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EFFECTS OF RESERVOIR WATER LEVELS ON YEAR-CLASS DEVELOPMENT AND THE ABUNDANCE OF HARVESTABLE FISH

by

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Qualitative results indicated that increased production of young fish consistently increases the abundance of harvestable-size fish within 1 to 4 years, barring catastrophic mortality of young fish before they recruit to a harvestable size. However, the abundance of large fish which results from recruitment of young fish could not be quantified because of variable rates of mortality and growth, as well as a lack of accurate age and growth data.

The single most important variable affecting the production of harvestable fish is mortality. Major sources of mortality such as starvation and predation often can be reduced by manipulating water levels during the growing season. Condition (weight at a discrete length) of largemouth bass was positively correlated to average surface area in summer and maximum change in area per year. Mortality due to starvation was apparently reduced by extensive spring flooding and above-average summer water levels. Above-normal water levels in summer also may reduce predatory mortality of young fishes by providing additional refuge from predators.

The degree to which a single year class of fish dominates a population apparently is influenced by the extent of annual and multiyear changes in water levels. Fish exhibited boom and bust patterns of recruitment in Bull Shoals Lake, Ark., where water levels changed extensively within and among years. In contrast, annual recruitment of fish was more uniform in John H. Kerr Lake, Va., where water levels varied less extensively within and among years than in Bull Shoals Lake.

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PREFACE

This report was prepared by the Aquatic Ecosystem Analysts (AEA) for the US Army Engineer Waterways Experiment Station (WES) under Purchase Order Number DACW39-84-M-0895, dated 4 January 1984. The study was part of the Environmental and Water Quality Operational Studies (EWQOS), Task II.E, "Environmental Effects of Fluctuating Reservoir Water Levels." The EWQOS Program, sponsored by the Office, Chief of Engineers (OCE), US Army, has been assigned to WES under the management of the Environmental Laboratory (EL). The OCE Technical Monitors for EWQOS were Mr. Earl Eiker, Dr. John Bushman, and Mr. James L. Gottesman.

This report was prepared by Mr. G. R. Ploskey and Dr. L. R. Aggus, Fishery Biologists of the AEA, and Dr. J. M. Nestler of the EL. The work was conducted under the direct supervision of Dr. Nestler and the general supervision of Mr. Mark Dortch, Chief, Water Quality Modeling Group; Mr. D. L. Robey, Chief, Ecosystem Research and Simulation Division; and Dr. John Harrison, Chief, EL. Dr. J. L. Mahloch is the Program Manager of EWQOS.

During the preparation of this report, COL Tilford C. Creel, CE, and COL Robert C. Lee, CE, were Commanders and Directors of WES and Mr. F. R. Brown was Technical Director. At the time of publication, COL Allen F. Grum, CE, was Director and Dr. Robert W. Whalin was Technical Director.

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EFFECTS OF RESERVOIR WATER LEVELS ON YEAR-CLASS DEVELOPMENT
AND THE ABUNDANCE OF HARVESTABLE FISH

PART I: INTRODUCTION

1. This report supplements findings of Technical Report E-84-8 (Ploskey, Nestler, and Aggus 1984), which documented quantitative relations between reservoir hydrologic events and the August abundance of fishes in small and intermediate size classes. Regression models developed in the previous report provided a predictive methodology for assessing effects of existing or proposed water-level regimes on fish reproductive success and the survival of young fish. Although above-average crops of small and intermediate-size fish usually resulted in above-average crops of large fish in 1 to 4 years, relations between hydrologic events and the abundance of large harvestable fishes could not be quantified. Relationships between reproductive success and the abundance of large fish 1 to 4 years later had to be demonstrated graphically because the amount of time required for small fish to grow to a harvestable size varied greatly among years (Ploskey, Nestler, and Aggus 1984).

2. As year-class development is currently understood, post-hatching survival often determines the abundance of large fish produced from a previous reproductive event. The chance of a young fish surviving to recruit to a fishery (attain a harvestable size) usually increases as it grows. Survival is often a function of size because increased size reduces mortality from hazards such as predation. Of course, many other factors such as disease and extreme physicochemical conditions also influence survival, but these factors are either unpredictable or less size specific than predation. If the strength of some year classes is determined more by the growth and survival of young-of-year (YOY) fish than by the number of YOY produced, cause-effect relations probably cannot be established between hydrology and the abundance of large fish unless effects on growth and survival can be quantified. Major hydrologic events usually determine reproductive success (Ploskey,

Nestler, and Aggus 1984), but after reproduction, recruitment to a harvestable size may be independent of the original hydrologic event if survival is significantly above or below average.

3. The purpose of this study is to examine in detail the development of year classes of fish to clarify the effects of previous reproductive events on the abundance of large fish. An important aspect of the study involves relating the condition (weight at a discrete length) of large largemouth bass to seasonal and annual water levels. Condition is an accepted index to growth and available food resources, which in turn affect survival. The process of producing crops of large fish (year-class development) warrants detailed study because the abundance of harvestable fish after major hydrologic events is the ultimate measure of the effects of water-level regimes on reservoir fisheries.

4. This study concentrates on fish and hydrologic data from Bull Shoals Lake, a hydropower storage reservoir in Arkansas. Some supplemental data from two other storage impoundments (John H. Kerr Lake, Va., and Clarks Hill Lake, Ga.) will be used. Information available for Bull Shoals Lake represents one of the longest continuous records of data on hydrology and fish in a warmwater reservoir.

5. Although the year-class development for several species is examined, efforts were concentrated on largemouth bass for several reasons. First, the largemouth bass is one of the most ubiquitous species in hydropower storage reservoirs. Second, it is one of the most valuable sport fish exploited by anglers. Third, and most important, it is representative of most warmwater fishes with regard to patterns of year-class development and response to water-level changes. The abundance of small, intermediate-, and large-size groups (see Ploskey, Nestler, and Aggus (1984), Appendix D, for size classification) of many species is positively correlated with the abundance of largemouth bass of about the same size (Appendix A of this report). Data used for correlation analysis are pooled from the three hydropower storage reservoirs discussed in the previous paragraph, and size definitions and scientific names are presented by Ploskey, Nestler, and Aggus (1984). Results suggest that the reproductive response of many species, as indexed by the abundance

of fish of small and intermediate size in August, is cued to about the same environmental conditions as the reproductive response of largemouth bass (see Ploskey, Nestler, and Aggus (1984) for relations between reproductive success and seasonal water levels). In addition, the abundance of intermediate-size largemouth bass was positively correlated to the abundance of all fishes and sport fishes when all sizes are pooled. Changes in the abundance of large fish of many species also are similar to those of largemouth bass.

6. Designating year classes is a convenient way to evaluate the contribution (numbers or biomass) of fish of different ages to a population at any point in time. In this report, year class refers to a cohort of fish hatched in the same year. For example, a YOY fish in 1973 would be assigned to the 1973 year class; in 1974, this 1973 year-class fish would be a yearling (Age 1); in 1978, a 1973 year-class fish would be Age 5.

PART II: AVAILABLE DATA AND METHODS

7. Hydrologic data used in this study included estimates of elevation on the last day of every month in Bull Shoals Lake, Ark. (1968-1980) and John H. Kerr Lake, Va. (1972-1979) (Figure 1), as well as average seasonal surface areas and storage ratios (mean monthly volume/total monthly discharge) in Bull Shoals Lake (1972-1981); Clarks Hill Lake, Ga. (1960-1967 and 1976-1979); and John H. Kerr Lake (1974-1979). Seasonal variables consisted of average monthly storage ratios in spring and fall; average surface area in spring, summer, and fall; and maximum change in area annually and in spring, summer, and fall. These variables were defined and derived by Ploskey, Nestler, and Aggus (1984).

8. Fishery data analyzed in this study consisted of 25 years of rotenone samples of fish communities in coves of the three storage reservoirs and spring electrofishing samples of largemouth bass in Bull Shoals Lake from 1969 to 1981. A detailed description of the rotenone sampling technique is presented in a paper by Grinstead et al. (1977); sampling dates and the species, sizes, and abundance of fish collected from the three reservoirs were described in Technical Report E-84-8 (Ploskey, Nestler, and Aggus 1984). Spring electrofishing samples of largemouth bass were taken at night during April from the Gunnel Fork arm of Bull Shoals Lake, a 200-ha embayment in the lower region of the lake. Bass were collected along the shore during two or more sampling runs around the embayment. Fish were marked during sampling runs and recaptured during a subsequent run. Population estimates were made using the Peterson method (Ricker 1975).

