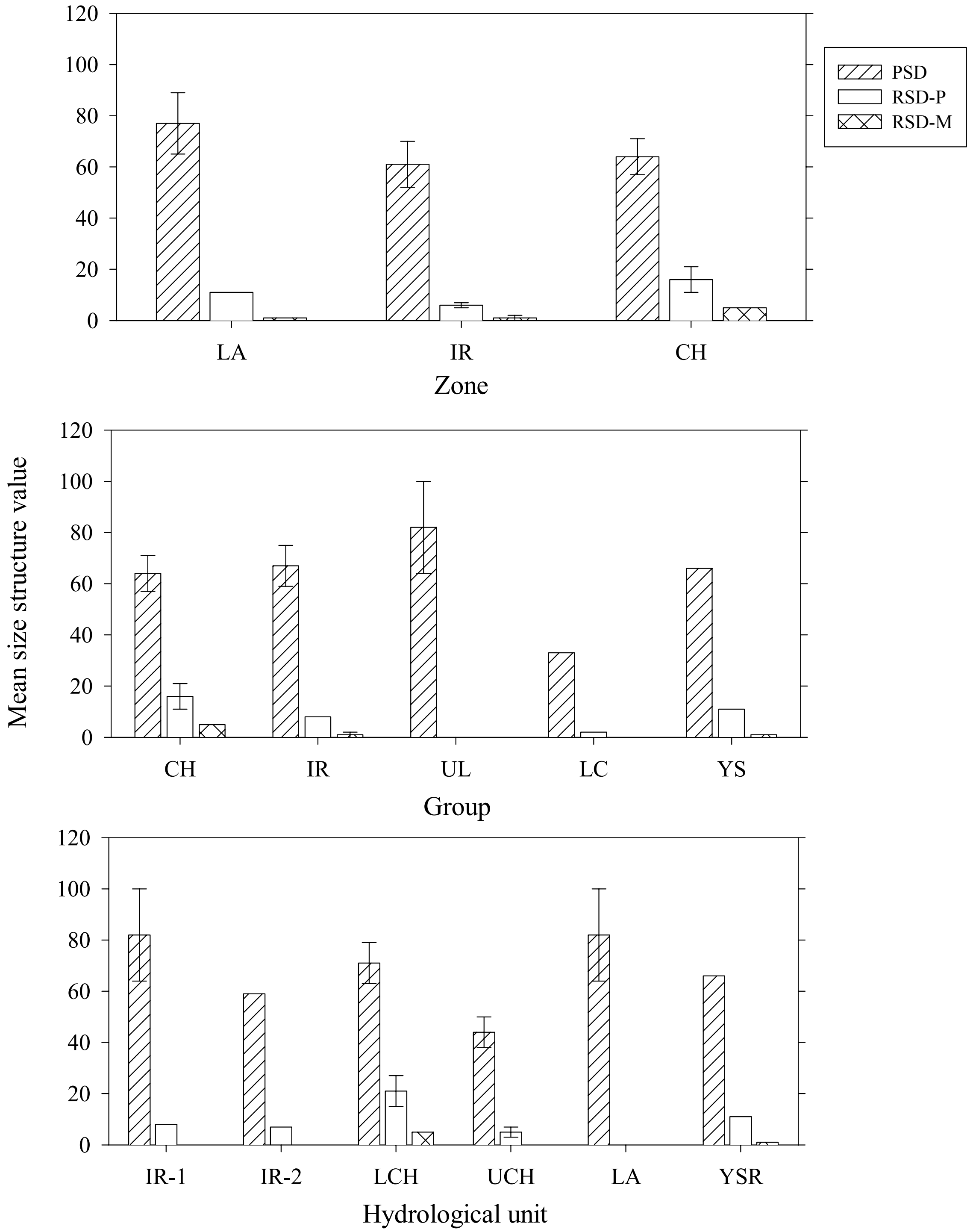

Figure 44. Mean size structure values for proportional stock density (PSD), relative stock density preferred (RSD-P), and relative stock density memorable (RSD-M) for channel catfish sampled in the Missouri and Yellowstone rivers by gill nets from 1996-1998 by zone (top panel), group (middle panel), and hydrological unit (bottom panel). Error bars delineate one standard error. See text for acronym definitions.

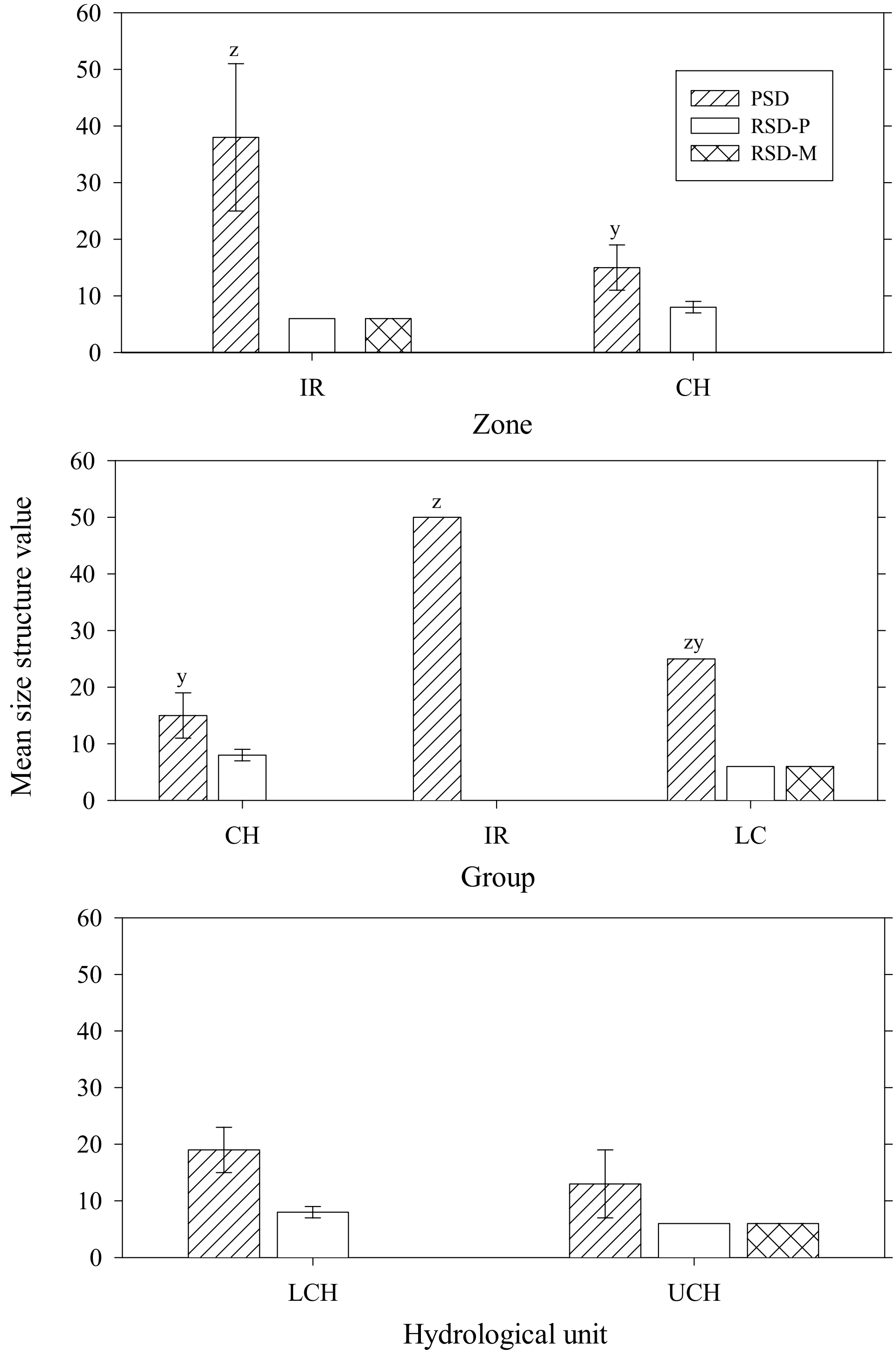

Figure 45. Mean size structure values for proportional stock density (PSD), relative stock density preferred (RSD-P), and relative stock density memorable (RSD-M) for flathead catfish sampled in the Missouri and Yellowstone rivers by boat electrofishing during 1996-1998 by zone (top panel), group (middle panel), and hydrological unit (bottom panel). Error bars delineate one standard error. See text for acronym definitions.

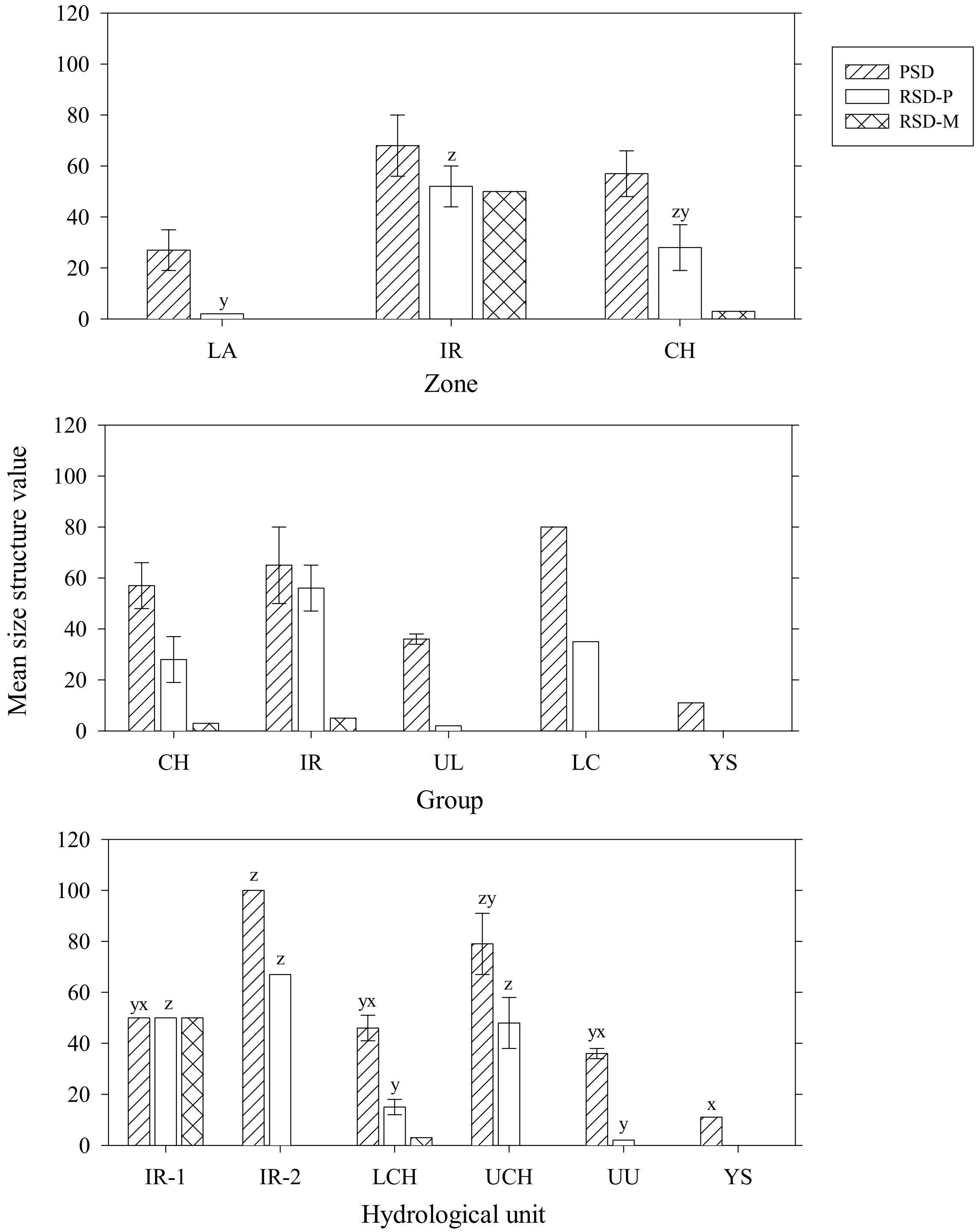

Figure 46. Mean size structure values for proportional stock density (PSD), relative stock density preferred (RSD-P), and relative stock density memorable (RSD-M) for freshwater drum sampled in the Missouri and Yellowstone rivers by boat electrofishing from 1996-1998 by zone (top panel), group (middle panel), and hydrological unit (bottom panel). Error bars delineate one standard error. See text for acronym definitions.

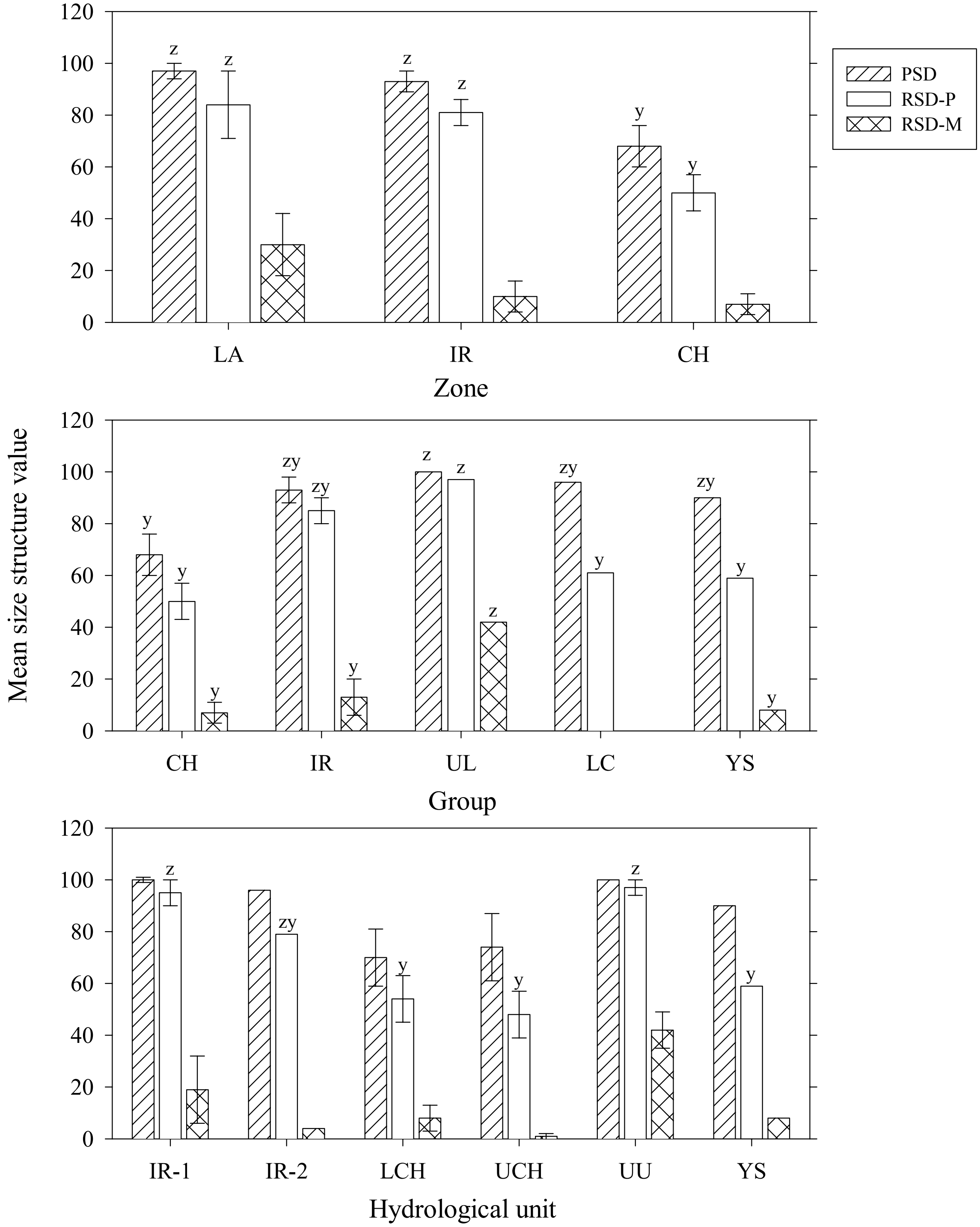

Figure 47. Mean size structure values for proportional stock density (PSD), relative stock density preferred (RSD-P), and relative stock density memorable (RSD-M) for river carpsuckers sampled in the Missouri and Yellowstone rivers by boat electrofishing from 1996-1998 by zone (top panel), group (middle panel), and hydrological unit (bottom panel). Error bars delineate one standard error. See text for acronym definitions.

