Methods for Including Reservoir Fishery Impacts in Reservoir Operations or Basinwide Assessments: A Case History for Black Bass in Bull Shoals Reservoir

by  Gene R. Ploskey, John M. Nestler, WES  
W. M. Bivin, Arkansas Game and Fish Commission
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Assessing Basinwide Impacts of Reservoir Operations

Methods for Including Reservoir Fishery Impacts in Reservoir Operations or Basinwide Assessments: A Case History for Black Bass in Bull Shoals Reservoir (TR EL-96-12)

ISSUE: Fishery biologists often associate strong year classes of many warmwater fishes with years of above-average inflow and water levels in reservoirs. In contrast, daily or weekly fluctuations may have negative effects on spawning and hatching. Negative correlations of catches of young-of-year fishes with flushing rate variables in mainstream reservoirs may result from high rates of water exchange that limit time available for nutrient processing and flush may young-of-year fish downstream from the reservoir. Standing crops of fish in storage reservoirs increase in response to increased rates of water exchange and area.

RESEARCH OBJECTIVE: The objective of this study was to compare three different methods for explaining the relationship between strong year classes in black bass to hydrologic parameters in a warmwater reservoir.

SUMMARY: Three methods area described for relating reproductive success of fish to reservoir hydrology, using the responses of young black bass in Bull Shoals Reservoir, Arkansas. (1) Hydrologic variables were calculated based upon inflow, release, volume, mean area, change in area, or selected ratios thereof from time segments ranging from one season to 2 years before fish sampling in August. This method produced 36 variables, many of them intercorrelated. Although time-consuming, this method provided the best, most easily interpreted predictive models. (2) Intercorrelation problems were avoided by using principal components as independent variables in regression analyses. Four components explained 95 percent of the variation. Although simple and fast, this method did not produce the most useful models. (3) Cosine functions were fit to monthly discharge of the unregulated White River (1920-49) and to end-of-month area of Bull Shoals Reservoir (1955-93). This method was time-consuming, but provided good explanations of variations in reservoir surface area and in largemouth and spotted bass standing crop. All three methods would be useful for quantifying effects of operations and hydrology on fish populations in multiple-use or basinwide assessments of water resources.

AVAILABILITY: The report is available on Interlibrary Loan Service from the U.S. Army Engineer Waterways Experiment Station (WES) Library, 3909 Halls Ferry Road, Vicksburg, MS 39180-6199; telephone (601) 634-2355. To purchase a copy, call the National Technical Information Service (NTIS) at (703) 487-4650. For help in identifying a title for sale, call (703) 487-4780. NTIS numbers may also be requested from the WES librarians.

About the Authors: The report was written by Mr. Gene R. Ploskey and Dr. John M. Nestler of the WES Environmental Laboratory and Mr. W. M. Bivin of Arkansas Game and Fish Commission. Point of contact at WES is Dr. Nestler, telephone (601) 634-3870.
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Preface

The research reported herein is part of a work unit entitled "Assessing Basin-Wide Impacts of Reservoir Operation," conducted as part of the Environmental Impact Research Program (EIRP), Work Unit 32882. The EIRP is sponsored by the Headquarters, U.S. Army Corps of Engineers (HQUSACE), and is assigned to the U.S. Army Engineer Waterways Experiment Station (WES) under the purview of the Environmental Laboratory (EL). Funding was provided under Department of Army Appropriation No. 96X3121GI, Construction General. EIRP was managed by Dr. Roger T. Saucier until the end of 1994, when EIRP's management was transferred to Dr. Russell F. Theriot. Technical Monitor during this study was Dr. John Bushman, HQUSACE.

The Principal Investigator for the study was Dr. John M. Nestler, Water Quality and Contaminant Modeling Branch (WQCM), Environmental Processes and Effects Division (EPED), EL. The study was conducted and the report prepared by Mr. Gene R. Ploskey and Dr. Nestler, both of WQCM, jointly with Mr. W. M. Bivin of the Arkansas Game and Fish Commission. Mr. Randy Sheldon, U.S. Army Engineer District, Little Rock, supplied hydrologic data for Bull Shoals Lake. Biologists with the Arkansas Game and Fish Commission and the former National Reservoir Research Program collected the 34 years of cove-rotenone sample data used in this study.