9. To examine the year-class development of a single species, we plotted the biomass (kilograms/hectare) of fish in specific size classes (25-mm for electrofishing samples and 25.4-mm for rotenone samples) for all years of record. Biomass was expressed as a fraction of the total biomass in all size groups sampled each year. Numbers per hectare in specific size classes were not plotted directly because numbers overemphasized the importance of small fishes and did not adequately illustrate the development of year classes, culminating in the recruitment of

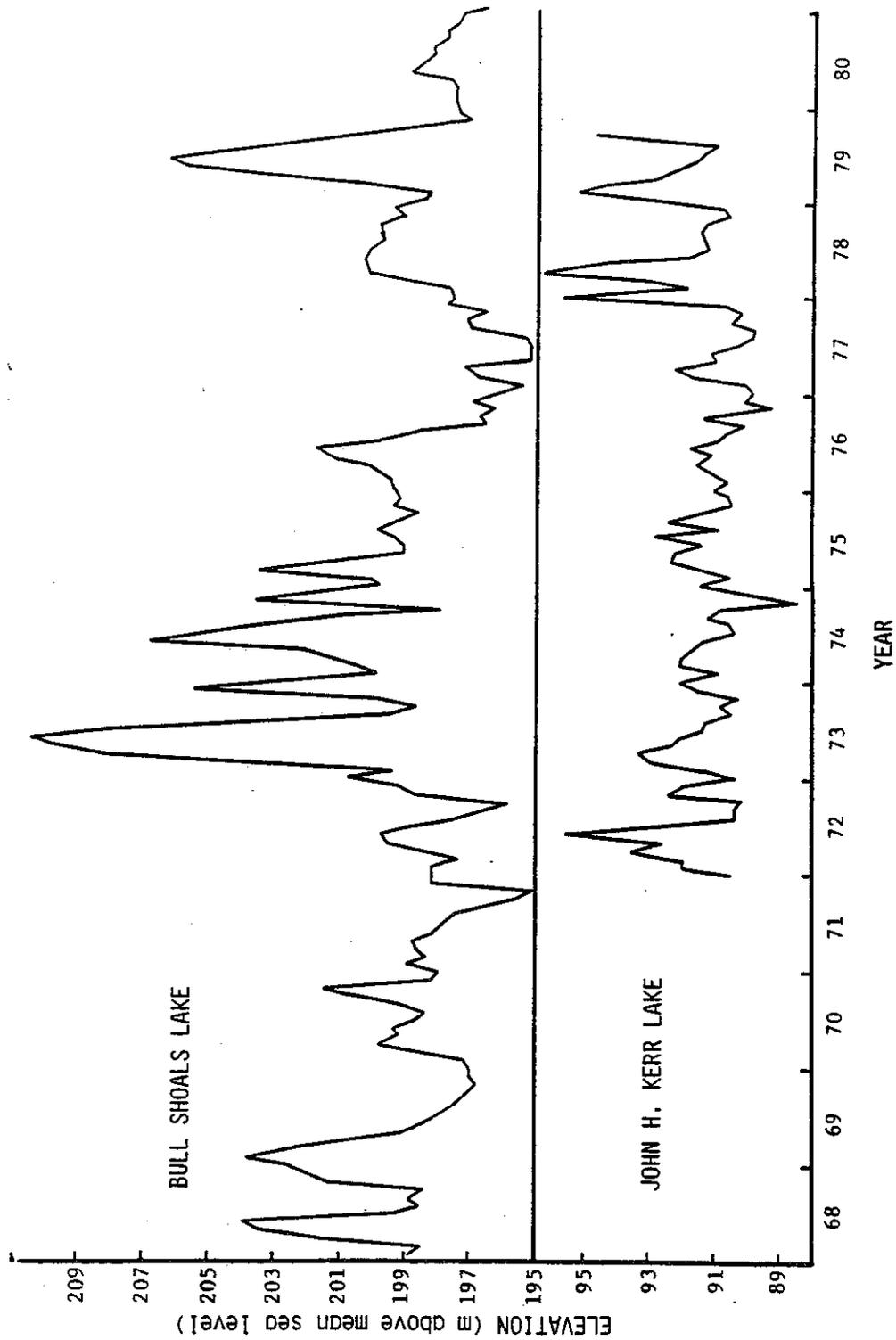


Figure 1. Monthly changes in the surface elevations of Bull Shoals Lake, Ark. (1968-1980), and John H. Kerr Lake, Va. (1972-1979)

young fish to harvestable sizes. Changes in length-frequency distributions over years indicated when strong year classes of fish were produced and how long they lasted. By expressing the biomass in every size class as a percent of the total in all size classes, we dampened distortions that often arise from year-to-year sampling variability. Different numbers of fish may be collected in some years solely because local environmental conditions make fish more or less vulnerable to sampling.

10. The relation between the biomass of young fish and the subsequent contribution of individual year classes to a fishery is best illustrated graphically, with biomass expressed as a percentage of total biomass of a species each year (as described in paragraph 9). Unfortunately, a graphical approach is useful only when a species is (a) sufficiently abundant in annual samples so that all size classes are well represented, and (b) grows large enough to permit division of length into a large number of equal classes. For example, the year-class development of sunfishes was difficult to represent graphically because 25.4-mm size classes available from rotenone samples were too large to separate into discrete age groups (often only six size classes were represented). After studying rotenone data from Bull Shoals Lake, we chose to illustrate the year-class development of gizzard shad, common carp, golden redhorse, and largemouth bass because these species were usually abundant and most size classes were well represented each year. These species also grow to 380 mm or longer, and length could be divided into 15 or more 25.4-mm size classes. We selected gizzard shad and redhorses as examples to illustrate year-class development in John H. Kerr Lake. In Clarks Hill Lake, a gap in sampling of consecutive years and poor representation of most adult fishes precluded a detailed examination of year-class development for any species.

11. Regression analysis on lagged data from the three hydropower storage reservoirs was used to evaluate positive relations between the abundance of small fish and that of large fish 1 to 4 years later. These relations should further justify the use of predictions of the abundance of young fishes (Ploskey, Nestler, and Aggus 1984) as a method for evaluating effects of hydrology on reservoir fisheries. From changes

in the length-frequency distributions of fish over years, we were able to derive an estimate of the number of years required for small fish to recruit to the large-size group (hereinafter referred to as "years-to-recruitment"). Estimates ranged from 1 to 4 years because of variable trophic conditions and growth. By adding "years-to-recruitment" to the year small fish were hatched, we attempted to correlate the biomass of small fish with the resulting biomass of large fish observed several years later. For example, the biomass of small largemouth bass in Bull Shoals Lake in 1975 was correlated with the biomass of large largemouth bass in 1978 by lagging the data 3 years, which was the estimated time required for most YOY largemouth bass in 1975 to recruit to a harvestable size of 317.5 mm. By contrast, the biomass YOY produced in the high-water year of 1973 was matched with the biomass of harvestable largemouth bass in 1974, because only 1 year was required for recruitment. After all possible combinations of years and biomass were lagged according to the estimated "years-to-recruitment," crops of large fish were regressed on crops of small fish of the same species or group in earlier years.

12. Condition (weight at a discrete length) is an index to the relative physical fitness of individual fish and reflects trophic conditions (that is, the adequacy of food resources in the environment). We estimated the average condition of large (>317.5 mm) largemouth bass in August and April using data from August rotenone and April electrofishing samples from Bull Shoals Lake. Calculation of average condition entailed the following steps:

- a. Taking the logarithm of individual weights (g) and lengths (mm) of all large largemouth bass sampled over the years.
- b. Regressing log (weight) on log (length) using estimates for individual fish to derive a standard length-weight equation for large largemouth bass in Bull Shoals Lake.
- c. Predicting weights of fish from actual lengths using the standard equation (step b).
- d. Dividing actual weight by predicted weight at the same length to generate estimates of relative condition for individual fish.

- e. Averaging the condition of all large largemouth bass sampled in the same year and in the same month.

Standard regression equations for predicting weight from length (step b above) were highly significant ($P \leq 0.0001$). Equations based on August rotenone and April electrofishing data had identical coefficients of determination ($r^2 = 0.94$) but were based on different numbers of largemouth bass (132 in August versus 730 in April). For any sample, an index of unity (actual weight/predicted weight = 1) from step e above reflects average condition; an index less than one indicates below-normal condition; and an index greater than one reflects above-average condition.

13. We also derived indices of condition for species other than largemouth bass from mean weights of fish in 25.4-mm size classes, as collected in standard rotenone samples. A lack of discrete length and weight measurements for other species prevented the use of the accurate method for calculating condition, as described in the previous paragraph. Instead, we had to assume that the midpoint of each 25.4-mm size class represented the average length of fish in each size class and that the mean weight of fish in a 25.4-mm size class represented the mean weight of fish at the midpoint length. If meaningful indices could be derived from size-class data, we hoped to explore relations between hydrologic events and the condition of many species.

14. To test the sensitivity and accuracy of indices of condition derived from size-class data, we compared derived condition for large largemouth bass to the actual condition of large largemouth bass calculated from individual length and weight measurements.