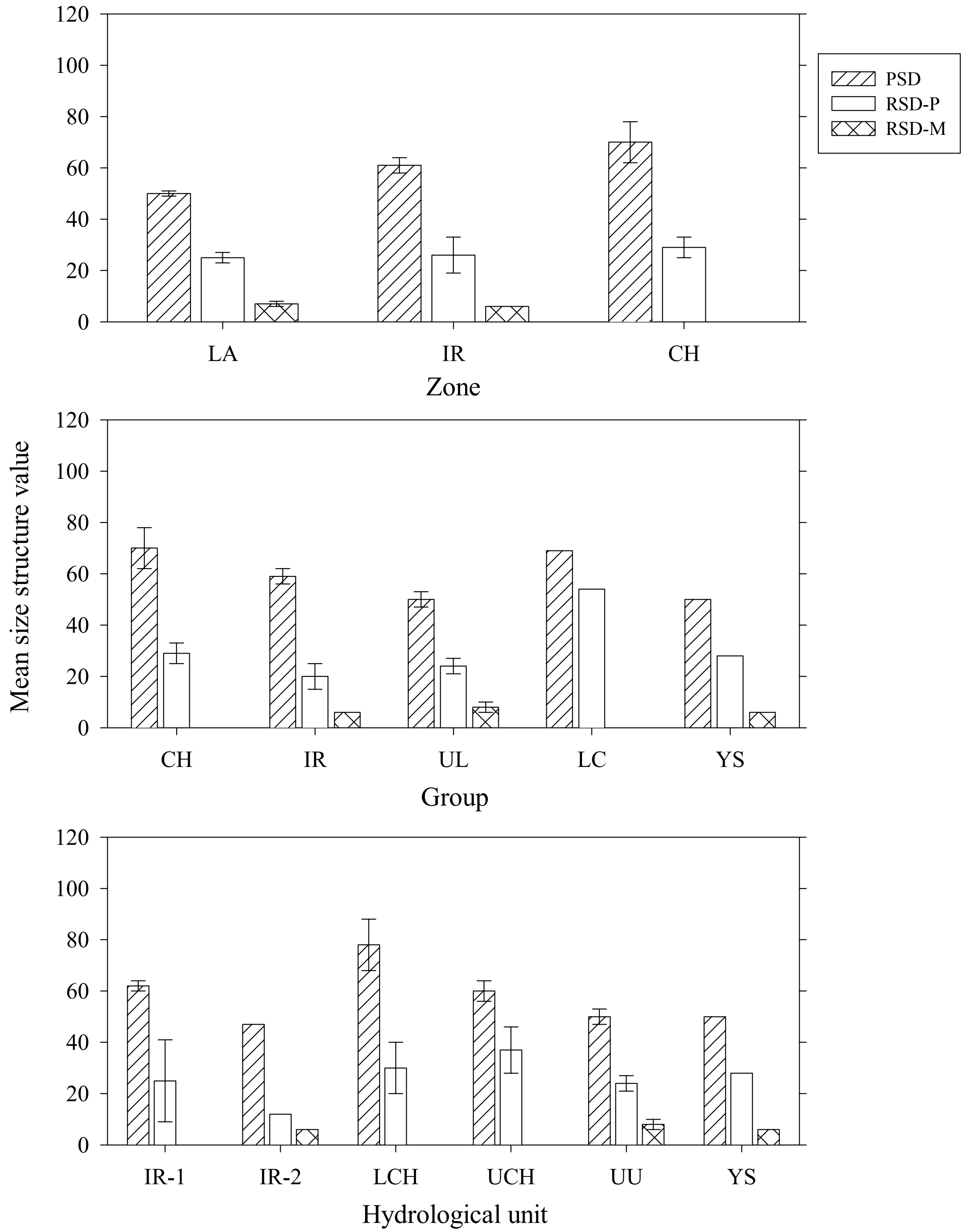

Figure 48. Mean size structure values for proportional stock density (PSD), relative stock density preferred (RSD-P), and relative stock density memorable (RSD-M) for sauger sampled in the Missouri and Yellowstone rivers by boat electrofishing from 1996-1998 by zone (top panel), group (middle panel), and hydrological unit (bottom panel). Error bars delineate one standard error. See text for acronym definitions.

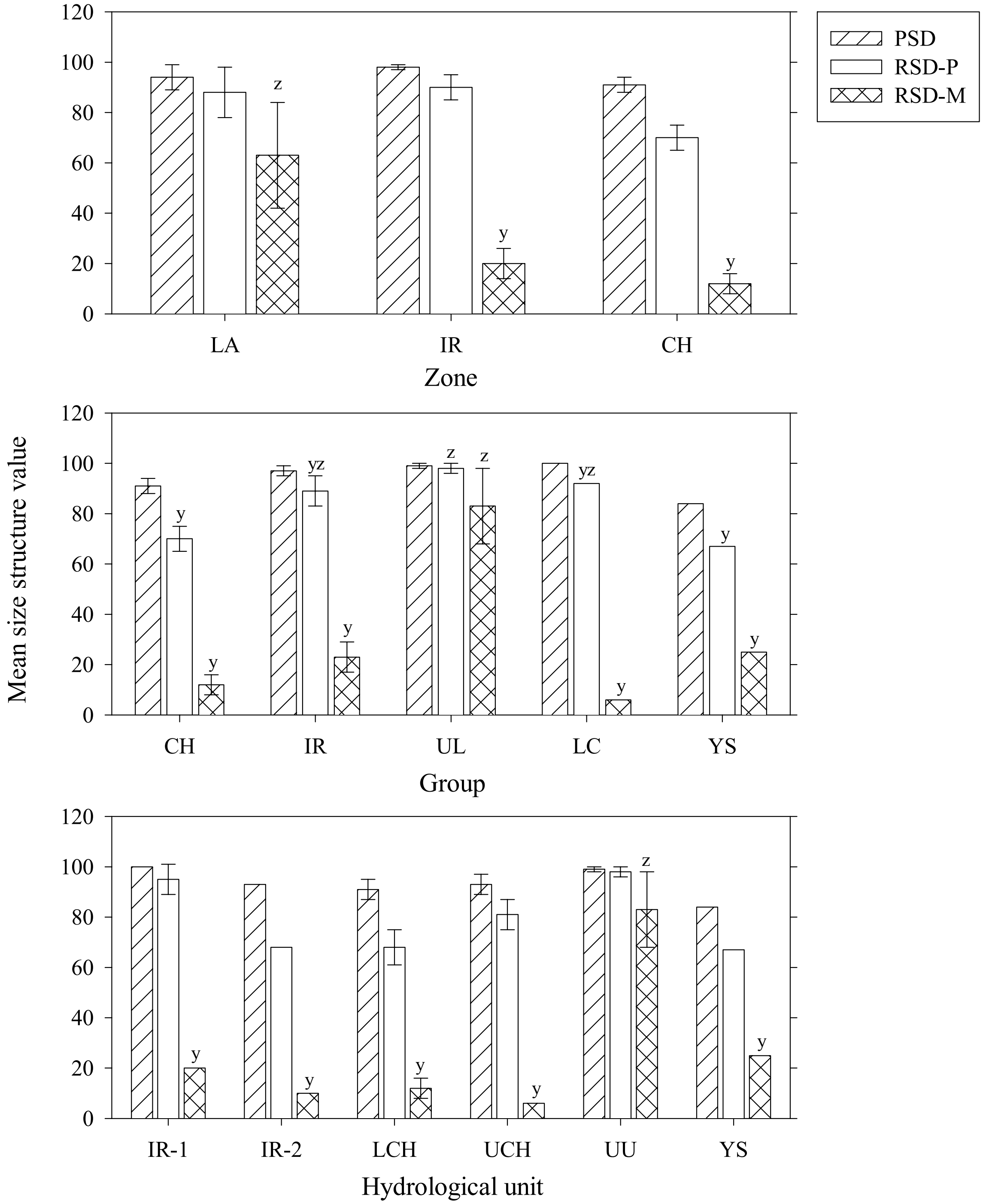

Figure 49. Mean size structure values for proportional stock density (PSD), relative stock density preferred (RSD-P), and relative stock density memorable (RSD-M) for shovelnose sturgeon sampled by drifting trammel nets from 1996-1998 in the Missouri and Yellowstone rivers by zone (top panel), group (middle panel), and hydrological unit (bottom panel). Error bars delineate one standard error. See text for acronym definitions.

Missouri River.

Survival

Total annual survival estimates were variable among species, segments, hydrological units, and groups (Table 15). Survival estimates varied longitudinally and were related to river kilometer (i.e., segments) for channel catfish (total annual survival = 0.837-0.0002[river kilometer] + 0.00000008 [river kilometer^2], P=0.06, R^2=0.75), freshwater drum (total annual survival = 0.657+0.00007[river kilometer], P=0.002, r^2=0.71), sauger (total annual survival = 0.548 + 0.00008[river kilometer], P=0.15, r^2=0.32), and shovelnose sturgeon (total annual survival = 0.770-0.00003 [river kilometer]+ 0.00000001 [river kilometer^2], P=0.001, R^2=0.85) (Figure 50). Interestingly, survival estimates tended to be lowest between river kilometers 496 and 915 (segments 19-23) for all species. Unsurprisingly, theoretical maximum age and maximum age of the sample were related to survival estimates and showed similar patterns (Table 15).

Survival of freshwater drum, sauger, and shovelnose sturgeon differed significantly among zones (Table 16). Survival was significantly lower in the channelized zone than the least-altered zone for freshwater drum, sauger, and shovelnose sturgeon (Table 15). Similarly, survival estimates were significantly lower in the channelized zone than the inter-reservoir group

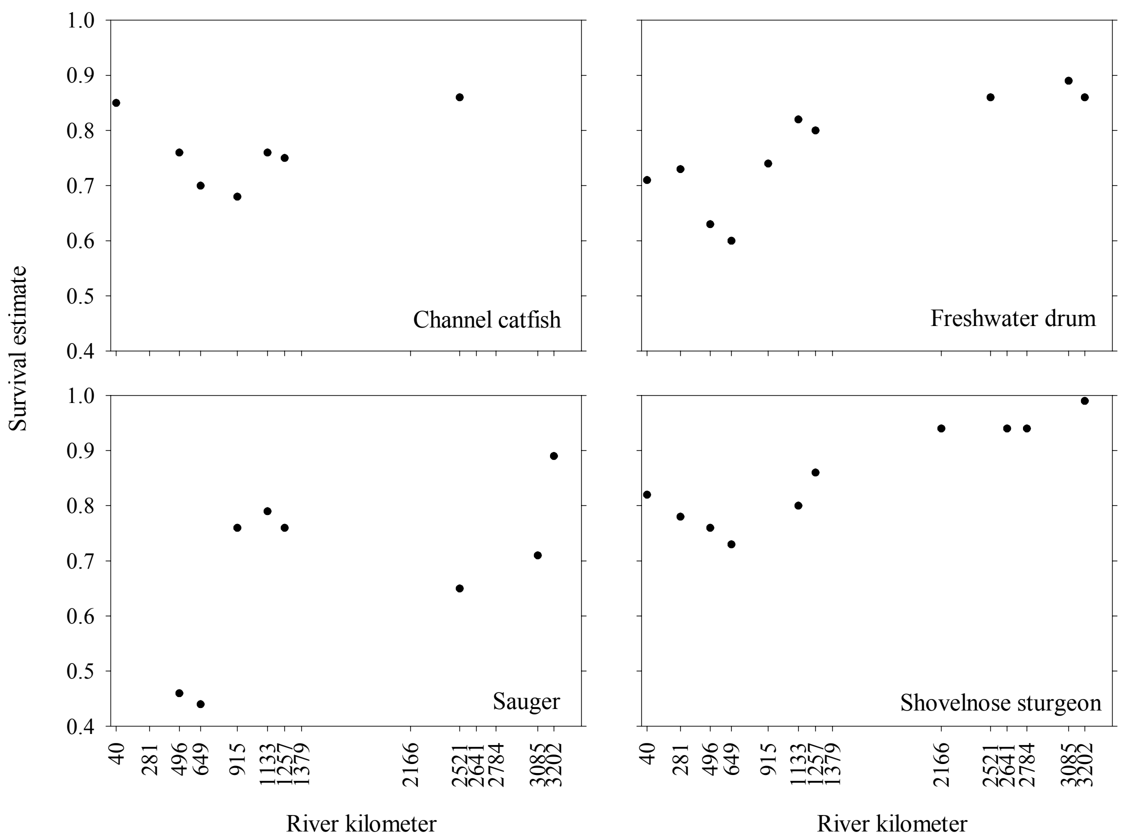

Figure 50. Total annual survival estimates by river kilometer for channel catfish, freshwater drum, sauger, and shovelnose sturgeon sampled in the Missouri River from 1996-1998. Total annual survival was estimated from pooling age-structure data from 1996 through 1998.

Table 15. Survival estimates, theoretical maximum age, age used, r^2, and P by species for segment, hydrological unit, and zone. Survival estimates, theoretical maximum age, r^2, and P are from catch curve analyses for fish sampled in the Missouri and Yellowstone rivers during 1996-1998. Note that segment 15 is also group Lewis and Clark (LC). See methods for all acronym definitions.