15. The procedure for deriving the size-class condition index involved the following steps:

- a. Calculating the mean weight for all fish in every 25.4-mm size class > 317.5 mm.
- b. Taking the logarithm of "1 + mean weight" and of the midpoint length of every size class.
- c. Regressing $\log(1 + \text{mean weight})$ on $\log(\text{midpoint length})$, using all size classes and years of data, to develop a standard length-weight regression equation.

- d. Predicting mean weight from the midpoint length of every size class, using the standard equation from c above.
- e. Calculating an index of condition for every size class sampled by dividing the mean weight of each size class by the predicted mean weight for the same size class.
- f. Calculating a mean index of condition for large largemouth bass by averaging condition indices for all size classes > 317.5 mm each year.

16. We also weighted (by number) the average size-class index for large largemouth bass to place more emphasis on the 25.4-mm size classes that contained more fish. In calculating a weighted index of condition from size-class data, we had to make two major assumptions: (a) the average length of fish in a single 25.4-mm size class was equal to the midpoint length of the size class, and (b) the lengths of fish in every size class were normally distributed, so that as the number of fish in each size class increased, the mean weight and length approached the true mean weight and midpoint length.

PART III: RESULTS AND DISCUSSION

Year-Class Development

17. Recruitment patterns of all species tested were highly variable in Bull Shoals Lake, but the occurrence of increased biomass of small fish in some years generally resulted in a substantial increase in the adult population for several successive years. Strong year classes of gizzard shad and carp produced in 1973 and 1978 (Figures 2 and 3) dominated populations of these species throughout the 11-year period of record. Strong year classes, apparently produced several years before data collection began, did not contribute significantly to the adult biomass of these species until the late 1970s.

18. Golden redhorse also periodically produced strong year classes that dominated the biomass of the population for years (Figure 4). Based on changes in the size distribution of yearling and older individuals (Figure 4), high production of YOY golden redhorse probably occurred in 1973, 1976, and 1978-1979 and contributed substantially to the adult biomass in subsequent years. If small golden redhorse had been well represented in cove samples (which they seldom were because of age-specific habitat preferences), recruitment patterns would be even more discernible.

19. In contrast to golden redhorse, small largemouth bass were better represented in cove samples than large bass because of age-specific differences in habitat selection. Crops of young largemouth bass were high in 1973 and 1978-1979 (Figure 5) and can be linked to increases in the proportion of adult fish in subsequent years, although not as conspicuously as for adults of the other species tested, because adult largemouth bass were not adequately represented in coves.

20. Similar treatment of 25-mm size classes of largemouth bass collected in springtime electroshocking samples from Bull Shoals Lake revealed that the strong year classes of YOY fish produced in 1973 and 1978-1979 indeed dominated the adult biomass for several years thereafter (Figure 6). The 1978-1979 year class is partially obscured by the

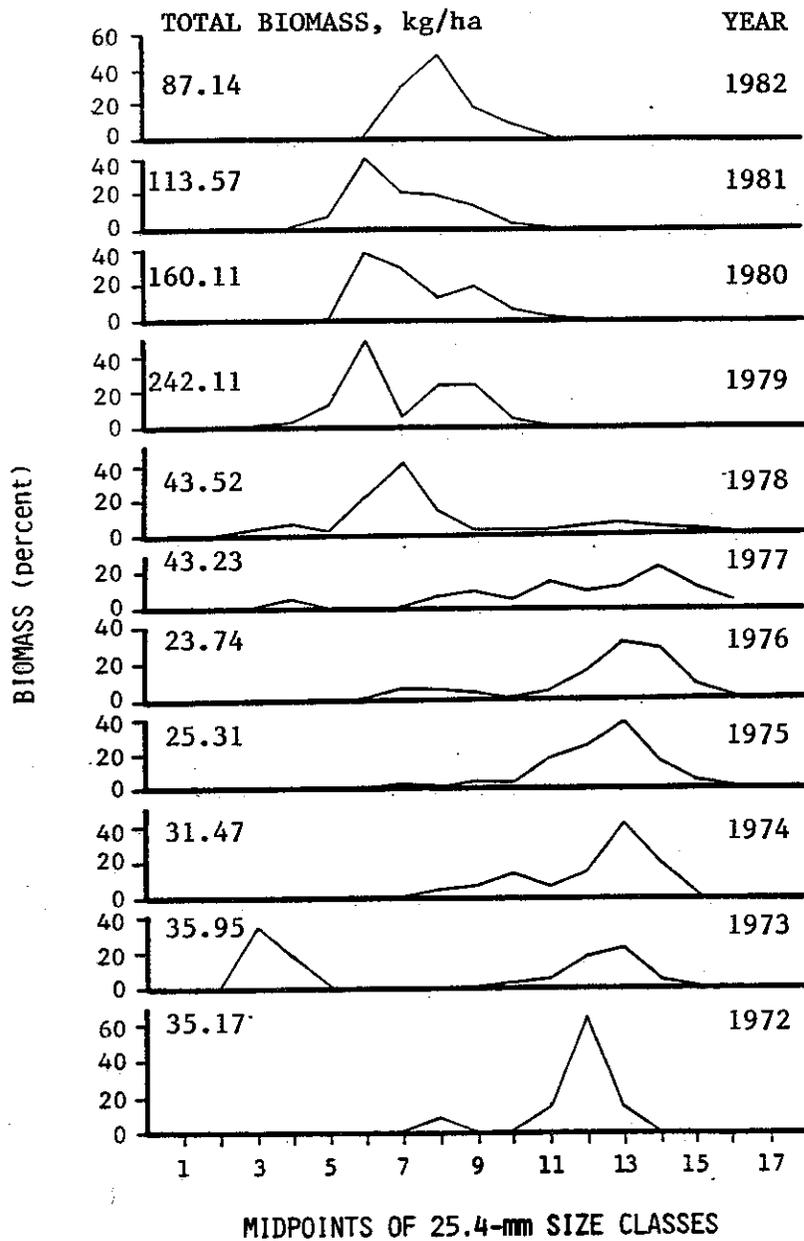


Figure 2. Length-frequency distributions of gizzard shad biomass in Bull Shoals Lake from 1972 to 1982. Biomass is expressed as a percentage of the total biomass of gizzard shad collected each year in August rotenone samples of coves.

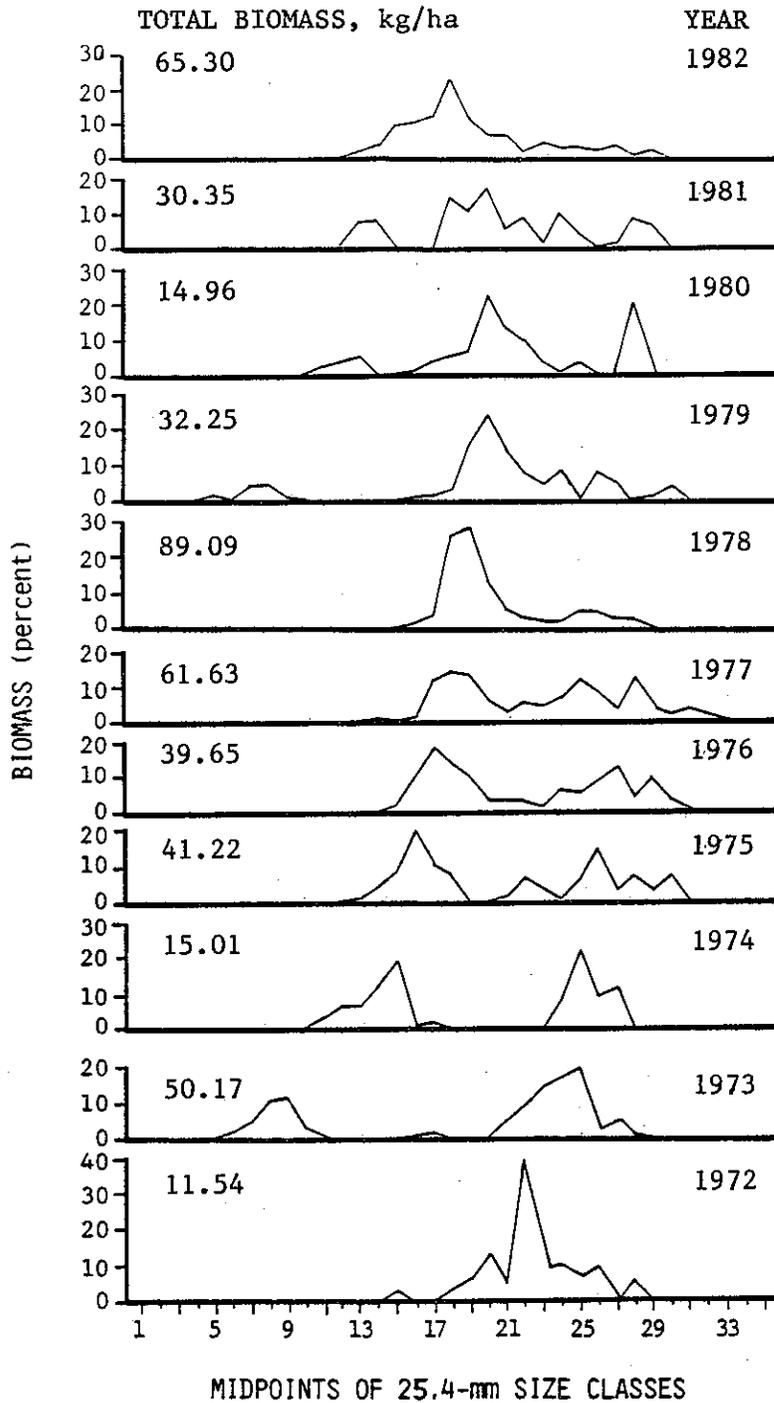


Figure 3. Length-frequency distributions of common carp biomass in Bull Shoals Lake from 1972 to 1982. Biomass is expressed as a percentage of the total biomass of common carp collected each year in August rotenone samples of coves.

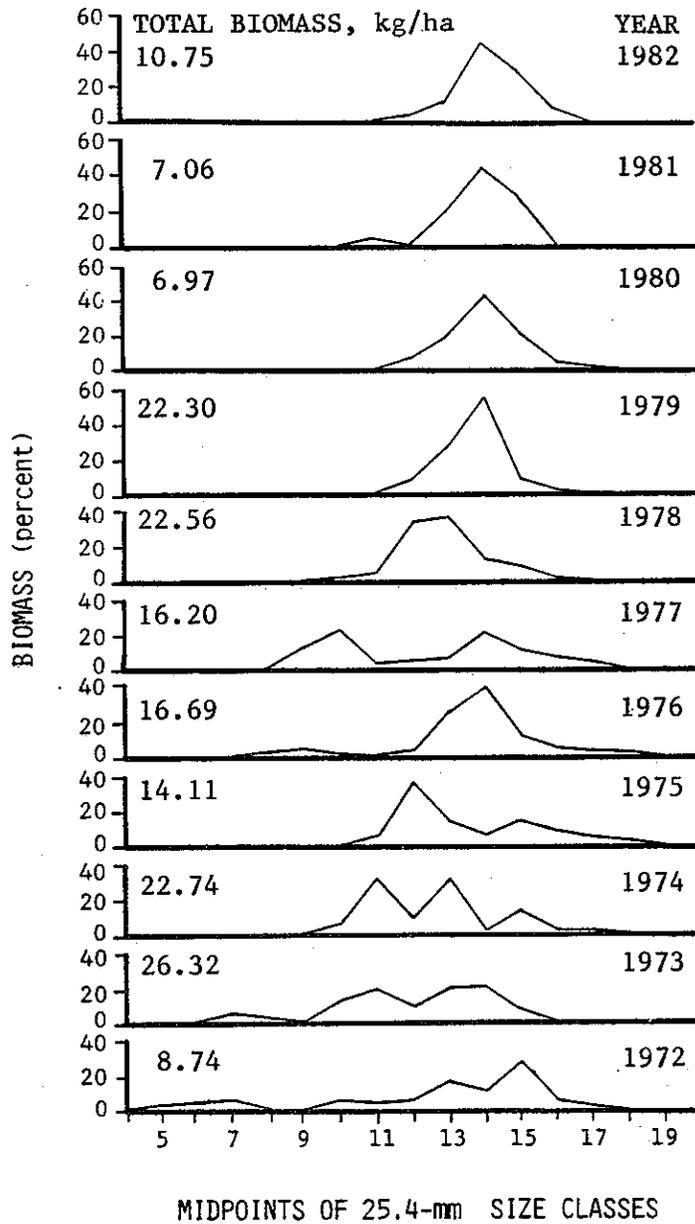


Figure 4. Length-frequency distributions of golden redhorse in Bull Shoals Lake from 1972 to 1982. Biomass is expressed as a percentage of the total biomass of golden redhorse collected each year in August rotenone samples of coves.

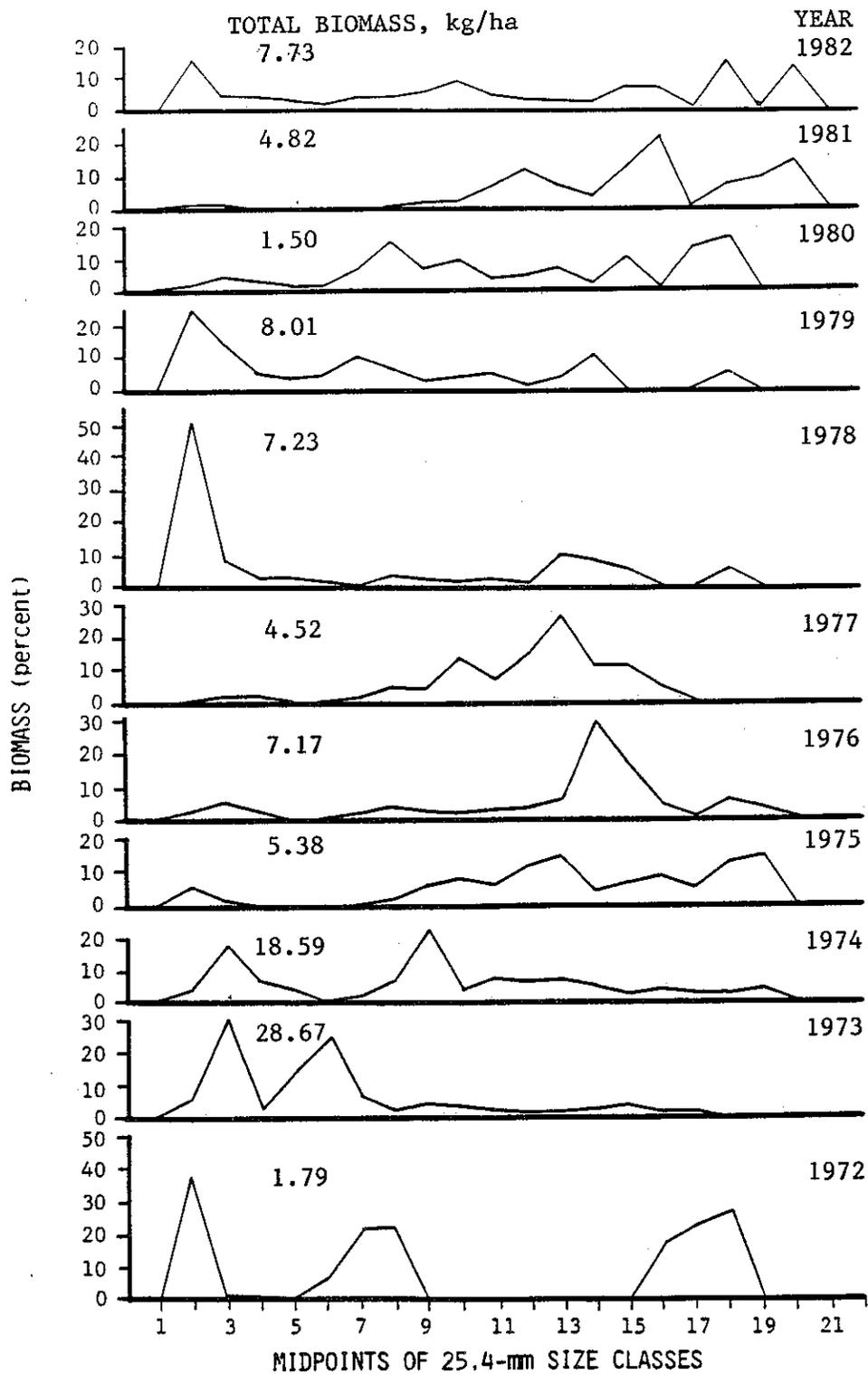


Figure 5. Length-frequency distribution of largemouth bass in Bull Shoals Lake from 1972 to 1982. Biomass is expressed as a percentage of the total biomass of largemouth bass collected each year in August rotenone samples of coves.