Species	Segment, hydrological unit, zone	Survival	Theoretical maximum age	Ages used	r^2	P
CNCF	9	0.88	28	1-14	0.30	0.05
	10	0.86	20	1-15	0.51	0.004
	15 (LC)	0.75	13	1-11	0.65	0.003
	17	0.76	12	1-8	0.61	0.02
	19	0.68	8	1-8	0.93	0.0001
	22	0.70	11	1-10	0.69	0.005
	23	0.76	13	1-8	0.31	0.15
	27	0.85	20	1-10	0.27	0.12
	LCH	0.76	18	1-10	0.61	0.007
	UCH	0.65	12	1-11	0.87	0.0001
	YS	0.88	28	1-14	0.30	0.05
	CH	0.71	16	1-10	0.73	0.002
	IR	0.82	26	1-15	0.65	0.0003
	LA	0.90	35	1-14	0.17	0.15
FWDM	3	0.86	22	2-22	0.70	0.0007
	5	0.89	23	0-17	0.35	0.03
	10	0.86	15	0-15	0.47	0.13
	15 (LC)	0.80	12	0-15	0.52	0.01
	17	0.72	7	0-8	0.47	0.13
	19	0.74	8	0-9	0.43	0.05
	22	0.60	8	0-9	0.74	0.001
	23	0.63	9	0-7	0.81	0.002
	25	0.73	12	0-14	0.86	0.0001
	27	0.71	12	0-12	0.83	0.0001

Species	Segment, hydrological unit, zone	Survival	Theoretical maximum age	Ages used	r^2	P
	LCH	0.65	12	0-14	0.87	0.0001
	UCH	0.75	13	0-15	0.68	0.0009
	CH	0.65	13	0-14	0.91	0.0001
	IR	0.89	24	0-27	0.40	0.01
	LA	0.84	22	0-22	0.84	0.0001
RVCS	9	0.73	12	0-11	0.58	0.0006
	19	0.60	7	0-7	0.95	0.0001
	22	0.61	9	0-7	0.98	0.0001
	25	0.70	9	0-9	0.58	0.03
	LCH	0.59	11	0-9	0.82	0.0007
	UCH	0.73	16	0-8	0.49	0.04
	YS	0.73	12	0-11	0.58	0.006
	CH	0.59	11	0-9	0.81	0.0009
	IR	0.74	17	0-11	0.44	0.03
	LA	0.73	13	0-11	0.57	0.008
SGER	3	0.89	15	1-16	0.71	0.009
	5	0.71	8	1-7	0.51	0.07
	10	0.65	7	1-7	0.88	0.002
	15 (LC)	0.76	8	1-7	0.59	0.04
	17	0.79	10	1-10	0.88	0.005
	19	0.76	7	1-7	0.41	0.12
	22	0.44	5	1-5	0.75	0.13
	23	0.46	5	1-5	0.76	0.13
	LCH	0.48	7	1-5	0.83	0.09
	UCH	0.67	10	1-10	0.86	0.0009
	UU	0.81	14	1-16	0.76	0.002
	YS	0.88	17	1-7	0.21	0.30
	CH	0.59	9	1-10	0.76	0.005

Species	Segment, hydrological unit, zone	Survival	Theoretical maximum age	Ages used	r^2	P
	IR	0.67	11	1-9	0.85	0.001
	LA	0.78	14	1-16	0.81	0.009
SNSG	3	0.99	46	8-34	0.66	0.27
	7	0.94	33	5-26	0.21	0.03
	8	0.94	25	5-27	0.31	0.02
	9	0.91	33	5-38	0.80	0.0001
	12	0.94	35	7-16	0.06	0.48
	15 (LC)	0.86	21	6-18	0.46	0.02
	17	0.80	20	6-19	0.73	0.0009
	22	0.73	17	5-15	0.72	0.0009
	23	0.76	18	5-17	0.61	0.002
	25	0.78	18	5-16	0.75	0.0003
	27	0.82	15	5-14	0.63	0.01
	IR-1	0.91	30	5-26	0.31	0.007
	IR-2	0.94	25	5-27	0.31	0.016
	LCH	0.69	19	5-17	0.79	0.0001
	UCH	0.79	21	5-19	0.55	0.002
	UU	0.97	63	5-37	0.11	0.08
	YS	0.91	33	5-38	0.80	0.0001
	CH	0.69	20	5-19	0.79	0.0001
	IR	0.90	37	5-28	0.49	0.0001
	LA	0.90	39	5-38	0.75	0.0001

Table 16. Probability and F values for comparisons of slopes from catch-curve regression lines by species and group for fish sampled in the Missouri and Yellowstone rivers during 1996-1998. If there was a significant difference in slope estimates among groups then analyses were paired by group.

Species	Group	F-value	P
Channel catfish	Overall	2.58	0.091
Freshwater drum	Overall	11.68	< 0.0001
	IR-LA	1.24	0.276
	CH-LA	19.23	0.0001
	CH-IR	25.33	< 0.0001
River carpsucker	Overall	1.17	0.326
Sauger	Overall	4.24	0.03
	IR-LA	3.46	0.086
	CH-LA	6.4	0.025
	CH-IR	0.86	0.372
Shovelnose sturgeon	Overall	16.52	< 0.0001
	IR-LA	0.04	0.838
	CH-LA	36.45	< 0.0001
	CH-IR	21.46	< 0.0001

for freshwater drum and shovelnose sturgeon (Tables 15 and 16).

Recruitment Deficiencies

Number of missing year classes (i.e., year-class failure) was highly variable among segments and species (Figure 51). In general, the number of missing year classes increased with river kilometer for channel catfish (number of missing year classes = -0.274+0.0013[river kilometer], P=0.003, r^2=0.55), freshwater drum (number of missing year classes = 1.00+0.001[river kilometer], P=0.022, r^2=0.39), and river carpsucker (number of missing year classes = -0.159+0.001[river kilometer], P=0.001, r^2=0.59) (Figure 51). Number of missing year classes decreased with increasing river kilometer for sauger (number of missing year classes = 3.63-0.0009[river kilometer], P=0.009, r^2=0.45). Number of missing year classes was highest for shovelnose sturgeon in the mid-river kilometers and was weakly correlated with river kilometer (number of missing year classes = 0.506+0.0007[river kilometer], P=0.07, r^2=0.24) – a polynomial model for shovelnose sturgeon did not improve the model.

Mean number of missing year classes differed significantly among zones for freshwater drum and shovelnose sturgeon (Figure 52). Mean number of missing year classes was lowest in the channelized zone and highest in the inter-reservoir zone for freshwater drum. Similarly, shovelnose sturgeon had the least number of missing year classes in the channelized zone (Figure 52).

Serial Discontinuity

Freshwater drum AG-0 in four of five IR segments was lower than predicted by the LA and CH segments (Table 17, Figure 22). AG-0 in segment 8 had relatively large negative PI and DD values, suggesting that AG-0 in segment 8 was more characteristic of populations in the segments furthest upstream than in the longitudinal position of segment 8. AG-0 for sand shiner in segment 15 had large positive PI and DD values (Table 18, Figure 22), sug-

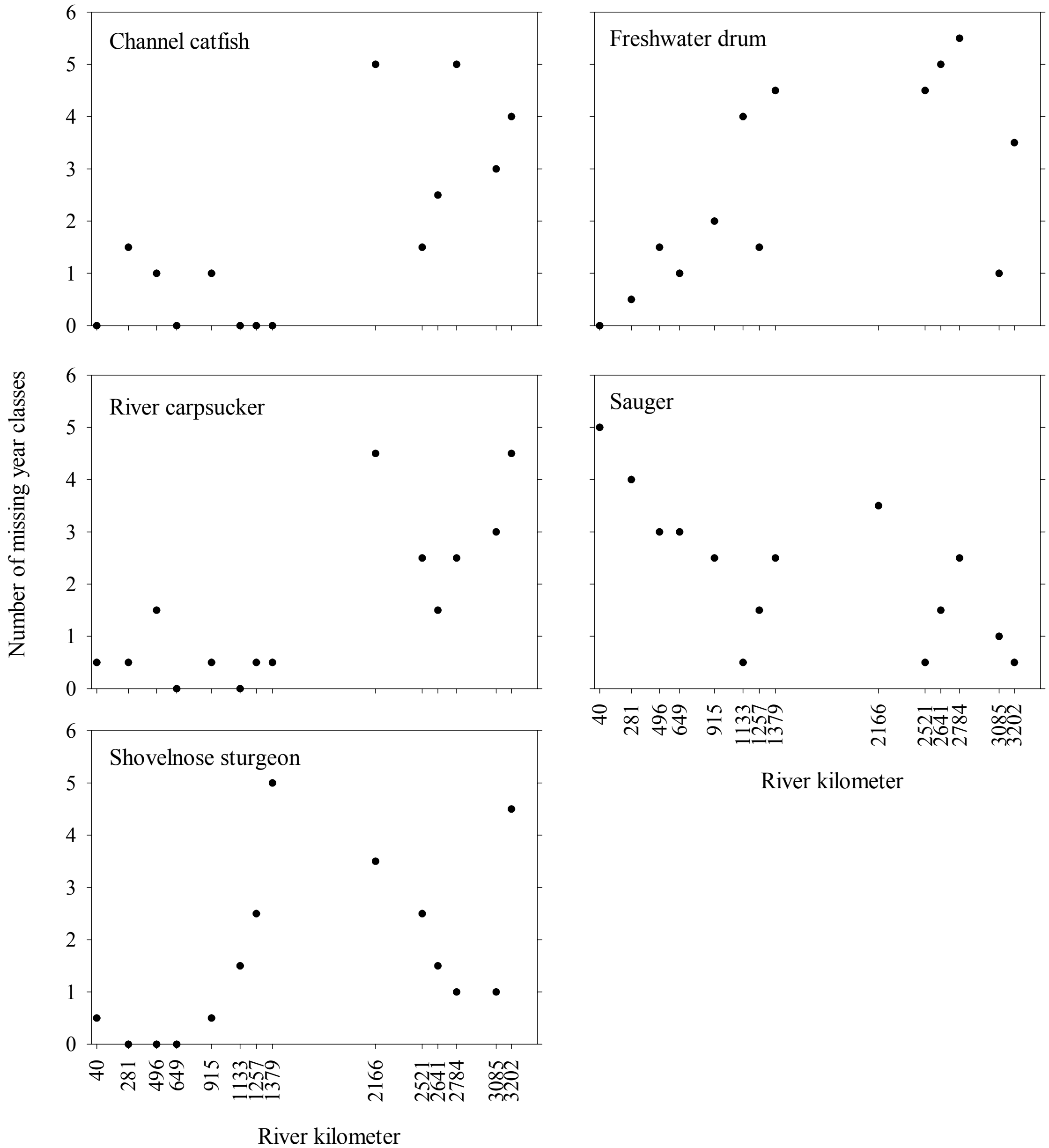

Figure 51. Number of missing year classes for channel catfish, freshwater drum, river carpsucker, sauger, and shovelnose sturgeon sampled in the Missouri River from 1997-1998. The data used for calculating the number of missing year classes was standardized by species (channel catfish, age 1-5; freshwater drum age 0-5; river carpsucker age 0-5; sauger, age 1-5; shovelnose sturgeon age 5-10). Missing year classes were calculated by year. Data for each year was considered a subsample not a replicate, thus no measure of variation could be estimated.

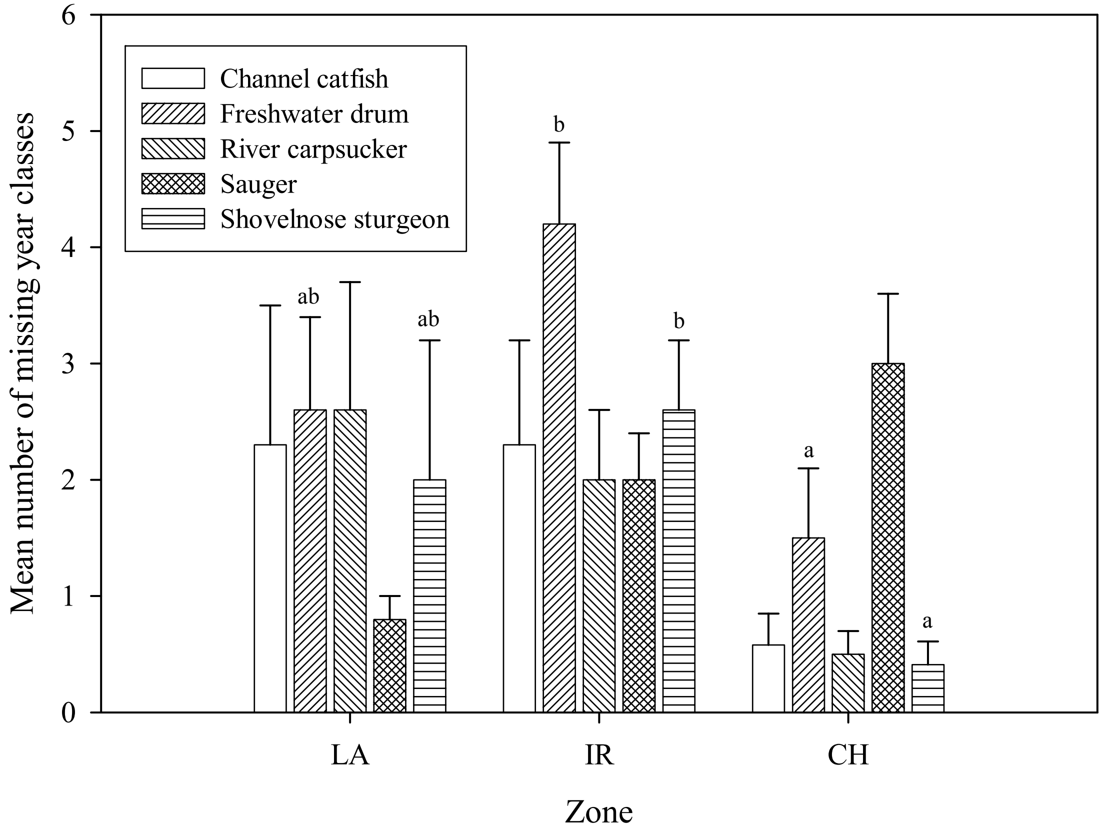

Figure 52. Mean number of missing year classes by zone for channel catfish, freshwater drum, river carpsucker, sauger, and shovelnose sturgeon sampled in the Missouri and Yellowstone rivers from 1997-1998. Error bars delineate one standard error.

Table 17. Observed and predicted segment midpoint and annual growth at age-0 (AG-0) values for freshwater drum in inter-reservoir segments of the Missouri River. Predicted values were derived from the AG-0 vs. distance regression shown in Figure 22. Parameter intensity and discontinuity distance were calculated as observed minus predicted. See Galat et al. 2001 for a detailed description of the serial discontinuity rationale and calculations.

Segment	Segment Midpoint	Observed AG-0	Predicted Midpoint	Predicted AG-0	Discontinuity Distance (km)	Parameter Intensity (AG-0)
Ft. Peck Lake						
7	2784	79	2918.4	80.3	-134.4	-1.3
8	2641	61	4755.1	81.7	-2114.1	-20.7
10	2521	86	2204.1	82.9	316.9	3.1
Lake Sakakawea						
12	2167	-	-	-	-	-
Lake Oahe, Sharpe, and Francis Case						
14	1380	91	1693.9	94.1	-313.9	-3.1
Lewis and Clark						
15	1257	91	1693.9	95.3	-436.9	-4.3

gesting that AG-0 in segment 15 was more characteristic of populations near the mouth than in the longitudinal position of segment 15. Five of six inter-reservoir segments had negative PI and DD for sauger AG-0 (Table 19, Figure 22). Negative PI and DD values were relatively large in segment 12, suggesting that sauger AG-0 in segment 12 was more characteristic of populations in the segments furthest up-

Table 18. Observed and predicted segment midpoint and annual growth at age-0 (AG-0) values for sand shiner in inter-reservoir segments of the Missouri River. Predicted values were derived from the AG-0 vs. distance regression shown in Figure 22. Parameter intensity and discontinuity distance were calculated as observed minus predicted. See Galat et al. 2001 for a detailed description of the serial discontinuity rationale and calculations.

Segment	Segment Midpoint	Observed AG-0	Predicted Midpoint	Predicted AG-0	Discontinuity Distance (km)	Parameter Intensity (AG-0)
Ft. Peck Lake						
7	2784	-	-	-	-	-
8	2641	-	-	-	-	-
10	2521	-	-	-	-	-
Lake Sakakawea						
12	2167	-	-	-	-	-
Lake Oahe, Sharpe, and Francis Case						
14	1380	-	-	-	-	-
Lewis and Clark						
15	1257	36	-529.4	29.9	1786.4	6.1

Table 19. Observed and predicted segment midpoint and annual growth at age-0 (AG-0) values for sauger in inter-reservoir segments of the Missouri River. Predicted values were derived from the AG-0 vs. distance regression shown in Figure 22. Parameter intensity and discontinuity distance were calculated as observed minus predicted. See Galat et al. 2001 for a detailed description of the serial discontinuity rationale and calculations.

Segment	Segment Midpoint	Observed AG-0	Predicted Midpoint	Predicted AG-0	Discontinuity Distance (km)	Parameter Intensity (AG-0)
Ft. Peck Lake						
7	2784	173	3154.2	181.9	-370.2	-8.9
8	2641	164	3529.2	185.3	-888.2	-21.3
10	2521	171	3237.5	188.2	-716.5	-17.2
Lake Sakakawea						
12	2167	147	4237.5	196.7	-2070.5	-49.7
Lake Oahe, Sharpe, and Francis Case						
14	1380	205	1820.8	215.6	-440.8	-10.6
Lewis and Clark						
15	1257	224	1029.2	218.5	227.8	5.5

stream than in the longitudinal position of segment 12. Four of five inter-reservoir segments had PI and DD values for smallmouth buffalo AG-0 characteristic of locations downstream (Table 20, Figure 22). Segment 7 was an exception, with AG-0 more characteristic of populations in the segments furthest upstream than in the longitudinal position of segment 7.