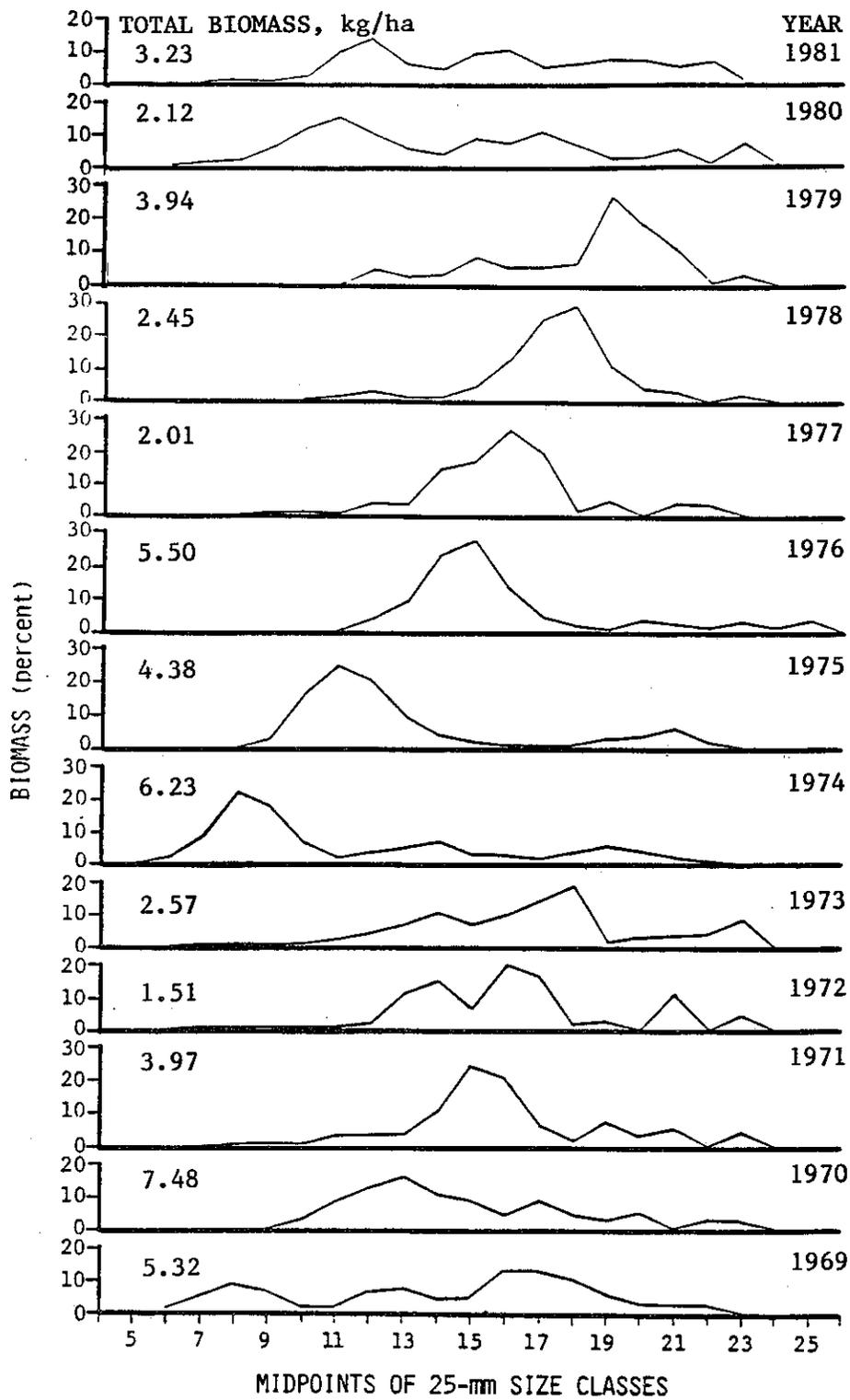


Figure 6. Length-frequency distributions of largemouth bass biomass in Bull Shoals Lake from 1969 to 1981. Biomass is expressed as a percentage of the total biomass of largemouth bass collected each year in April electro-fishing samples.

many remaining fish from the 1973 year class. Young bass do not appear in the figure until their second year of life, when electroshocking was done in April. We began sampling bass by electroshocking in 1969, and a strong year class produced in 1968 appeared as Age 1 Fish (150-225 mm) when data collection began. These fish dominated the population until 1973.

21. Strong year classes of the four species examined above almost invariably originated in years when water levels were high (1973 and 1978-1979), or at least significantly higher than those of the preceding year (Figure 1). Largemouth bass also produced a strong year class in 1968, as indicated by electroshocking data (Figure 6). These results indicate that the periodic large fluctuations in pool levels exert an overriding influence on the size and age structure of several important species in Bull Shoals Lake.

22. Annual recruitment of smaller fish to the adult population was more consistent in John H. Kerr Lake than in Bull Shoals Lake, although strong single year classes of gizzard shad (Figure 7) and red-horses (Figure 8) did occur. Consequently, domination of the reservoir fishery by a single year class of fish was not as pronounced in John H. Kerr Lake as in Clarks Hill Lake.

23. The degree to which a single year class dominates an adult population apparently varies among reservoirs of the same type (e.g., hydropower storage) because of differences in the extent of annual and multiyear changes in water levels. In Bull Shoals Lake, extreme annual variations in water levels (Figure 1) apparently caused boom and bust cycles of year classes (see Figures 2-6), whereas relatively uniform and less extensive annual changes in water levels in John H. Kerr Lake permitted some successful reproduction and recruitment in most years (Figures 7 and 8). Water levels in John H. Kerr Lake fluctuated less than those of Bull Shoals Lake and within approximately the same vertical range every year (Figure 1). In addition, the two multipurpose reservoirs were operated differently. Although the storage allocated for power generation was similar ($1.24 \times 10^9 \text{ m}^3$ in Bull Shoals Lake versus $1.27 \times 10^9 \text{ m}^3$ in John H. Kerr Lake), flood control storage in Bull

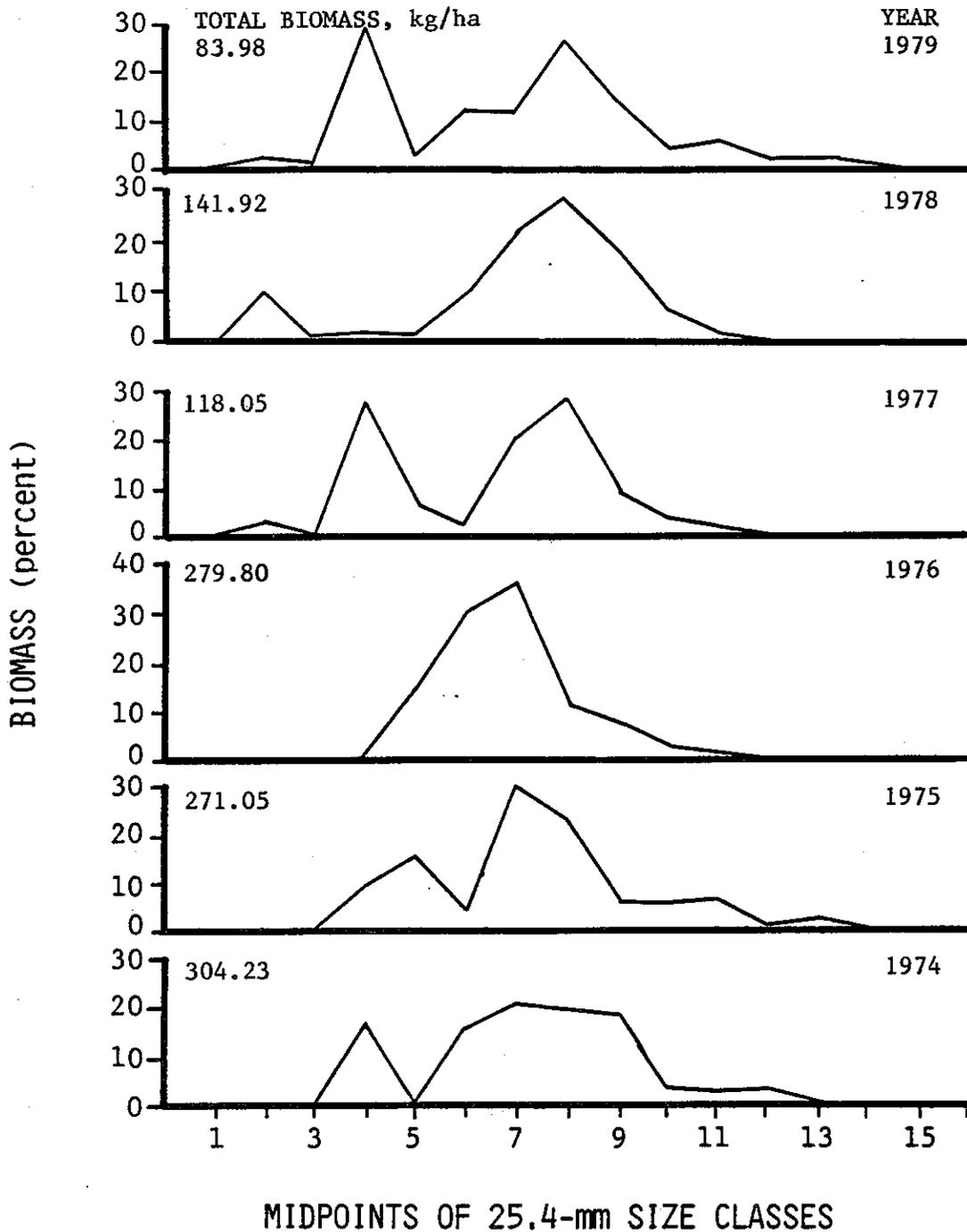


Figure 7. Length-frequency distributions of gizzard shad in John H. Kerr Lake from 1974 to 1979. Biomass is expressed as a percentage of the total biomass of gizzard shad collected each year in August rotenone samples of coves.

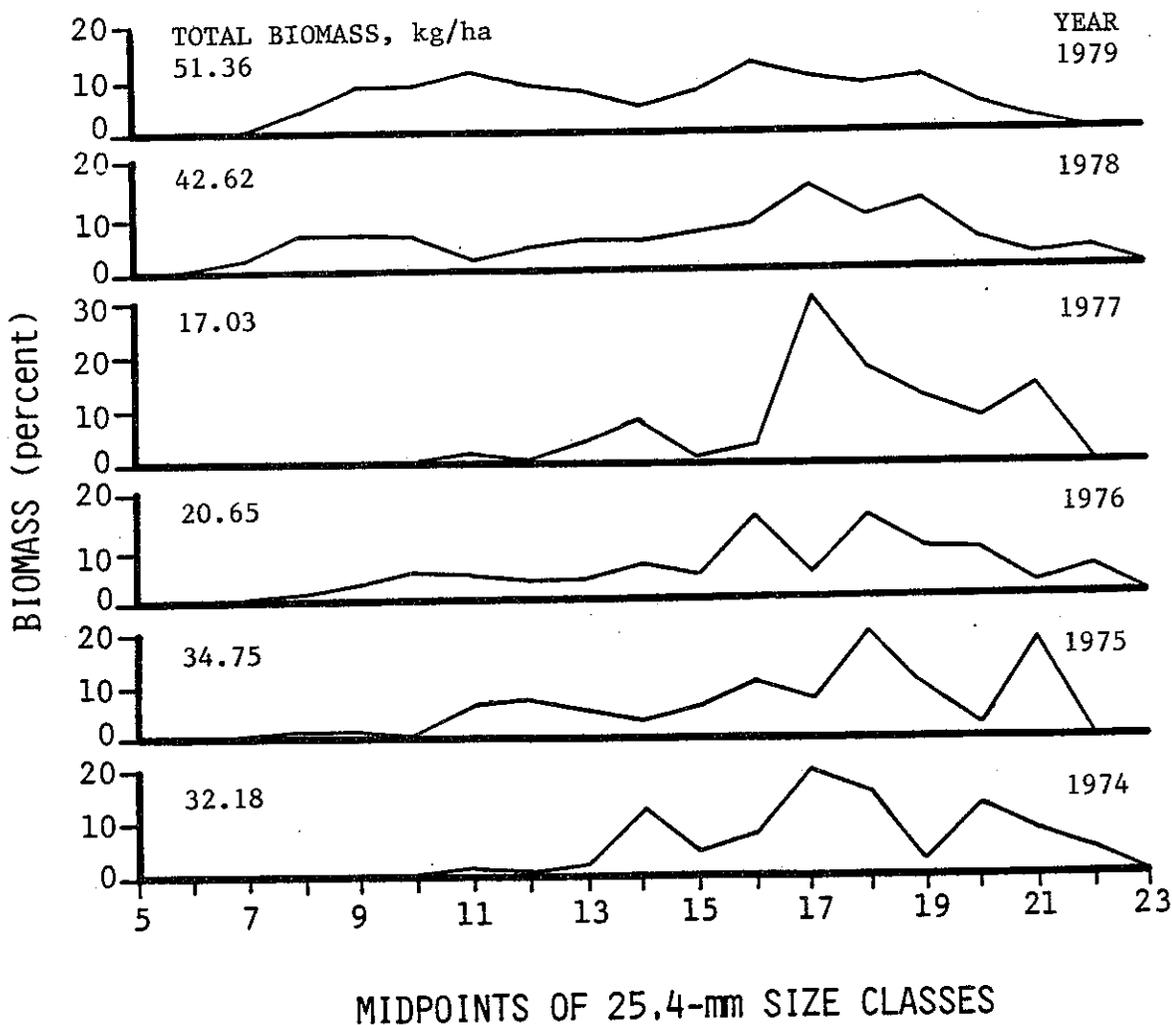


Figure 8. Length-frequency distributions of redhorses in John H. Kerr Lake from 1974 to 1979. Biomass is expressed as a percentage of the total biomass of redhorses collected each year in August rotenone samples of coves.

Shoals Lake ($2.91 \times 10^9 \text{ m}^3$) was 1.85 times larger than that in Kerr Lake ($1.58 \times 10^9 \text{ m}^3$). Unlike John H. Kerr Lake, Bull Shoals Lake also fluctuated over multiyear cycles due to consecutive years of drought and flooding (Figure 1). "Wet" years generally occurred at 5- to 7-year intervals, inundating large areas that had not been flooded for several years.

24. Although the degree to which a single year class dominates a population may vary directly with the magnitude of annual water-level

changes, patterns of year-class development were similar for reservoirs of the same operational classification. Ploskey, Nestler, and Aggus (1984) were able to correlate the abundance of small and intermediate-size fish to seasonal changes in surface area in reservoirs of the same type (e.g., hydropower storage), and in this study, the biomass of small fishes was related qualitatively to the biomass of large fish 1 to 4 years later.

25. Adverse effects of widely fluctuating water levels that significantly impair year-class development in most years can be compensated for by moderating drawdowns after spawning to enhance the survival of fish after a strong year class is produced. Because highly successful reproduction is usually limited to years of flooding (a relatively unpredictable phenomenon), attempts to manipulate water levels to produce strong year classes of fish may fail unless they coincide with a "wet" year. However, in wet years when the abundance of small fish is usually high in August, maintenance of above-average summer and fall water levels should increase the survival of young fish (Ploskey, Nestler, and Aggus 1984) and maximize year-class strength. To further compensate for the negative effects of extreme water-level changes, attempts should be made to provide adequate water levels during spring and summer of nonflooding years to increase the frequency of moderate year-class development, while still taking advantage of strong year classes in years of flooding.

26. Reservoirs without widely fluctuating water levels could benefit from some flooding of the surcharge zone in spring (assuming there is no serious conflict with other authorized project purposes) to maximize reproductive success. However, these reservoirs generally have some recruitment of fish every year, and thus are not as dependent upon suitable water-level changes.

27. Using the lagging process described in paragraph 11 and regression analysis, we were able to establish that the biomass of most harvestable sport and commercial fishes was positively related to the biomass of small fish of the same species or group that occurred 1 to 4 years earlier. Species or groups for which positive relations could

be identified were as follows: all sport fishes, largemouth bass, carp-suckers, crappies, common carp, and spotted bass at $P < 0.01$; flathead catfish, white crappie, and bluegills at $P < 0.05$; and sunfishes, golden redhorse, and channel catfish at $P < 0.10$.

28. These findings strongly support the hypothesis that the biomass of most harvestable-size sport and commercial fishes is determined to a significant extent by the abundance of these fishes when they were YOY in August, 1 to 4 years earlier. The variation in the biomass of large fish that was unexplained by the biomass of small fish in earlier years (one minus the coefficient of determination) ranged from 5 to 67 percent for the fish and year examined. Unexplained variation is primarily due to variations in mortality during year-class development and, perhaps, differences in sampling efficiency. If mortality were constant, we could more accurately estimate the biomass of large fish from a known biomass of small fish in earlier years. Unfortunately, widely varying rates of annual mortality make quantification impossible.

29. We did not list the regression equations described above because they were specific to the years and mortality rates observed. In addition, the regression equations were not considered to have quantitative value because predictions could only reflect proportional changes in the abundance of large fish from 1 to 4 years after a change in the abundance of small fish. Also, the process of lagging data was inexact for several reasons. First, we were forced to rely on changes in length-frequency distributions to estimate "years-to-recruitment" because no accurate age and growth data were available. As a result, our estimates reflect only the growth of an average fish in a year class and do not account for individuals of the same age that grew faster or slower than average. Second, some degree of subjectivity was involved in the lagging process whenever estimated growth rates were questionable or reflected the growth of less than about 60 percent of the fish assigned to a year class.