Shovelnose sturgeon AG-m in four of five IR segments was lower than predicted by the LA and CH segments (Table 21, Figure 25). AG-m in segments 10 and 14 were much lower than predicted, resembling AG-m expected near the mouth. AG-m in segment 15 was greater than predicted, resembling AG-m expected in the segments furthest upstream.

Table 20. Observed and predicted segment midpoint and annual growth at age-0 (AG-0) values for smallmouth buffalo in inter-reservoir segments of the Missouri River. Predicted values were derived from the AG-0 vs. distance regression shown in Figure 22. Parameter intensity and discontinuity distance were calculated as observed minus predicted. See Galat et al. 2001 for a detailed description of the serial discontinuity rationale and calculations.

Segment	Segment Midpoint	Observed AG-0	Predicted Midpoint	Predicted AG-0	Discontinuity Distance (km)	Parameter Intensity (AG-0)
Ft. Peck Lake						
7	2784	196	4305.4	170.6	-1521.4	25.4
8	2641	159	2089.8	168.2	551.2	-9.2
10	2521	132	473.1	166.2	2047.9	-34.2
Lake Sakakawea						
12	2167	-	-	-	-	-
Lake Oahe, Sharpe, and Francis Case						
14	1380	133	532.9	147.1	847.1	-14.1
Lewis and Clark						
15	1257	122	-125.7	145.1	1382.7	-23.1

Table 21. Observed and predicted segment midpoint and annual growth at length-at-maturity (AG-m) values for shovelnose sturgeon in inter-reservoir segments of the Missouri River. Predicted values were derived from the AG-m vs. distance regression shown in Figure 25. Parameter intensity and discontinuity distance were calculated as observed minus predicted. See Galat et al. 2001 for a detailed description of the serial discontinuity rationale and calculations.

Segment	Segment Midpoint	Observed AG-m	Predicted Midpoint	Predicted AG-m	Discontinuity Distance (km)	Parameter Intensity (AG-m)
Ft. Peck Lake						
7	2784	24	2153.8	24.8	630.2	-0.8
8	2641	-	-	-	-	-
10	2521	22	615.4	24.5	1905.6	-2.5
Lake Sakakawea						
12	2167	23	1384.6	24	782.4	-1
Lake Oahe, Sharpe, and Francis Case						
14	1380	21	-153.8	23	1533.8	-2
Lewis and Clark						
15	1257	25	2923.1	22.8	-1666.1	2.2

Freshwater drum L-m in segments 8 and 14 was much lower than predicted by the LA and CH segments (Table 22, Figure 28), resembling L-m expected in the segments furthest upstream. L-m in segments 7, 10 and 15 was slightly higher than predicted. Shovelnose sturgeon L-m in segment 10 was much lower than predicted by the LA and CH segments (Table 23, Figure 28). L-m in segment 12 was higher than predicted.

Serial discontinuity was evident for W_r of sauger. Mean W_r values were below predicted values for all inter-reservoir segments (Table 24). Thus, sauger populations in the inter-reservoir segments were more similar to sauger populations 1,005 to 4,517 km upstream, where W_r values were

Table 22. Observed and predicted segment midpoint and mean length at age of maturity (L-m) values for freshwater drum in inter-reservoir segments of the Missouri River. Predicted values were derived from the L-m vs. distance regression shown in Figure 28. Parameter intensity and discontinuity distance were calculated as observed minus predicted. See Galat et al. 2001 for a detailed description of the serial discontinuity rationale and calculations.

Segment	Segment Midpoint	Observed L-m	Predicted Midpoint	Predicted L-m	Discontinuity Distance (km)	Parameter Intensity (L-m)
Ft. Peck Lake						
7	2784	228	2384.3	217.8	399.7	10.2
8	2641	196	3639.2	221.5	-998.2	-25.5
10	2521	229	2345.1	224.5	175.9	4.5
Lake Sakakawea						
12	2167	-	-	-	-	-
Lake Oahe, Sharpe, and Francis Case						
14	1380	193	3756.9	253.6	-2376.9	-60.6
Lewis and Clark						
15	1257	272	658.8	256.7	598.2	15.3

Table 23. Observed and predicted segment midpoint and mean length at age of maturity (L-m) values for shovelnose sturgeon in inter-reservoir segments of the Missouri River. Predicted values were derived from the L-m vs. distance regression shown in Figure 28. Parameter intensity and discontinuity distance were calculated as observed minus predicted. See Galat et al. 2001 for a detailed description of the serial discontinuity rationale and calculations.

Segment	Segment Midpoint	Observed L-m	Predicted Midpoint	Predicted L-m	Discontinuity Distance (km)	Parameter Intensity (L-m)
Ft. Peck Lake						
7	2784	400	2864.5	402.2	-80.5	-2.2
8	2641	405	2681.3	406.1	-40.3	-1.1
10	2521	341	5025.6	409.4	-2504.6	-68.4
Lake Sakakawea						
12	2167	440	1399.3	419	767.7	21
Lake Oahe, Sharpe, and Francis Case						
14	1380	423	2022	440.5	-642	-17.5
Lewis and Clark						
15	1257	425	1948.7	443.9	-691.7	-18.9

lower for sauger populations. Parameter intensity values varied from -2 to -9 (Table 24).

Despite the relatively high coefficient of determination for the river kilometer-W_r relationship for shovelnose sturgeon, mean W_r exhibited serial discontinuity. Mean W_r values were below predicted levels at river kilometer 2,784 and 2,641 (below Ft. Peck Reservoir; inter-reservoir segments 7 and 8; Table 25). Similarly, mean W_r values were below predicted levels for inter-reservoir segments 12 and 15 (Table 25). Parameter intensity values varied from -4 to -9 for inter-reservoir segments 7, 8, 12, and 15. Shovelnose sturgeon populations at segments 7, 8, 12, and 15 were more similar to shovelnose sturgeon 466 to 1,213 km downstream (i.e., discontinuity distance; Table 25). Conversely, mean W_r values were above predicted levels for inter-reservoir segments 10 and 14 (Table

Table 24. Observed and predicted segment and mean relative weight *(W_r)* values for stock-length sauger. The predicted values were derived from the segment-W_r regression from data collected on sauger in the Missouri River from 1996-1998. Parameter intensity and discontinuity distance were calculated as observed minus predicted.

Segment	Segment Midpoint	Observed W_r	Predicted Midpoint	Predicted W_r	Discontinuity Distance (km)	Parameter Intensity (W_r)
Ft. Peck Lake						
7	2784	73	6684	81	-3900	-8
8	2641	73	6684	81	-4043	-8
10	2521	79	3526	81	-1005	-2
Lake Sakakawea						
12	2167	73	6684	82	-4517	-9
Lake Oahe, Sharpe, and Francis Case						
14	1380	76	5105	83	-3725	-7
Lewis and Clark						
15	1257	80	3000	84	-1743	-4

Table 25. Observed and predicted segment and mean relative weight *(W_r)* values for preferred-length shovelnose sturgeon. The predicted values were derived from the segment-W_r regression from data collected on shovelnose sturgeon in the Missouri River from 1996-1998. Parameter intensity and discontinuity distance were calculated as observed minus predicted.

Segment	Segment Midpoint	Observed W_r	Predicted Midpoint	Predicted W_r	Discontinuity Distance (km)	Parameter Intensity (W_r)
Ft. Peck Lake						
7	2784	94	1571	103	1213	-9
8	2641	95	1701	102	940	-7
10	2521	106	3130	101	-609	5
Lake Sakakawea						
12	2167	95	1701	99	466	-4
Lake Oahe, Sharpe, and Francis Case						
14	1380	103	2740	93	-1360	10
Lewis and Clark						
15	1257	84	272	92	985	-8

25). Discontinuity distance values indicated that shovelnose populations in segment 10 and 14 were more similar to shovelnose sturgeon 609 to 1,360 km upstream.

Survival estimates exhibited serial discontinuity for freshwater drum, shovelnose sturgeon, and sauger (Tables 26-28). However, the difference between observed and predicted survival estimates was minimal for shovelnose sturgeon and freshwater drum. Similarly, discontinuity distance values were low for freshwater drum and shovelnose sturgeon (Tables 26 and 28). Parameter intensity and discontinuity distance were relatively high for sauger, but segments 10 and 15 exhibited opposite patterns (Table 27). The observed survival rate was higher than predicted for segment 15. Consequently, discontinuity distance indicated that survival of the sauger population in segment 15 was similar to populations 1,192 km upstream.

Number of missing year classes exhib-

Table 26. Observed and predicted segment and survival estimates for freshwater drum. The predicted values were derived from the segment-survival regression from data collected on freshwater drum in the Missouri River from 1996-1998. Parameter intensity and discontinuity distance were calculated as observed minus predicted.

Segment	Segment Midpoint	Observed Survival	Predicted Midpoint	Predicted Survival	Discontinuity Distance (km)	Parameter Intensity (Survival)
Ft. Peck Lake						
10	2521	0.86	2836	0.84	-315	0.02
Lewis and Clark						
15	1257	0.80	1940	0.75	-683	0.05

Table 27. Observed and predicted segment and survival estimates sauger. The predicted values were derived from the segment-survival regression from data collected on sauger in the Missouri River from 1996-1998. Parameter intensity and discontinuity distance were calculated as observed minus predicted.

Segment	Segment Midpoint	Observed Survival	Predicted Midpoint	Predicted Survival	Discontinuity Distance (km)	Parameter Intensity (Survival)
10	2521	0.65	1327	0.76	1194	-0.11
Lewis and Clark						
15	1257	0.76	2449	0.64	-1192	0.12

Table 28. Observed and predicted segment and survival estimates for shovelnose sturgeon. The predicted values were derived from the segment- survival regressions from data collected on shovelnose sturgeon in the Missouri River from 1996-1998. Parameter intensity and discontinuity distance were calculated as observed minus predicted.

Segment	Segment Midpoint	Observed Survival	Predicted Midpoint	Predicted Survival	Discontinuity Distance (km)	Parameter intensity (Survival)
Ft. Peck Lake						
7	2784	0.94	2754	0.94	30	0
8	2641	0.94	2754	0.93	-113	0.01
Lake Sakakawea						
12	2167	0.94	2754	0.9	-587	0.04
Lewis and Clark						
15	1257	0.86	1594	0.83	-337	0.03

ited discontinuity, but was highly variable among segments, species, and segments within species (Tables 29-32). For example, discontinuity distance varied from 24 to 4,328 and parameter intensity varied from 0 to 4. In general, observed number of missing year classes was less than or equal to predicted number of missing year classes for channel catfish and river carpsucker (Tables 29 and 30). Conversely, observed number of missing year classes was often greater than predicted for sauger and shovelnose sturgeon (Tables 31 and 32). For example, shovelnose sturgeon populations in segments 10, 12, 14, and 15 had number of missing year classes similar to populations 409 to 4,328 kilometers upstream where number of missing year classes was greater.

Segment 12 (below Lake Sakakawea) had the greatest percentage of negative PIs of all the inter-reservoir segments (Table 33). Conversely, segments 15 (below Lewis and Clark Lake) and 10 (below Ft. Peck Lake) had the smallest percentages of negative PIs. The growth metrics and W_r had negative PI for most species and segments, missing year classes had a mixture of negative and positive PIs, while survival PIs were mostly positive (Table 33).

Table 29. Observed and predicted segment and number of missing year classes for channel catfish. The predicted values were derived from the segment-number of missing year class regression from data collected on channel catfish in the Missouri River from 1996-1998. Parameter intensity and discontinuity distance were calculated as observed minus predicted.

Segment	Segment Midpoint	Observed Survival	Predicted Midpoint	Predicted Survival	Discontinuity Distance (km)	Parameter intensity (Survival)
Ft. Peck Lake						
10	2521	2	1960	3	561	-1
Lake Sakakawea						
12	2167	5	4960	2	-2793	3
Lake Oahe, Sharpe, and Francis Case						
14	1380	0	-40	1	1420	-1
Lewis and Clark						
15	1257	0	-40	1	1297	-1

Table 30. Observed and predicted segment and number of missing year classes for river carpsucker. The predicted values were derived from the segment-number of missing year class regression from data collected on river carpsucker in the Missouri River from 1996-1998. Parameter intensity and discontinuity distance were calculated as observed minus predicted.

Segment	Segment Midpoint	Observed Survival	Predicted Midpoint	Predicted Survival	Discontinuity Distance (km)	Parameter intensity (Survival)
Ft. Peck Lake						
7	2784	3	2808	3	-24	0
8	2641	2	1899	3	742	-1
10	2521	3	2808	3	-287	0
Lake Sakakawea						
12	2167	5	4626	2	-2459	3
Lake Oahe, Sharpe, and Francis Case						
14	1380	1	990	1	390	0
Lewis and Clark						
15	1257	1	990	1	267	0

Table 31. Observed and predicted segment and number of missing year classes for sauger. The predicted values were derived from the segment-number of missing year class regression from data collected on sauger in the Missouri River from 1996-1998. Parameter intensity and discontinuity distance were calculated as observed minus predicted.

Segment	Segment Midpoint	Observed Survival	Predicted Midpoint	Predicted Survival	Discontinuity Distance (km)	Parameter intensity (Survival)
Ft. Peck Lake						
7	2784	3	1270	1	1514	2
8	2641	2	2270	1	371	1
10	2521	1	3720	1	-1199	0
Lake Sakakawea						
12	2167	4	270	2	1897	2
Lake Oahe, Sharpe, and Francis Case						
14	1380	3	1270	2	110	1
Lewis and Clark						
15	1257	2	2270	3	-1013	-1

Table 32. Observed and predicted segment and number of missing year classes for shovelnose sturgeon. The predicted values were derived from the segment-number of missing year class regression from data collected on shovelnose sturgeon in the Missouri River from 1996-1998. Parameter intensity and discontinuity distance were calculated as observed minus predicted.

Segment	Segment Midpoint	Observed Survival	Predicted Midpoint	Predicted Survival	Discontinuity Distance (km)	Parameter intensity (Survival)
Ft. Peck Lake						
7	2784	1	1126	2	1658	-1
8	2641	2	1819	2	822	0
10	2521	3	2930	2	-409	1
Lake Sakakawea						
12	2167	4	4041	2	-1874	2
Lake Oahe, Sharpe, and Francis Case						
14	1380	5	5708	1	-4328	4
Lewis and Clark						
15	1257	3	2930	1	-1673	2

Relationships Among Growth, Condition, Size Structure, Survival and Recruitment

Correlation Analysis by Species

To examine relationships among all variables, we calculated all pair-wise Pearson correlation coefficients by species using segment-level estimates of variables (Tables 34-38). Because of data limitations, these correlation matrices were attempted only for channel catfish, freshwater drum, river carpsucker, sauger and shovelnose sturgeon. Significant correlations included both positive and negative relationships in all these species except river carpsucker, in which all relationships were positive.