Condition of Large Largemouth Bass

30. Analysis of variance on the relative condition of largemouth

bass > 317.5 mm, by year, indicated that there were significant differences ($P < 0.05$) among years for both April and August estimates from Bull Shoals Lake. However, Duncan's Multiple Range Test showed that only the years of extreme condition differed significantly. Additionally, significant differences were observed between the condition of fish in April and August of the same year; April and August estimates were not correlated ($r = -0.14$; $P = 0.66$). Figure 9 illustrates changes in condition from April 1970 through August 1981.

31. Annual and seasonal changes in condition, leading to maxima in August 1973 and 1979 and minima in April 1978 and August 1980, can be

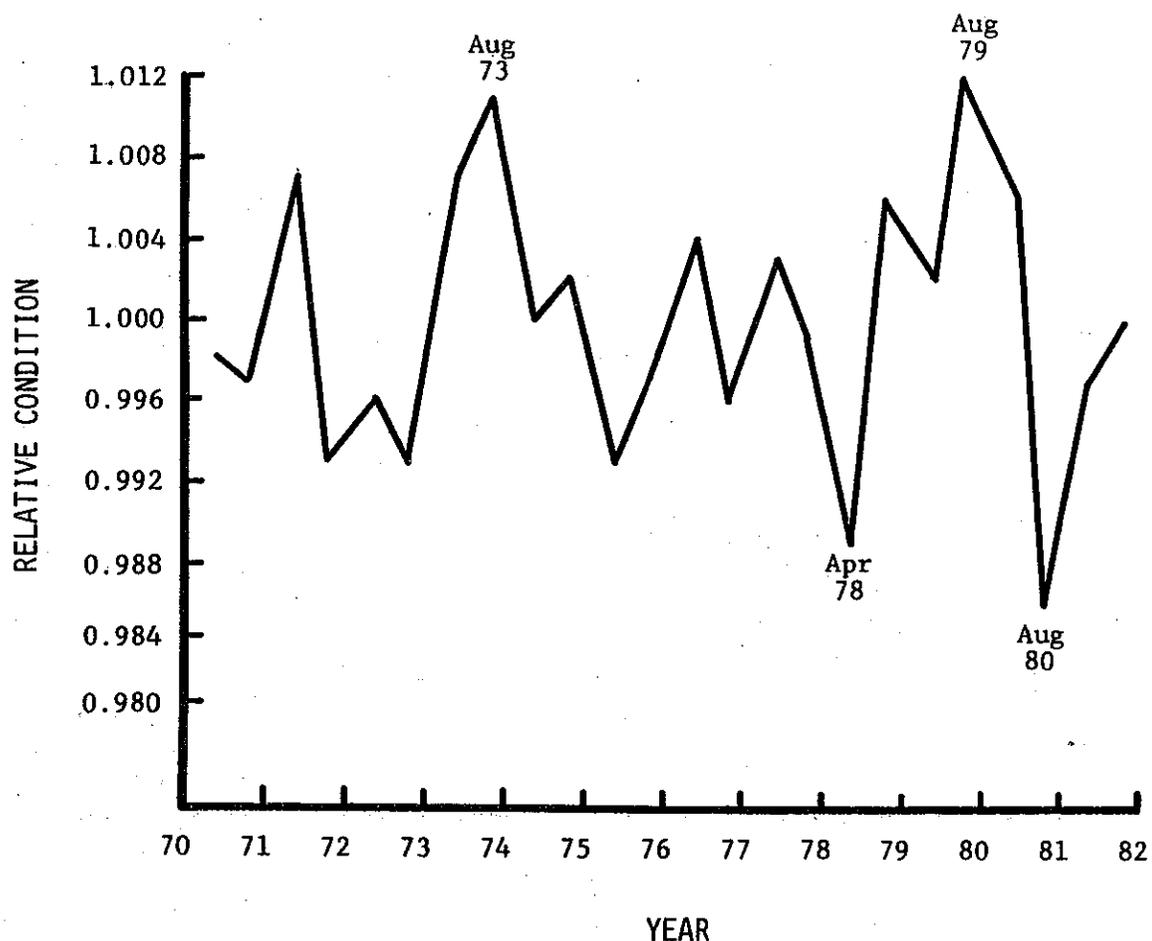


Figure 9. Changes in the relative condition of large (>317.5-mm) largemouth bass from 1970 to 1982 in Bull Shoals Lake. April and August estimates were plotted every year.

explained by trophic conditions created by water levels or temperature. Water levels in spring 1973 and 1979 were the highest recorded from 1972 to 1981 (Figure 1) and were followed in August 1973 and 1979 by the greatest abundance of young fish observed over the same 10-year period. Thus, the condition of largemouth bass > 317.5 mm was also exceptionally high (Figure 9). Fish of all species that were < 165 mm and available as forage for bass > 317.5 mm exhibited a biomass of 235 and 230 kg/ha in August 1973 and 1979, respectively. These biomass estimates represented 90 percent of the total biomass of all fish in 1973 and 87 percent in 1979. In an average year, usually less than 30 percent of total fish biomass is represented by fish < 165 mm.

32. Condition of large largemouth bass declined significantly between April 1977 and April 1978 (Figure 9) because of low water levels and poor prey production. Throughout most of 1977, surface elevations in Bull Shoals Lake were the lowest observed from 1972 to 1981 (Figure 1), averaging about 197 m (above mean sea level). As a result, the total biomass of small fish (< 165 mm) of all species in August 1977 was only 38.9 kg/ha or 14 percent of the total biomass of fish of all sizes. The poor condition of largemouth bass in April 1978 resulted from a poor forage base due to extremely low water levels in 1977 and a die-off of threadfin shad during the unusually cold winter of 1977-1978. Threadfin shad density (numbers per hectare) declined from 66.6 to zero between August 1977 and August 1978.

33. The extremely low condition of largemouth bass > 317.5 mm in August 1980 (Figure 9), following a steady decline since April, was more difficult to explain. Only four bass were collected in August, and mean condition estimates were less precise than in other years. In addition, water levels in Bull Shoals Lake in 1980 were low and relatively stable (Figure 1) because of drought. As a result, the biomass of YOY prey (prey ≤ 140 mm) in August 1980 was only 33.9 kg/ha, 14 percent of the total biomass of fish of all sizes. This scarcity of small prey may have contributed to the decline in condition of bass between April and August 1980. However, there was no shortage of prey between 140 and 165 mm (60 kg/ha), and largemouth bass have been reported to swallow

prey up to one-half their body length (Lawrence 1958), although they may not selectively feed on these larger, faster prey.

34. Another partial explanation concerns water temperatures and the distribution of large largemouth bass in relation to prey. If largemouth bass sought refuge in deep water from high water temperatures in coves, as reported by Coutant (1975) and Hall and Werner (1977), bass may have been somewhat isolated from prey. In addition, metabolic rate is an exponential function of temperature in fish, and high temperatures in 1980 would have increased the forage demands of bass above normal levels. Water temperatures were exceptionally high in summer 1980, averaging 31.5° C at the surface, 31° C at 3 m, and 30° C at 6 m on 15 July, as compared with temperatures of 25-29° C in other years.

35. Significant annual and seasonal changes in condition observed in this study support findings of Ploskey and Jenkins (1982), who demonstrated seasonal prey shortages for piscivores in DeGray Lake, Ark. Apparently, water levels in spring and summer play a key role in determining the condition of predators because they influence YOY prey production. Therefore, attempts to increase reproductive success by maintaining high spring and summer water levels should improve prey production and ultimately sport fish condition and survival.

Condition Indices Derived from Size-Class Data

36. We were unsuccessful in deriving a meaningful index of condition for large fish using size-class data from August rotenone samples. Unweighted and weighted indices derived from size-class data for large largemouth bass were not correlated with actual condition in August. Furthermore, size-class condition indices were not correlated with hydrologic variables, even at the 15-percent level of significance.

37. A major problem in calculating the condition of fish in a size class is that the only estimate of mean length is the midpoint of a size class. Condition indices calculated from size-class data apparently could not be correlated with actual condition for largemouth bass for two reasons. First, the mean weight of bass in a single size class

was determined more by the length of bass within the size class than by actual condition of individual fish. A single fish should be in good condition when well fed and in poor condition when starved. However, if fish in one size class were shorter (on average) than the midpoint length of the size class, the mean weight of fish in that size class would be less than expected for fish with a mean length equal to the midpoint length. As a result, a condition index would suggest that fish in the size class were in poor shape. Table 1 shows the minimum, mean, and maximum weights of a single fish in different size classes, as well as the maximum error when length was equal to the extremes of the size class, instead of the midpoint. Maximum errors (Table 1) are progressively larger for small size classes of bass because differences between extreme and mean weight were higher for small than for large size classes.