In channel catfish, AG-0 was negatively correlated with Survival and positively correlated with MYC. AG-m was positively correlated with L-m, W_r S-Q and RSD-P, but negatively correlated with Survival and MYC. L-m was negatively correlated with Surv, and W_r S-Q was posi-

Table 33. Summary of the sign of parameter intensities (PI) for population metrics in inter-reservoir segments of the Missouri River. Negative PI is represented by "-", positive PI by "+", zero PI by "0", and no value by ".". Species are abbreviated as follows: cncf=channel catfish, fwdm=freshwater drum, rvcs=river carpsucker, snsn=sand shiner, sger=sauger, snsg=shovelnose sturgeon, smbf=smallmouth buffalo. Population metrics are abbreviated as follows: W_r=relative weight, S=survival, MYC=missing year classes, AG-0=annual growth at age-0, AG-m=annual growth at length at maturity, L-m=mean length at age of maturity. Regression sign indicates whether the slope of the regression of the population metric vs. distance from the mouth of the Missouri River is positive or negative. Percent negative indicates the percentage of negative PI values.

	cncf	fwdm			rvcs	snsn	snsg					sger				smbf	
Segment	MYC	AG-0	L-m	S	MYC	AG-0	AG-m	L-m	W_r	S	MYC	AG-0	W_r	S	MYC	AG-0	% Neg.
7	.	-	+	.	0	.	-	-	-	0	+	-	-	.	-	+	50
8	.	-	-	.	+	.	.	-	-	+	0	-	-	.	-	-	73
10	+	+	+	+	0	.	-	-	+	.	-	-	-	-	0	-	50
12	-	.	.	.	-	.	-	+	-	+	-	-	-	.	-	.	80
14	+	-	-	.	0	.	-	-	+	.	-	-	-	.	-	-	75
15	+	-	+	+	0	+	+	-	-	+	-	+	-	+	+	-	38
Regression Sign	+	-	-	+	+	-	+	-	+	+	+	-	-	+	-	+	
Percent Negative	25	80	40	0	17	0	80	83	67	0	67	83	100	50	67	80	

Table 34. Pearson correlations of channel catfish growth, condition, size structure, survival and recruitment variables in segments of the Missouri and lower Yellowstone rivers. Variables are abbreviated as follows: AG-0=annual growth at age-0, AG-m=annual growth at age at maturity, L-m=mean length at age of maturity, W_r S-Q=condition of stock-quality size fish, W_r Q-P=condition of quality-preferred sized fish, W_r P-M=condition of preferred-memorable sized fish, PSD=proportional stock density, RSD-P=relative stock density-preferred, Surv=survival, MYC=number of missing year classes. Numbers below correlation coefficients are sample size (n). Asterisks indicate *P*-value levels as follows: * 0.01<=*P*<0.05, ** 0.001<=*P*<0.01, *** 0.0001<=*P*<0. 001, **** *P*<0.0001. Dashes indicate n<5.

	Variable								
Variable	AG-m	L-m	W_r S-Q	W_r Q-P	W_r P-M	PSD	RSD-P	Surv	MYC
AG-0	-0.17	-0.01	0.07	0.08	-	0.06	-0.49	-0.74*	0.57*
	15	15	13	15		14	14	8	15
AG-m		0.94****	0.67*	0.48	-	-0.11	0.55*	-0.78*	-0.52*
		15	13	15		14	14	8	15
L-m			0.44	0.42	-	-0.11	0.51	-0.83*	-0.35
			13	15		14	14	8	15
W_r S-Q				0.67*	-	-0.02	0.09	-0.4	-0.3
				13		12	12	8	13
W_r Q-P					-	-0.24	-0.11	-0.56	-0.18
						14	14	8	15
W_r P-M						-	-	-	-
PSD							0.27	0.49	0.51
							14	8	14
RSD-P								-0.23	-0.23
								8	14
Surv									<0.01
									8

Table 35. Pearson correlations of freshwater drum growth, condition, size structure, survival and recruitment variables in segments of the Missouri and lower Yellowstone rivers. Variables are abbreviated as follows: AG-0=annual growth at age-0, AG-m=annual growth at age at maturity, L-m=mean length at age of maturity, W_r S-Q=condition of stock-quality size fish, W_r Q-P=condition of quality-preferred sized fish, W_r P-M=condition of preferred-memorable sized fish, PSD=proportional stock density, RSD-P=relative stock density-preferred, Surv=survival, MYC=number of missing year classes. Numbers below correlation coefficients are sample size (n). Asterisks indicate *P*-value levels as follows: * 0.01<=*P*<0.05, ** 0.001<=*P*<0.01, *** 0.0001<=*P*<0. 001, **** *P*<0.0001. Dashes indicate n<5.

	Variable								
Variable	AG-m	L-m	W_r S-Q	W_r Q-P	W_r P-M	PSD	RSD-P	Surv	MYC
AG-0	0.80**	0.81***	-0.74*	-0.75	-	0.31	0.78*	-0.75*	-0.38
	13	13	8	6		8	8	10	14
AG-m		0.92****	-0.55	-0.66	-	0.05	0.6	-0.79**	-0.41
		13	7	6		8	8	10	13
L-m			-0.73	-0.91*	-	0.34	0.66	-0.84**	-0.43
			7	6		8	8	10	13
W_r S-Q				0.91*	-	-0.29	-0.75	0.91**	0.53
				5		6	6	7	8
W_r Q-P					-	-0.87*	-0.97**	0.5	0.31
						6	6	6	6
W_r P-M						-	-	-	-
PSD							0.68	0.01	-0.15
							8	8	8
RSD-P								-0.31	0.01
								8	8
Surv									0.4
									10

Table 36. Pearson correlations of river carpsucker growth, condition, size structure, survival and recruitment variables in segments of the Missouri and lower Yellowstone rivers. Variables are abbreviated as follows: AG-0=annual growth at age-0, AG-m=annual growth at age at maturity, L-m=mean length at age of maturity, W_r S-Q=condition of stock-quality size fish, W_r Q-P=condition of quality-preferred sized fish, W_r P-M=condition of preferred-memorable sized fish, PSD=proportional stock density, RSD-P=relative stock density-preferred, Surv=survival, MYC=number of missing year classes. Numbers below correlation coefficients are sample size (n). Asterisks indicate *P*-value levels as follows: * 0.01<=*P*<0.05, ** 0.001<=*P*<0.01, *** 0.0001<=*P*<0. 001, **** *P*<0.0001. Dashes indicate n<5.

				Variable					
Variable	AG-m	L-m	W_r S-Q	W_r Q-P	W_r P-M	PSD	RSD-P	Surv	MYC
AG-0	0.26	0.26	-0.37	-0.28	-0.16	-0.3	-0.3	-	-0.31
	15	15	7	10	15	14	14		15
AG-m		0.75**	-0.71	-0.4	0.21	0.17	0.41	-	0.61*
		15	7	10	15	14	14		15
L-m			-0.28	0.33	0.14	0.44	0.66*		0.71**
			7	10	15	14	14		15
W_r S-Q				0.43	0.17	0.13	-0.14	-	0.18
				7	7	7	7		7
W_r Q-P					0.48	0.41	0.4	-	0.61
					10	10	10		10
W_r P-M						-0.07	0.03	-	0.26
						14	14		15
PSD							0.87****	-	0.58
							14		14
RSD-P								-	0.84****
									14
Surv									-

Table 37. Pearson correlations of sauger growth, condition, size structure, survival and recruitment variables in segments of the Missouri and lower Yellowstone rivers. Variables are abbreviated as follows: AG-0=annual growth at age-0, AG-m=annual growth at age at maturity, L-m=mean length at age of maturity, W_r S-Q=condition of stock-quality size fish, W_r Q-P=condition of quality-preferred sized fish, W_r P-M=condition of preferred-memorable sized fish, PSD=proportional stock density, RSD-P=relative stock density-preferred, Surv=survival, MYC=number of missing year classes. Numbers below correlation coefficients are sample size (n). Asterisks indicate *P*-value levels as follows: * 0.01<=*P*<0.05, ** 0.001<=*P*<0.01, *** 0.0001<=*P*<0. 001, **** *P*<0.0001. Dashes indicate n<5.

				Variable					
Variable	AG-m	L-m	W_r S-Q	W_r Q-P	W_r P-M	PSD	RSD-P	Surv	MYC
AG-0	0.78**	0.66	0.28	0.26	0.62	0.78**	0.62	-0.47	0.32
	14	6	6	8	6	10	10	8	14
AG-m		0.82*	0.29	0.53	0.64	0.37	0.76*	-0.04	-0.01
		6	6	8	6	10	10	8	14
L-m			-0.26	-0.15	-	-0.08	0.3	-	0.42
			6	6		6	6		6
W_r S-Q				0.68	-	-0.39	0.8	-	-0.97**
				6		6	6		6
W_r Q-P					-	0.22	0.62	-	0.46
						6	6		8
W_r P-M						0.24	0.1	-	-0.53
						5	5		6
PSD							0.36	-0.71	0.81**
							10	6	10
RSD-P								-0.28	-0.02
								6	10
Surv									-0.74*
									8

Table 38. Pearson correlations of shovelnose sturgeon growth, condition, size structure, survival and recruitment variables in segments of the Missouri and lower Yellowstone rivers. Variables are abbreviated as follows: AG-0=annual growth at age-0, AG-m=annual growth at age at maturity, L-m=mean length at age of maturity, W_r S-Q=condition of stock-quality size fish, W_r Q-P=condition of quality-preferred sized fish, W_r P-M=condition of preferred-memorable sized fish, PSD=proportional stock density, RSD-P=relative stock density-preferred, Surv=survival, MYC=number of missing year classes. Numbers below correlation coefficients are sample size (n). Asterisks indicate *P*-value levels as follows: * 0.01<=*P*<0.05, ** 0.001<=*P*<0.01, *** 0.0001<=*P*<0. 001, **** *P*<0.0001. Dashes indicate n<5.

				Variable					
Variable	AG-m	L-m	W_r S-Q	W_r Q-P	W_r P-M	PSD	RSD-P	Surv	MYC
AG-0	-0.35	0.55	-	0.13	-0.32	0.15	0.06	0.05	0.2
	12	15		9	14	15	15	11	15
AG-m		-0.43	-	0.8	0.27	0.2	0.27	0.59	0.13
		12		6	11	12	12	9	12
L-m			-	-0.47	-0.76**	-0.22	-0.42	-0.82**	-0.27
				9	14	15	15	11	15
W_r S-Q				-	-	-	-	-	-
W_r Q-P					0.70*	-0.02	0.02	0.55	-0.24
					9	9	9	8	9
W_r P-M						0.18	0.51	0.80**	0.33
						14	14	10	14
PSD							0.80***	0.31	0.56*
							15	11	15
RSD-P								0.59	0.74**
								11	15
Surv									0.73*
									11

tively correlated with W_r Q-P (Figure 53).

In freshwater drum, AG-0 was positively correlated with AG-m, L-m and RSD-P, and negatively correlated with W_r S-Q and Survival. AG-m was positively correlated with L-m and negatively correlated with Survival. L-m was negatively correlated with W_r Q-P and Survival. W_r S-Q was positively correlated with W_r Q-P and Survival. W_r Q-P was negatively correlated with PSD and RSD-P (Figure 54).

In river carpsucker, AG-m was positively correlated with L-m and MYC. L-m was positively correlated with RSD-P and MYC. PSD was positively correlated with RSD-P, and RSD-P was positively correlated with MYC (Figure 55).

In sauger, AG-0 was positively correlated with AG-m and PSD. AG-m was positively correlated with L-m and RSD-P. W_r S-Q was negatively correlated with MYC, PSD was positively correlated with MYC, and Survival was negatively correlated with MYC (Figure 56).

In shovelnose sturgeon, L-m was negatively correlated with W_r P-M and Survival. W_r Q-P was positively correlated with W_r P-M, and W_r P-M was positively correlated with Survival. PSD was positively correlated with RSD-P and MYC. RSD-P was positively correlated with MYC, and Survival was positively correlated with MYC (Figure 57).

Multivariate Analyses

Relative weight, size structure, survival, missing year classes, and mean back-calculated length at age of maturity for all species (i.e., freshwater drum, river carpsucker, sauger, and shovelnose sturgeon) pooled were used to discriminate among zones in the Missouri River (Figure 58). The first canonical factor was statistically significant (P = 0.01), had an eigenvalue of 1.47, and accounted for 82% of the total variability. The raw canonical coefficients for canonical factor 1 can be computed by:

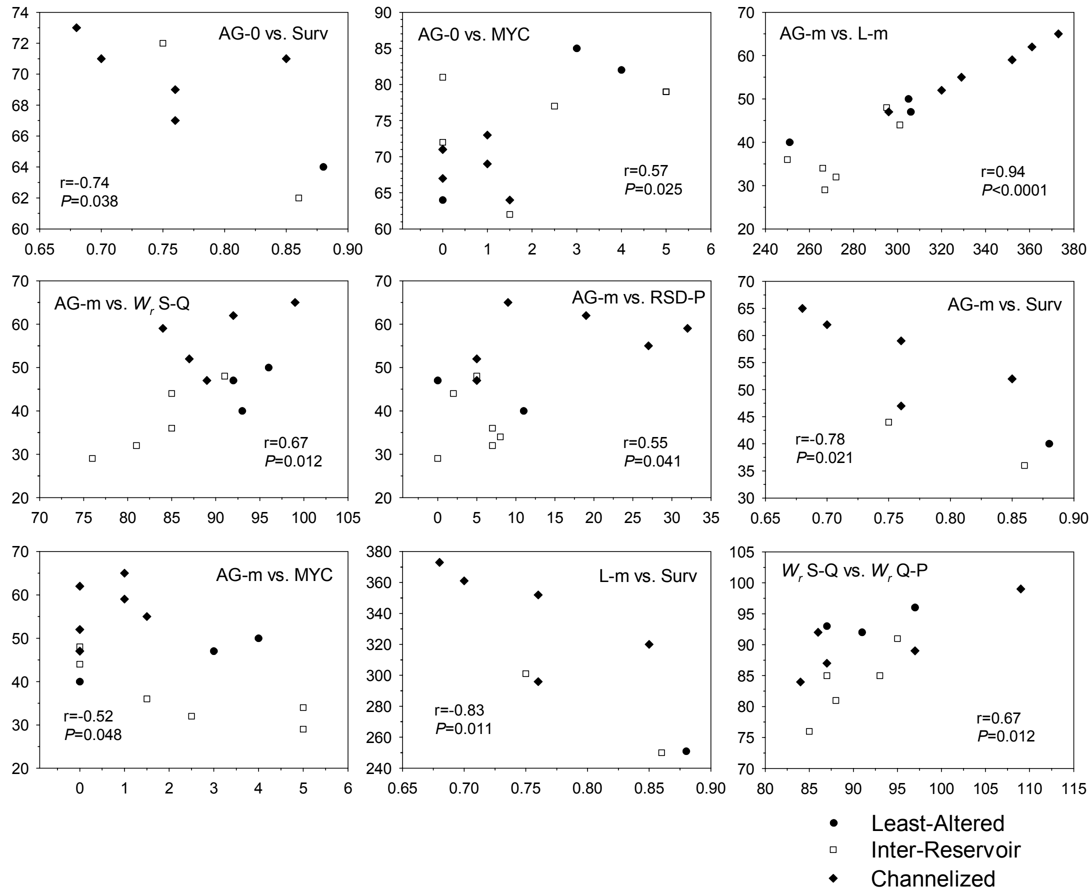

Figure 53. Scatterplots of significant (α<0.05) correlations of channel catfish growth, condition, size structure, survival and recruitment variables in segments of the Missouri and lower Yellowstone rivers. Variables are abbreviated as follows: AG-0=annual growth at age-0, AG-m=annual growth at age at maturity, L-m=mean length at age of maturity, W_r S-Q=condition of stock-quality size fish, W_r Q-P=condition of quality-preferred sized fish, W_r P-M=condition of preferred-memorable sized fish, PSD=proportional stock density, RSD-P=relative stock density-preferred, Surv=survival, MYC=number of missing year classes. In each scatterplot, the first variable listed is plotted on the Y-axis. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points.

canonical factor 1 = -0.10 (relative weight) +0.03 (size structure) + 13.7 (survival) + 0.10 (number of missing year classes) -0.01 (mean back-calculated length at age of maturity). Canonical factor 2 was not significant (P = 0.27) and only accounted for 18% of the variability, thus it was not useful in discriminating among zones. Bivariate centroids differed significantly among zones. The centroid for the channelized zone differed significantly between the inter-reservoir (P = 0.07) and least-altered (P=0.008) zones. Centroids did not differ significantly (P = 0.33) between the inter-reservoir and least-altered zones.