Table 1
Minimum and Maximum Possible Weights of a Single Largemouth
 Bass in Several 25.4-mm Size Classes*

Size Class range, mm	Minimum Weight kg	Mean Weight kg	Maximum Weight kg	± Maximum Error percent	
>317.5-342.9	0.415	0.504	0.597	-17.7	18.5
>342.9-368.5	0.597	0.696	0.801	-14.2	15.1
>368.5-393.7	0.801	0.910	1.028	-12.0	13.0
>393.7-419.1	1.028	1.146	1.273	-10.3	11.1
>419.1-444.5	1.273	1.405	1.543	- 9.4	9.8
>444.5-469.9	1.543	1.687	1.838	- 8.5	9.0
>469.9-495.3	1.838	1.995	2.156	- 7.9	8.1

* Maximum error was calculated by subtracting the mean weight from the minimum or maximum possible weights, dividing by the mean weight, and multiplying by 100.

38. An additional problem associated with accurately approximating mean weight for a size class was that, in most cases, too few fish were represented in an individual size class. The three smallest size classes, for which the potential error in accurately approximating mean weight was the highest (Table 1), contained more fish than the four

large ones. Thus, although the error in approximating mean weight decreased for larger size classes, the chance of mean length deviating from the midpoint length increased, as sample size decreased. Numbers of large largemouth bass in 25.4-mm size classes collected in August rotenone samples from Bull Shoals Lake (Table 2) illustrate that in 50 percent of the years sampled there were 1.1 or fewer fish per hectare represented in four of the seven size classes; in 30 percent of all size classes and years shown, no fish were represented. The chance of incorrectly approximating the actual condition of fish in a size class is simply too great when the number of fish present is so low. Even when 15.2 bass per hectare were present in the 342.9- to 368.5-mm size class in 1976, we estimated that the error in accurately estimating condition was 14 percent, because mean length was 2.6 mm below the midpoint length.

Table 2
Numbers of Largemouth Bass per Hectare in 25.4-mm Size
Classes in Every Year of Rotenone Sampling of Coves
in Bull Shoals Lake

Year	Size Class, mm						
	>317.5- 342.9	>342.9- 368.5	>368.5- 393.7	>393.7- 419.1	>419.1- 444.5	>444.5- 469.9	469.9- 495.3
1972*	0	0	0	0.9	0.9	0.9	0
1973*	0	2.2	3.3	3.3	1.1	1.1	0
1974	2.5	6.2	2.5	2.5	1.2	1.2	1.2
1975	8.5	1.3	1.4	1.3	1.4	1.4	1.4
1976	3.5	15.2	5.9	1.2	0	1.1	1.1
1977	13.2	4.4	4.4	1.5	0	0	0
1978	5.6	4.2	1.4	0	0	1.3	0
1979*	2.5	5.0	0	0	0	1.3	0
1980*	1.1	0	1.1	0	1.1	0	0
1981*	3.3	1.1	3.3	4.4	0	1.1	0

* Years in which 1.1 or fewer largemouth bass were represented in four of the seven size classes.

PART IV: CONCLUSIONS AND RECOMMENDATIONS

39. Qualitative results from this study indicate that increased production of small fish consistently increases the abundance of harvestable fish within 1 to 4 years, barring catastrophic mortality of young fish before they recruit to a harvestable size. Plots of changes in length-frequency distributions of select species over 6- to 10-year periods illustrated patterns of year-class development, and how growth, mortality, and the initial biomass of young fish interact to determine the biomass of large fish in later years. Regression analysis of lagged data on the biomass of small and large fish also showed that changes in the biomass of large fish were primarily determined by the biomass of small fish 1 to 4 years before. However, regression equations were specific to the reservoirs and years examined because of unpredictable annual variations in mortality, and therefore were of low predictive value for other impoundments. Although the abundance of small and intermediate-size fish of most species in August can be predicted from reservoir hydrologic data (Ploskey, Nestler, and Aggus 1984), we were unable to quantify similar relations for fish of harvestable size. Quantification attempts were thwarted by variable rates of mortality and growth among years and reservoirs, as well as the lack of accurate age and growth information.

40. The most important variable affecting the production of harvestable fish is mortality. Although many causes of post-hatching mortality are uncontrollable, major causes such as starvation and predation can be reduced by providing above-average water levels during the growing season, especially when YOY prey production is high due to spring flooding. Positive relations were documented between the condition (weight at a discrete length) of large largemouth bass and average summer surface area as well as maximum change in area per year. Above-average water levels in spring increase the production of aquatic plants, invertebrates, and YOY fishes, which serve as food for fish (Ploskey, Nestler, and Aggus 1984), and increased forage production reduces the chances of mortality by starvation. Above-average water levels in summer

also provide more food, but equally important, they increase available refuge for young fish, thereby reducing predatory mortality.

41. Although similar patterns of year-class development were observed in two different hydropower storage reservoirs and year-class production appeared to be controlled by similar environmental conditions, the degree to which a single year class dominates a population was related to the extent of annual and multiyear changes in water levels. Bull Shoals Lake, with sizable annual fluctuations and large year-to-year differences in average pool levels, had boom and bust patterns of fish recruitment, whereas John H. Kerr Lake, with moderate water-level changes, had more consistent fish recruitment.

42. To compensate for adverse effects of extreme annual or multi-year changes in water levels, summer and fall water levels should be maintained as high as possible in years of high spring runoff when reproductive success is high, as long as conflicts with other project purposes, such as flood control, do not result. Maintenance of above-average summer and fall water levels improves condition and survival of YOY fishes. In addition, efforts could be made to provide adequate spring and summer water levels (as described by Ploskey, Nestler, and Aggus 1984) during some average hydrologic years to obtain moderate reproduction and recruitment. In other words, efforts can be made to maximize the yield of large fish from periodic strong year classes while improving recruitment somewhat in otherwise poor years.

43. Storage reservoirs without extreme fluctuations in water levels and with fairly uniform fish recruitment can be considered free of adverse effects of water-level fluctuation. However, our findings suggest that even if annual recruitment is fairly consistent from year to year, year-class strength is significantly increased in years of above-average inflow, if more extensive spring flooding of the surcharge zone occurs.

44. We recommend the use of the regression equations derived by Ploskey, Nestler, and Aggus (1984) to assess impacts of water levels or operational regimes on reservoir fisheries. These equations can be used to predict the August abundance of small and intermediate-size fish from

hydrologic data for the previous fall, spring, and summer. Although the predicted abundance of young fishes may not always reflect proportional changes in the abundance of large fish in later years, it is the most reliable index available today.

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APPENDIX A: FISHES EXHIBITING POPULATION CHANGES
SIMILAR TO LARGEMOUTH BASS

Species or Group	Statistics		
	r	P	N
<u>Small</u>			
Black basses	0.99	0.0001	25
Spotted bass	0.94	0.0001	10
Common carp	0.91	0.0337	5
Flathead catfish	0.86	0.0013	10
All species	0.81	0.0001	25
Golden redhorse	0.78	0.0081	10
White bass	0.75	0.0012	15
Gizzard shad	0.73	0.0002	21
Redhorses	0.72	0.0010	17
Bluegill	0.67	0.0003	25
Threadfin shad	0.65	0.0025	19
Sport fishes	0.63	0.0008	25
Green sunfish	0.63	0.0008	25
Sunfishes	0.60	0.0014	25
Temperate basses	0.45	0.0517	20
Yellow perch	0.44	0.1004	15
Crappies	0.41	0.0450	24
Minnows	0.38	0.0637	25
White crappie	0.37	0.1063	20
<u>Intermediate</u>			
Black basses	0.99	0.0001	25
Common carp	0.89	0.0001	13
Golden redhorse	0.86	0.0001	10
White bass	0.78	0.0006	15
Warmouth	0.75	0.0001	16
Redhorses	0.72	0.0011	17
Sport fishes	0.71	0.0001	25
Temperate bass	0.70	0.0006	20
Threadfin shad	0.65	0.0059	16
Yellow perch	0.60	0.0526	11
Green sunfish	0.56	0.0040	25
Sunfish	0.53	0.0104	25
Bluegill	0.44	0.0264	25
Gizzard shad	0.34	0.0949	25
<u>Large</u>			
Black basses	0.98	0.0001	25
Yellow perch	0.89	0.0009	11
Pikes	0.86	0.0061	8
All species	0.66	0.0004	25
Freshwater drum	0.62	0.0536	10
Sunfishes	0.61	0.0012	25
Redhorses	0.56	0.0120	19
Gizzard shad	0.55	0.0046	25
Sport fishes	0.53	0.0068	25
Common carp	0.46	0.0267	24
Warmouth	0.44	0.0910	16
Carp suckers	0.39	0.1201	17
Crappies	0.30	0.1703	23

Note: Species or groups of fish divided into small, intermediate, or large sizes whose abundance was positively correlated ($\alpha < 0.20$) with that of largemouth bass of the same size in three hydropower storage reservoirs. Statistics presented are defined as follows:
r = correlation coefficient, P = probability of a larger F statistic, and N = sample size.