Relative weight, survival, and number of missing year classes was used to discriminate among zones for freshwater drum (Figure 59). The first canonical factor was statistically significant (P = 0.05), had an eigenvalue of 54, and accounted for 98% of the total variability. The raw canonical co-

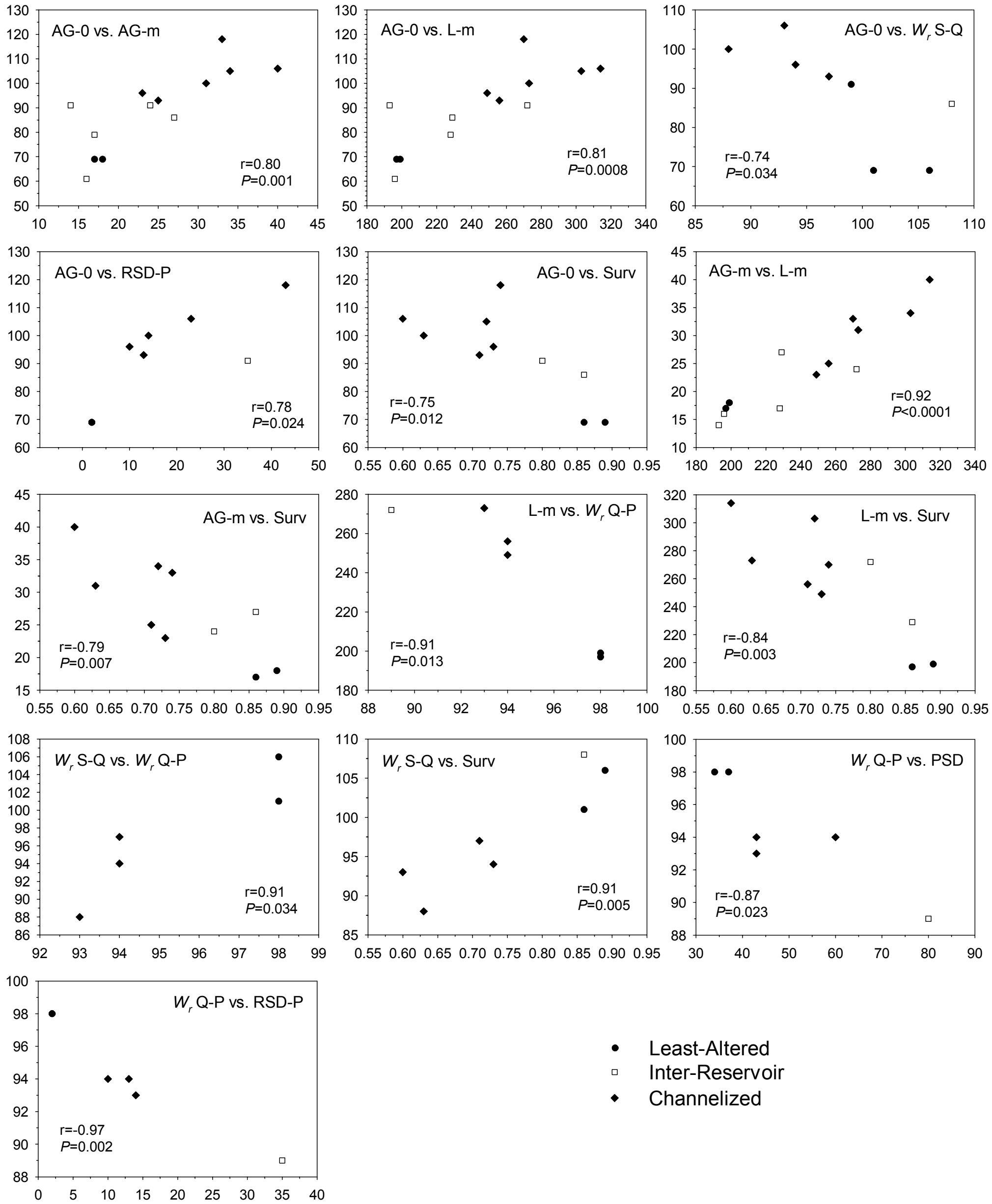

Figure 54. Scatterplots of significant (α<0.05) correlations of freshwater drum growth, condition, size structure, survival and recruitment variables in segments of the Missouri and lower Yellowstone rivers. Variables are abbreviated as follows: AG-0=annual growth at age-0, AG-m=annual growth at age at maturity, L-m=mean length at age of maturity, W_r S-Q=condition of stock-quality size fish, W_r Q-P=condition of quality-preferred sized fish, W_r P-M=condition of preferred-memorable sized fish, PSD=proportional stock density, RSD-P=relative stock density-preferred, Surv=survival, MYC=number of missing year classes. In each scatterplot, the first variable listed is plotted on the Y-axis. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points.

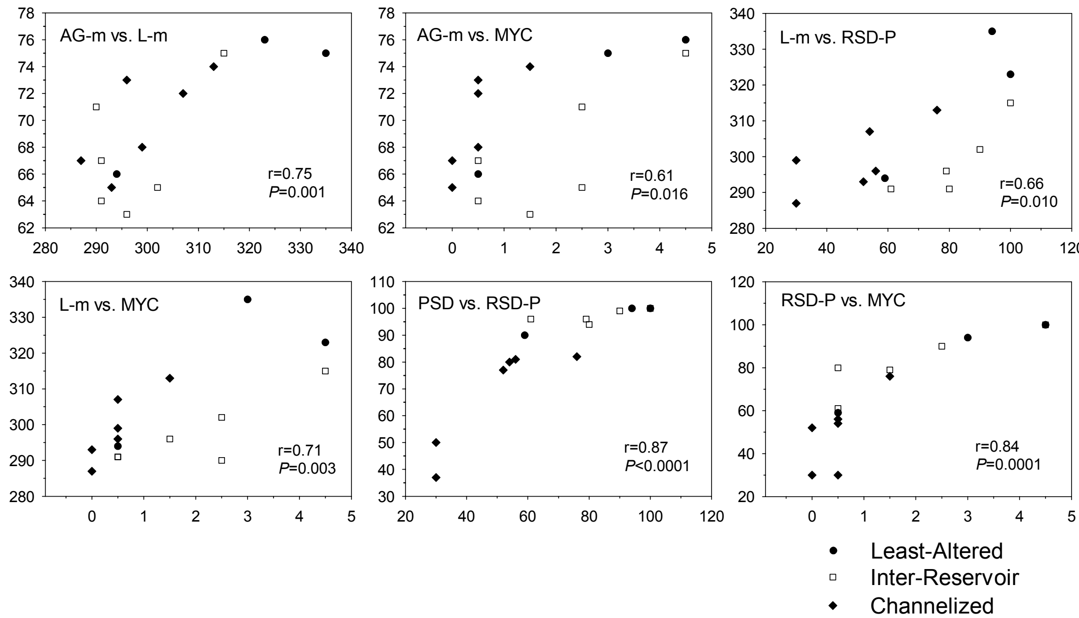

Figure 55. Scatterplots of significant (α<0.05) correlations of river carpsucker growth, condition, size structure, survival and recruitment variables in segments of the Missouri and lower Yellowstone rivers. Variables are abbreviated as follows: AG-0=annual growth at age-0, AG-m=annual growth at age at maturity, L-m=mean length at age of maturity, W_r S-Q=condition of stock-quality size fish, W_r Q-P=condition of quality-preferred sized fish, W_r P-M=condition of preferred-memorable sized fish, PSD=proportional stock density, RSD-P=relative stock density-preferred, Surv=survival, MYC=number of missing year classes. In each scatterplot, the first variable listed is plotted on the Y-axis. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points.

efficients for canonical factor 1 can be computed by: canonical factor 1 = 0.46 (relative weight) + 5.8 (survival) + 1.8 (number of missing year classes). Canonical factor 2 was not significant (P = 0.35) and only accounted for 2% of the variability, thus it was not useful in discriminating among zones. Bivariate centroids differed significantly among zones. The centroid for the channelized zone differed significantly between the inter-reservoir (P = 0.03) and least-altered (P=0.06) zones. Centroids did not differ significantly (P = 0.19) between the inter-reservoir and least-altered zones.

Size structure, number of missing year classes, and mean back-calculated length at age 1 was used to discriminate among zones for river carpsucker (Figure 60). The first canonical factor was statistically significant (P = 0.008), had an eigenvalue of 1.9, and accounted for 73% of the total variability. The raw canonical coefficients for canonical factor 1 can be computed by: canonical factor 1 = 0.10 (size structure) - 0.24 (number of missing year classes) -0.15 (mean back-calculated length at age 1). Canonical factor 2 was significant (P = 0.05), had an eigenvalue of 0.70, and accounted for 27% of the variability. The raw canonical coefficients for canonical factor 1 can be computed by: -0.10 (size structure) + 0.92 (number of missing year classes) -0.04 (mean back-calculated length at age 1). Bivariate centroids differed significantly between the channelized and inter-reservoir (P=0.05) and least-altered zones (P= 0.01). In addition, the inter-

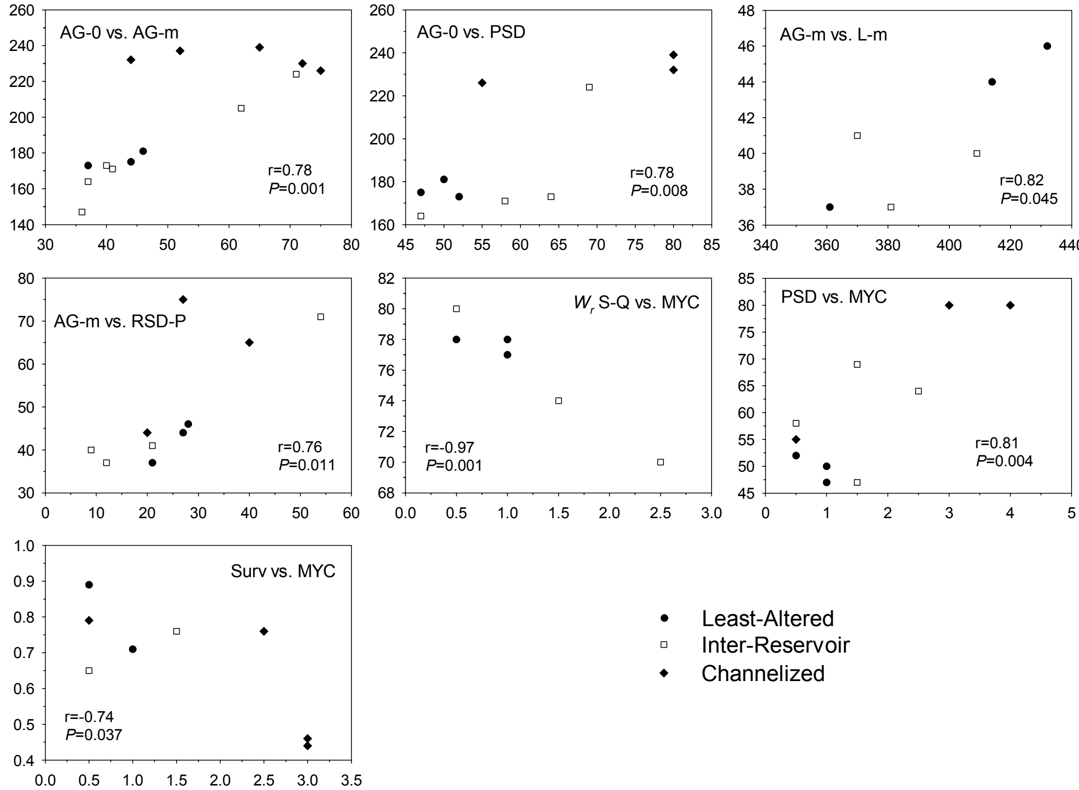

Figure 56. Scatterplots of significant (α<0.05) correlations of sauger growth, condition, size structure, survival and recruitment variables in segments of the Missouri and lower Yellowstone rivers. Variables are abbreviated as follows: AG-0=annual growth at age-0, AG-m=annual growth at age at maturity, L-m=mean length at age of maturity, W_r S-Q=condition of stock-quality size fish, W_r Q-P=condition of quality-preferred sized fish, W_r P-M=condition of pre-ferred-memorable sized fish, PSD=proportional stock density, RSD-P=relative stock density-preferred, Surv=survival, MYC=number of missing year classes. In each scatterplot, the first variable listed is plotted on the Y-axis. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points.

reservoir zone differed significantly from the least-altered zone (P=0.06).

Relative weight, size structure, survival, number of missing year classes, and mean back-calculated length at age of maturity was used to discriminate among zones for shovelnose sturgeon (Figure 61). The first canonical factor was statistically significant (P = 0.003), had an eigenvalue of 13.1, and accounted for 61% of the total variability. The raw canonical coefficients for canonical factor 1 can be computed by: canonical factor 1 = 0.71 (relative weight) + 0.02 (size structure) -73.3 (survival) +0.67 (number of missing year classes) - 0.06 (mean back-calculated length at age of maturity). Canonical factor 2 was also significant (P = 0.01), had and eigenvalue of 8.3, accounted for 39% of the total variability. The raw canonical coefficients for canonical factor 2 can be computed by: canonical factor 2 = -0.24 (relative weight) - 0.03 (size structure) +44.5 (survival) + 0.14 (number of missing year classes) -0.02 (mean back-calculated length at age of maturity). Bivariate centroids differed significantly among zones. The centroid for the channelized zone differed significantly be-

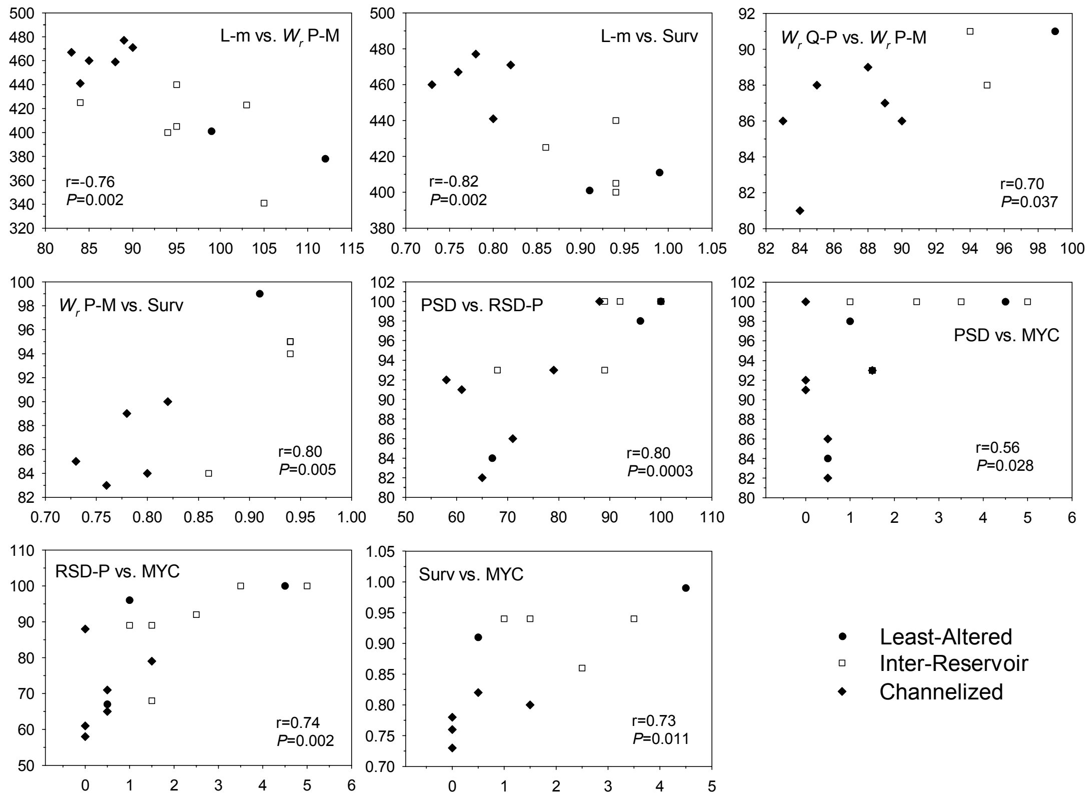

Figure 57. Scatterplots of significant (α<0.05) correlations of shovelnose sturgeon growth, condition, size structure, survival and recruitment variables in segments of the Missouri and lower Yellowstone rivers. Variables are abbreviated as follows: AG-0=annual growth at age-0, AG-m=annual growth at age at maturity, L-m=mean length at age of maturity, W_r S-Q=condition of stock-quality size fish, W_r Q-P=condition of quality-preferred sized fish, W_r P-M=condition of preferred-memorable sized fish, PSD=proportional stock density, RSD-P=relative stock density-preferred, Surv=survival, MYC=number of missing year classes. In each scatterplot, the first variable listed is plotted on the Y-axis. Symbols identify zones as indicated in the lower right corner of the figure. r and *P* values are for all data points.

tween the inter-reservoir (P = 0.04) and least-altered (P=0.02) zones. In addition, centroids differed significantly (P = 0.02) between the inter-reservoir and least-altered zones.

DISCUSSION

Our growth results showed a complex mix of responses, varying among species, among sizes within species, and to a lesser extent in time. The complexity of these results reflects the complexity of physiological, ecological and life-history differences among species, and the range of environmental differences found throughout a large-river system such as the Missouri.

Perhaps the strongest and most consistent pattern in the growth analyses was the decline in growth rate with fish length and age. Size-specific LOWESS regressions all clearly portrayed a decline in expected annual growth as fish length increases. Age-specific analyses of annual growth increment indicated highly significant age

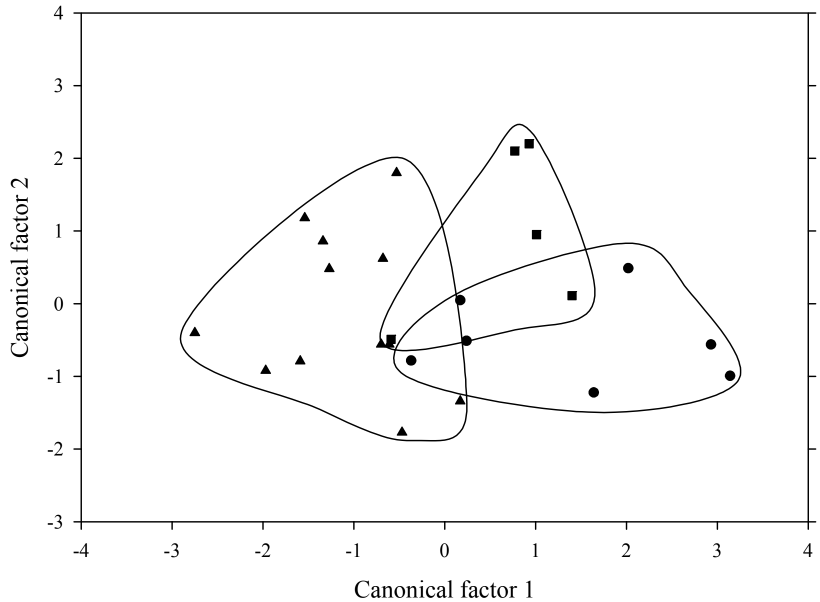

Figure 58. Canonical discriminant function analysis for least-altered (circles), inter-reservoir (squares), and channelized (triangles) zones in the Missouri River from 1996-1998. Canonical factors were derived from relative weight, size structure, survival, number of missing year classes and mean back-calculated length at age of maturity for channel catfish, freshwater drum, river carpsucker, sauger, and shovelnose sturgeon.

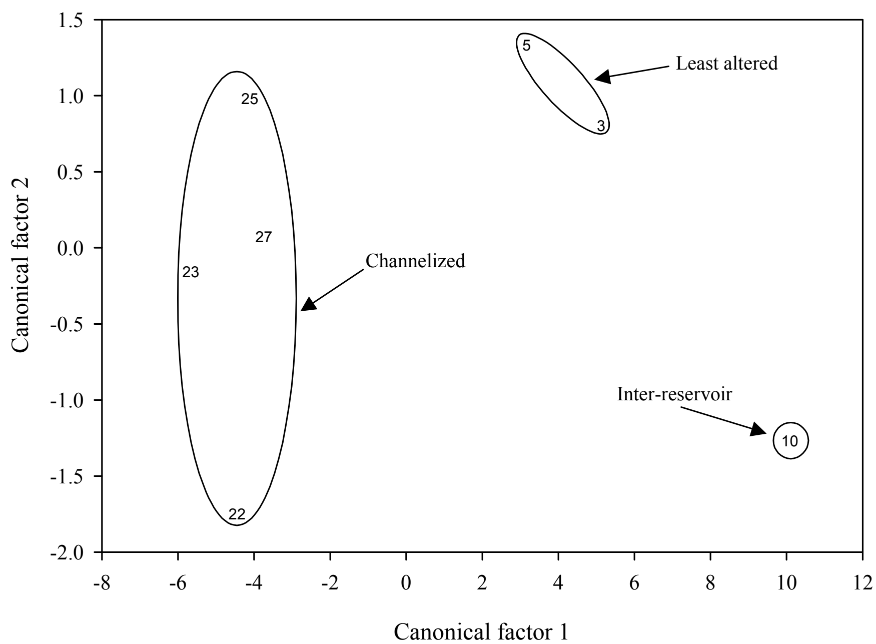

Figure 59. Canonical discriminant function analysis for freshwater drum sampled from least-altered, inter-reservoir, and channelized zones in the Missouri River from 1996-1998. Canonical factors scores were derived from freshwater drum relative weight of stock- to quality-length, survival, and number of missing year classes. Numbers within the ellipses represent segment.

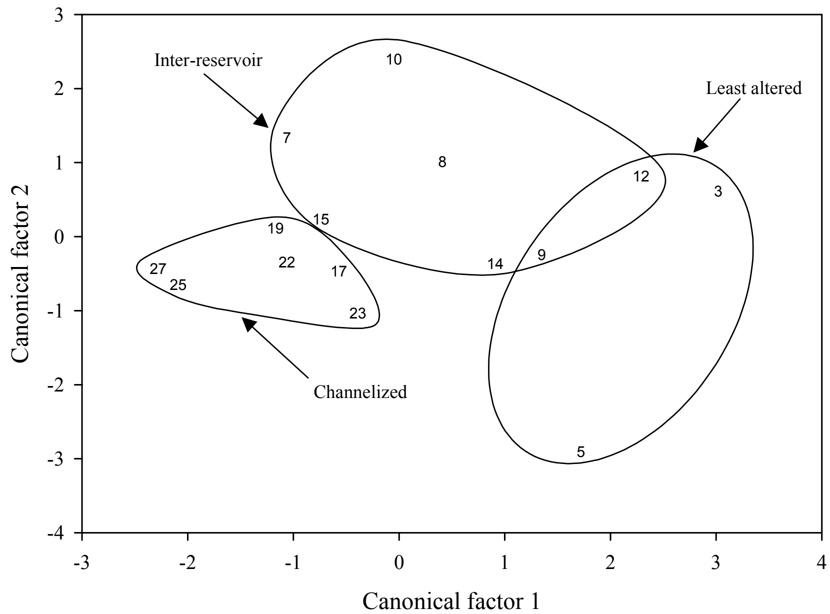

Figure 60. Canonical discriminant function analysis for river carpsucker sampled from least-altered, inter-reservoir, and channelized zones in the Missouri River from 1996-1998. Canonical factors scores were derived from sauger relative weight of stock-length, relative stock density of preferred length, number of missing year classes and mean back-calculated length at age 1. Numbers within the ellipses represent segment.

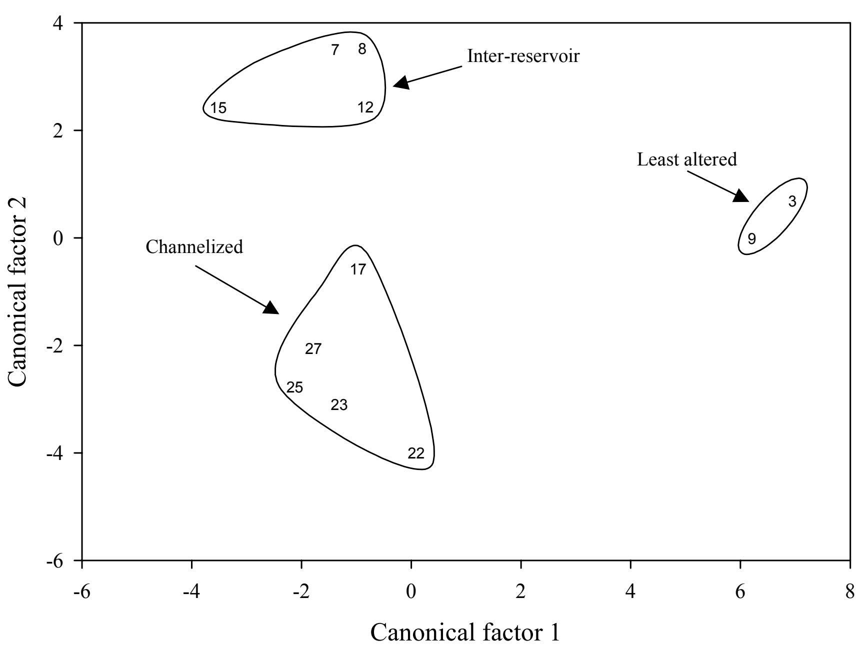

Figure 61. Canonical discriminant function analysis of shovelnose sturgeon sampled from least-altered, inter-reservoir, and channelized zones in the Missouri River from 1996-1998. Canonical factors scores were derived from shovelnose sturgeon relative weight of preferred-length, relative stock density of memorable length, survival, number of missing year classes and mean back-calculated length at age of maturity. Numbers within the ellipses represent segment.

effects for all species. These strong age effects were expected, and are consistent with patterns found throughout the growth literature. Application of the VBGF was based on the assumption of this age-related decline in annual growth rate, and the majority of the VBGFs fit the data well.

Year effects were statistically significant in many of our growth analyses, but in some cases these effects interacted with spatial groupings (segments, hydrological units or zones) and were difficult to interpret. These interactions presumably reflect local variation in weather, habitat conditions and resource availability occurring asynchronously over time. However, length at age 1 varied significantly with years and consistently across one or more spatial groupings in emerald shiner, flathead catfish, freshwater drum, plains minnow, shovelnose sturgeon, sicklefin chub and western silvery minnow. First year growth appeared to be faster in older individuals than in fish collected at younger ages in two of the three long-lived species in this group, freshwater drum and shovelnose sturgeon. This pattern matches the well-known Lee's phenomenon, and thus should be interpreted cautiously because of the possibility that the pattern is a sampling or methodological artifact rather than a true representation of a temporal growth trend. Results indicate that first year growth was fastest in 1993 and slowest in 1996 in the other long-lived species, flathead catfish. There was no consistency in which years had the fastest and slowest first year growth among the short-lived species, emerald shiner, plains minnow, sicklefin chub and western silvery minnow. Only plains minnow had a significant year effect in our age-specific analyses of annual growth increments. Both analyses of plains minnow showed the same temporal pattern, fastest growth in 1996 and slowest in 1995. In summary, we found significant yearly growth variation in some species, but no consistent pattern was seen among species. Furthermore, growth of several species appeared not to vary significantly among years.

Location effects were statistically significant in several of our growth analyses, reflecting a variety of environmental influences. In any large river system, differences along the river potentially represent influences of all the major physical and chemical variables that define the river continuum, such as changes in depth, velocity, turbidity, diel temperature variation, substrate, food resources and many other factors. The Missouri river encompasses nearly a 10^{o} range in latitude and significant changes in geography and climate, which adds even more potentially important environmental variation to drive changes in growth. Perhaps the most interesting observation is that the complete range of responses to these gradients was observed in every growth variable examined. First year growth varied significantly among segments in freshwater drum, river carpsucker, sauger and smallmouth buffalo, and whereas growth declined with increasing distance from the mouth of the Missouri River in the first three species, it increased in smallmouth buffalo. Length at maturity varied significantly among segments in channel catfish, freshwater drum, river carpsucker, shovelnose sturgeon and smallmouth buffalo. Length declined with distance from the mouth in channel catfish, freshwater drum and shovelnose sturgeon, increased in smallmouth buffalo, and was not significantly related to distance from the mouth in river carpsucker.

Distance from the mouth of the Missouri River and latitude are highly correlated ($r=0.98$, $P<0.0001$) among the 15 segments studied, so it is impossible to disentangle the potential effects of the latitudinal gradient from the suite of other factors that change along the river's course. For example, mean summer water temperature was significantly correlated (r=-0.73, *P*=0.002) with distance from the mouth, so although it is tempting to interpret longitudinal growth trends as responses to temperature differences, this must be done with the understanding that other potentially important factors may play a role. The case for temperature being the primary environmental driver of longitudinal gradients in growth is supported by Galat et al. (2001), who reported that from a suite of environmental variables potentially important to fish, temperature varied the most significantly and predictably along the river's course. Growth of several species showed relationships with temperature. First year growth of blue sucker, freshwater drum and sauger was positively correlated with temperature, but first year growth of smallmouth buffalo was negatively correlated with temperature. Growth rate at length of maturity of channel catfish, freshwater drum and sauger was positively correlated with temperature. Length at maturity of channel catfish, freshwater drum and shovelnose sturgeon was positively correlated with temperature. The majority of significant relationships were positive, implying that warmer temperatures in the lower Missouri River contributed to faster growth in these species. However, several species showed no relationship with temperature, and age-0 smallmouth buffalo grew fastest in colder segments. It is also noteworthy that for species positively correlated with temperature, the correlations with distance from the mouth and latitude are stronger in most cases. Temperature is likely an important determining factor of growth rates in all these species, but its influence is probably overridden by other factors in some species and augmented in others.

Superimposed on the longitudinal gradient of temperature from the cool, high latitude areas upstream to the warm, low latitude areas downstream, are cold areas below the large, hypolimnetic-release dams in the central portion of the river. Galat et al. (2001) reported that mean summer water temperatures in these areas were below what would be predicted based on their longitudinal position along the river. They suggested that this along with similar depression of turbidity, and perhaps other factors, justifies considering these areas as discontinuities in the normal river continuum (Stanford and Ward 1983). The lower portion of the Missouri River has been extensively constrained and channelized for navigation. These broad differences in human alteration were the basis for classifying river segments a priori into three zones: LA, IR and CH. We found significant growth variation among the three zones for several species. However, because the zones essentially group segments into three longitudinal categories, significant zone effects could be driven by temperature or other factors associated with the river continuum rather than the discrete type of human alteration implied in the zone classification. Significant zone effects in blue sucker, channel catfish, freshwater drum, sauger and shovelnose sturgeon all reflect the following rank order in growth among zones: LA<IR<CH. Because this rank order corresponds to the latitudinal gradient and associated correlates, it is difficult to separate the potential effects of human alteration from natural environmental differences

The growth relationships among species we identified illustrate both similarities and differences in how species responded across the 15 segments studied, and also some interesting changes in pair-wise relationships during the life cycle. Seven of nine significant pair-wise correlations for AG-0 were positive, three of four significant correlations for AG-m were positive, and all four significant pair-wise correlations for L-m were positive. This suggests that the majority of species observed responded similarly to environmental differences among segments, although the negative relationships are a reminder that some species pairs responded differently. Curiously, the relationships of channel catfish growth with emerald shiner and freshwater drum changed during the life cycle, being positive and negative, respectively, for AG-0 and changing to negative and positive for AG-m. The change in channel catfish and emerald shiner might be explained in part by the differences in life span and body size, with the responses diverging as differences in body size and presumably resource needs increases. Similar growth responses of mature channel catfish and freshwater drum might be expected, since they are both long-lived species and mature at similar sizes, but the reason for a negative correlation in first year growth of these species is unclear.

By independently estimating growth rates at two points in the life cycle, the first year of life and the year of maturity, we were able to assess whether species respond similarly to environmental differences at different points in their life cycle. We had sufficient data to examine this relationship for channel catfish, freshwater drum, river carpsucker, sauger and shovelnose sturgeon. Growth in the first year and year of maturity was positively correlated only in freshwater drum and sauger; no relationship was evident in the other three species. This suggests that in terms of growth, freshwater drum and sauger respond to environmental differences consistently throughout their life cycles, whereas the other species respond differently as they develop.

Condition, survival, and number of missing year classes exhibited longitudinal variation that was predictable at the segment, zone, and group scales. Longitudinal gradients in abiotic variables have been documented in other large rivers (Vannote 1980; Allan 1995); however, we are unaware of any studies that have conducted such a comprehensive longitudinal and latitudinal analysis of fish condition, size structure, survival, and recruitment in a single river. The population-level variables we evaluated limited our analyses to species that were relatively long-lived, present in over half the segments, had multiple year classes present in a sample, and had relatively large sample sizes. Thus, analyses were limited to common carp, channel catfish, flathead catfish, freshwater drum, river carpsucker, sauger, and shovelnose sturgeon. The species used in our analyses represent a variety of habitat uses (e.g., main channel, tributary mouths, secondary channels) and feeding guilds (e.g., benthic insectivores, piscivores). Despite that the variables we selected could not be used on all fishes sampled, we believe the species in our analyses represent the long-lived (> age 3) component of the Missouri River's benthic fish assemblage.

Condition varied longitudinally, but patterns differed among species. For example, condition declined for shovelnose sturgeon and increased for sauger from upstream to downstream. Therefore, factors influencing condition were not similar among species at the spatial scale studied (~ 3,000 river kilometers). Sauger was the only species that had an increasing trend in condition for all length categories from upstream to downstream. Longitudinal trends in condition varied among length categories for some species. Thus, factors influencing condition were not similar for length categories within a species; this likely being a function of differential environmental and anthropogenic influences during ontogeny.

Most species had highest condition values in the least-altered zone. Only P-M common carp and sauger had higher condition values in the channelized zone. Large-scale patterns in condition are likely a function of food availability, water temperature, and anthropogenic disturbances. For example, Megargle (1997) suggested that the Missouri River above Ft. Peck reservoir has higher benthic invertebrate abundance than lower reaches because the upper portion of the river has more gravel and cobble substrate. Longitudinal variation is also exhibited in prey fish; for example, gizzard shad *Dorosoma cepedianum*, a common prey item for sauger, is absent above Lake Oahe (Berry et al. 2004). The effects of food abundance on variation in condition have been widely studied (Gabelhouse 1991; Neumann and Willis 1995; Guy et al. 2002) in lentic systems.

The effects of reservoirs on condition were apparent in segments directly below reservoirs. Condition of shovelnose sturgeon was low below Ft. Peck Lake, Lake Sakakawea, and Lewis and Clark Lake. Interestingly, segment 10 below Ft. Peck Lake had higher condition values than predicted. Segment 10 is directly below the Yellowstone River and it is likely that the Yellowstone River is ameliorating the effects of Ft. Peck Lake on condition. Similarly, the Niobrara River enters at the bottom of segment 14, which had higher than predicted condition values for shovelnose sturgeon, and is ameliorating the disturbance from reservoirs. Galat et al. (2001) found that tributaries can ameliorate the effects of dams with respect to water temperature and turbidity.

Condition of saugers was influenced by reservoirs in all inter-reservoir segments. Tributaries did not appear to ameliorate the effects of reservoirs on sauger condition, and condition of sauger was atypically low in the least-altered zone (Montana). McMahon and Gardner (2001) documented a decline in sauger populations throughout Montana and suggested that drought, water withdraws, and competition with walleye were likely causes for the decline. Factors influencing condition of sauger in the upper Missouri and lower Yellowstone rivers merit further study.

Despite lower condition values in the channelized portion of the Missouri River for most species and length categories, condition appeared to be near or above 90 for all species except shovelnose sturgeon and sauger. Thus, channelization does not appear to have a profound detrimental effect on condition of common carp, river carpsucker, freshwater drum, channel catfish, or flathead catfish. Conversely, condition values of shovelnose sturgeon were below 90 in the channelized segments, except for segment 27 near the confluence with the Mississippi River. Importantly, shovelnose sturgeon is the only obligate main channel species we studied. Common carp, river carpsucker, freshwater drum, channel catfish, and flathead catfish are more generalist with respect to habitat use and are found in tributary mouths and secondary channels (Galat et al. 2004). Thus, low condition values observed in shovelnose sturgeon in channelized segments may be a function of changes in channel morphology caused by channelization. Low velocity habitat in main channel areas has been substantially reduced by strategic placement of dikes and revetments in the Missouri River below Sioux City, Iowa (Latka et al. 1993). Therefore, shovelnose sturgeon subjected to high velocities in the channelized portion of the river likely have increased metabolic costs for maintaining position and moving relative to fish in low-velocity areas. Thus, the plasticity in condition for shovelnose sturgeon along the Missouri River is likely a function of water temperature (below hypolimnetic releases from reservoirs) and velocity.

Our a priori prediction was that condition would increase from upstream to downstream based on longitudinal increases in productivity and growing season (Martin et al. 1980; Braaten and Guy 2002), but would be negatively influenced by reservoirs (i.e., serial discontinuity concept; Ward and Stanford 1983). However, sauger was the only species that followed our prediction and this is likely a function of increased food availability (gizzard shad abundance), reduced competition with other percids, and an earlier switch to piscivory in lower segments of the Missouri River. High condition of fishes in the upper segments of the Missouri River could be a function of longevity and subsequent accumulation of energy reserves. Several studies have shown that fish longevity increases from southern to northern latitudes (Colby and Nepszy 1981; Beverton 1987). Similarly, it has been well documented that birds and mammals are heavier for a given size in northern climates than southern climates as an adaptive mechanism to conserve or radiate body heat, depending on climate (Bergmann's rule). Lindsey (1966) found that fish exhibited a similar pattern and suggested that the pattern was related to small size and greater specialization in the tropics, heat conservation or other physiological processes related to surface-volume ratio, or selection of large adult size for high reproductive potential in northern climates. If the mechanism influencing the variation in condition was only water temperature then we would predict shovelnose sturgeon to have high condition values below reservoirs with hypolimnetic release, but the opposite occurred.

Observed patterns in size structure were similar to condition; for example, size structure (especially RSD-P and RSD-M) values tended to be higher in upstream segments. Conversely, sauger and channel catfish had higher size structure values in the lower Missouri River. However, the longitudinal pattern in size structure was not as clear as for other population metrics (i.e., condition, survival, and recruitment), and many of the zone, group, and hydrological unit comparisons did not differ significantly because of sample size limitations and high variability. Although we were unable to conduct serial discontinuity analyses on size structure data, it was evident that reservoirs might negatively influence size structure. The effect of reservoirs on size structure was most pronounced above and below Ft. Peck Lake for river carpsucker, sauger, and shovelnose sturgeon. Similar to the longitudinal variation in condition, the observed large-scale longitudinal patterns in size structure were likely a function of increased longevity in northern latitudes (Beverton 1987) and indeterminate growth of fishes.

Survival estimates clearly followed a longitudinal pattern from upstream to downstream for freshwater drum, sauger, and shovelnose sturgeon. However, sauger did not have an opposite pattern in survival relative to the other species as was observed in condition and size structure. Thus, the mechanism influencing survival of sauger differed from condition and size structure. Braaten and Guy (2002) suggested that fish populations in the lower Missouri River had fast growth rates and relatively short life spans and the opposite pattern for populations further north. The trend we observed in survival for channel catfish, freshwater drum, sauger, and shovelnose sturgeon corroborate findings by Braaten and Guy (2002), and supports our apriori prediction that survival increases from downstream to upstream. Large-scale patterns in survival and growth are likely a function of water temperature and growing season (Colby and Nepszy 1981; Beverton 1987; Beamesderfer and

North 1995). There were no consistent patterns in survival estimates regarding the influence of reservoirs on riverine segments. Population survival estimates may be insensitive to changes to river morphology caused by dams. All species had declines in survival estimates in segments 22 and 23. These segments were near St. Joseph and Kansas City, Missouri. It is likely that anthropogenic factors associated with high-density urban areas influenced survival of the benthic species we studied. Przybylski (1996) documented that growth and ultimate length of roach *Rutilus rutilus* was influenced by anthropogenic river modifications and water pollution from agricultural and industrial sources (i.e., high chloride, nitrogen, and phosphorus). This is an area worthy of further study.

Number of missing year classes (i.e., year-class failure) varied longitudinally and was related to river kilometer. Similar to the data for condition and size structure, sauger exhibited an opposite pattern relative to channel catfish, freshwater drum, river carpsucker, and shovelnose sturgeon. That is, sauger had the highest number of missing year classes in the lower segments of the Missouri River. Similar to the other metrics, the large-scale longitudinal patterns in year-class failure are likely a function of water temperature. The "warmwater" species (i.e., channel catfish, freshwater drum, river carpsucker, and shovelnose sturgeon) had more year-class failures in the upper segments of the Missouri River; conversely, the "coolwater" species (i.e., sauger) had more year-class failures in the lower segments. Idiosyncrasies in the longitudinal pattern of year-class failure were related to reservoirs. For example, segment 12 (below Lake Sakakawea) had the highest deviations from the predicated number of missing year classes for channel catfish, river carpsucker, and sauger; and segment 14 (below Lake Francis Case) had the highest number of missing year classes for shovelnose sturgeon. Reservoir operation causing fluctuating or reduced flow can negatively influence recruitment of fishes (Nelson and Walburg 1977).

Correlation analyses and scatterplots of all variables by species identified several patterns in the relationships among growth, condition, size structure, survival and recruitment. Only 25% of the significant relationships between growth variables and condition variables were positive. This is consistent with previous studies (Gutreuter and Childress 1990; Gabelhouse 1991; Liao et al. 1995) rejecting the commonly held idea that growth and condition are positively correlated. All of the significant relationships between growth variables and size structure variables were positive. This is logical, since faster growth leads to larger body size. None of the significant relationships of growth variables with survival were positive. This suggests a tradeoff between growth rate and survival in riverine species, and is worthy of further study. Because of the observational nature of this study and the fact that there were several non-significant relationships not accounted for in these percentages, their generality is uncertain.

Population metrics pooled for the benthic fishes moderately discriminated among the least-altered, inter-reservoir, and channelized zones. The lack of discrimination was likely a function of variation within the population metrics of the benthic fishes. For example, longitudinal variation in a given population metric was not similar for all species, sauger often deviated from other species (piscivory and the only "coolwater" species). Similarly, the response in population metrics to reservoirs was not similar among species. Habitat generalists were often less affected by anthropogenic changes than habitat specialists. Further, tributaries within inter-reservoir segments appear to have variable effects on the population metrics.

Relative weight, size structure indices, survival, number of missing year classes, mean back-calculated length at age 1, and mean back-calculated length at age of maturity were useful in discriminating among zones when individual species were examined. We were able to discriminate among zones for freshwater drum, river carpsucker, and shovelnose sturgeon. However, the discrimination among zones for river carpsucker was not as clear as for the other species. River carpsucker are generalists with respect to habitat requirements (Pflieger 1997) and this may account for the observed similarity among zones. The lack of discrimination among zones for the other species was largely due to missing population metric data. The ordination of zones using population metric data illustrates the unique population characteristics among species along the Missouri River. However, we are unaware of any historical data to determine if these patterns existed prior to anthropogenic modifications. We surmise that longitudinal variation was evident prior to construction of dams and channelization, and population metrics varied along a continuum rather than exhibiting discrete zonation. However, population characteristics now exhibit zonation because of reservoirs fragmenting populations and changing the physical characteristics of the Missouri River. Many of the species we studied are capable of long-distance movements (Pflieger 1997), thus the differences between the channelized zone and least-altered zones would have been less prior to population fragmentation by dams. The effect of reservoir fragmentation on population characteristics is most evident above and below Ft. Peck Lake. The comparison above and below the reservoir is unique to the Missouri River system because both areas are at similar latitudes, unlike other above and below reservoir comparisons. Further, the above reservoir segments are the most "natural" reach of the Missouri River (Galat and Lipkin 2000, Galat et al. 2001). The effect of a reservoir was similar to latitude for some population metrics because of the change in water temperature from hypolimnetic releases.

We found that anthropogenic modifications to the river (i.e., dams) can alter population metrics independently of latitudinal effects. The effects of reservoirs on population metrics were clear for many species; however, major tributaries (i.e., Yellowstone River, Niobrara River) ameliorated the effects of reservoirs on population metrics for the species that could use those tributaries during their life cycle. Many of the population metrics in Segment 12 were unfavorable relative to other segments. Segment 12 is the most isolated segment in the Missouri River; that is, there are no tributaries that enter the segment at the scale of the Yellowstone, Niobrara, Platte, or Kansas rivers. Despite that segment 15 is the only unchannelized area of the lower Missouri River, condition and recruitment of shovelnose sturgeon were lower than expected. The patterns observed in the population metrics below segment 15 may be related to the cumulative effects of reservoirs on river function.

The goal of this study was to assess population-level characteristics of fifteen fish species in the Missouri and lower Yellowstone rivers, and explore spatial patterns of these characteristics in relation to natural environmental gradients, flow regimes, and human alteration. This study is the largest of it's kind ever attempted, both in spatial scale and breadth of species included. We accomplished our objectives and have provided a wealth of data to dissect the myriad patterns and relationships exhibited by a diverse fish assemblage exposed to a highly complex mix of environmental factors, both natural and anthropogenic. Understanding these patterns and relationships in large rivers is critical for management and restoration.

Previous research suggests that the population status of fishes at risk within the Missouri River varies geographically. The healthiest populations of most species occur in the upper, least-altered Missouri River and its major tributaries (Hesse et al. 1989, White and Bramblett 1993). The section of greatest population decline is the middle and lower Missouri River in areas of degraded channels downstream from mainstem reservoirs (Hesse and Mestl 1993; Berry et al. 2004). The lower channelized Missouri River in Missouri may be somewhat intermediate as Pflieger and Grace (1987) found stable populations of several species, many of which Hesse (1994) reported as declining in Nebraska. Although we conclude that the fish population metrics we measured were not profoundly affected in the lower channelized area, they may not be the best measures of the impacts of channelization. Tributaries in the lower Missouri River may provide refugia for fish populations, partially offsetting the negative effects of a degraded main channel. Relative abundance and diversity of obligate main channel species (Berry et al. 2004) are apparently more sensitive indicators of negative impacts of channelization and impoundment than the populations characteristics we measured are, as was shown by Galat and Zweim**h**ller (2001) for riverine fishes in other north-temperate rivers. We surmise that fish populations below reservoirs are the most negatively affected, especially those areas without large tributaries. Tributaries are critical to maintaining healthy fish populations in the Missouri River. Additional degradation of tributaries such as the Yellowstone, Platte and Kansas rivers could further jeopardize fish populations in the Missouri River ecosystem.

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