Technical reviews of this report were provided by Mses. L. Toni Schneider and Dottie Hamlin-Tillman.

This investigation was performed under the general supervision of Dr. John W. Keeley, Director, EL; Mr. Donald L. Robey, Chief, EPED; and Dr. Mark S. Dortch, Chief, WQCM.

At the time of the publication of this report, Director of WES was Dr. Robert W. Whalin. Commander was COL Bruce K. Howard, EN.
This report should be cited as follows:


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1 Introduction

Background

Fishery biologists often associate strong year classes of many warmwater fishes with years of above-average inflow and water levels in reservoirs. Hydrologic patterns increasing year-class strength usually involve substantial increases in the inundated area, occur over several seasons or years, and may be accentuated by topography, soil conditions, and vegetation (Wood and Pfitzer 1960; Ploskey 1986). In contrast, daily or weekly fluctuations may have negative effects on spawning and hatching (Shields 1957; Bennett 1975; Heisey, Mathur, and Magnusson 1980; Bennett, Maughan, and Jester 1985; Kohler, Sheenan, and Sweatman 1993), although not necessarily year-class strength (Gasaway 1970; Estes 1971; Kohler, Sheenan, and Sweatman 1993). Responses of many species are positive and more pronounced in hydropower storage reservoirs—storage ratio (mean volume/annual discharge) > 0.165 years—than they were in hydropower mainstream impoundments—storage ratio < 0.165 years (Aguss and Lewis 1977). Negative correlations of catches of young-of-year (age-0) fishes with flushing rate variables in mainstream reservoirs (Ploskey, Agus, and Nestler 1984, 1993) may result from high rates of water exchange that limit time available for nutrient processing and flush many young-of-year fish downstream from the reservoir. Standing crops of fish in storage reservoirs increase in response to increased rates of water exchange and area. In such years, flushing rate and standing crop approach values more typically observed in productive mainstream impoundments (Agus and Lewis 1977).

Successful reproduction and development of strong year classes of fish with years of high water inundating vegetation in reservoirs are repeatedly documented in the literature (Benson 1968; Beckman and Elrod 1971; Nelson and Walburg 1977; Nelson 1978; Ploskey 1986; Kohler, Sheenan, and Sweatman 1993). Catches of many young fishes are highest in high-water years, in spite of substantial dilution by increased water volume. Years of high inflow in storage reservoirs increase surface area to absorb solar insolation, inundation of terrestrial areas, nutrient loadings (Westerdahl et al. 1981; Johnson and Ford 1987), and primary and secondary production (Benson and Cowell 1967; Mitchell 1975; Vollenweider 1975; Ostrofsky and Duthie 1978; McCammon and von Geldern 1979; Grimard and Jones 1982). Flooded vegetation affords
fishes optimum spawning and nursery habitat, e.g., yellow perch (Beckman and Elrod 1971), northern pike (Benson 1968; Hassler 1970), buffaloes (Moen 1974), and common carp (Gabel 1974), that enhance their survival (Martin et al. 1981).

Responses of largemouth bass (*Micropterus salmoides*) and to a lesser extent spotted bass (*M. punctulatus*) often have been studied because of black bass prominence in warmwater fisheries and their sensitivity to water-level changes (Jenkins 1970). Smallmouth bass (*M. dolomieu*) responses are different from those of largemouth and spotted bass (Aggus and Elliott 1975), underscoring the need for care in assigning a species to a reproductive guild (Austen, Bayley, and Menzel 1994). Many factors are believed to be linked to increased reproductive success of largemouth bass responses in wet years, including increased nutrient loading (Wright 1950; Wood 1951; Shirley and Andrews 1977; Aggus 1979), primary production (Benson 1968), and inundation of vegetated terrestrial vegetation (Bryant and Houser 1971; von Geldern 1971; Keith 1975; Aggus and Elliott 1975; Rainwater and Houser 1975; Houser and Rainwater 1975; Shirley and Andrews 1977; Strange, Kittrell, and Broadbent 1982). Inundation of terrestrial vegetation usually increases food availability, condition factors, or growth (Moffet 1943; Stroud 1948; Wright 1950; Jackson 1958; Applegate, Mullan, and Morais 1967; Mullan and Applegate 1968; Allan and Romero 1975; Aggus and Elliot 1975; Houser and Rainwater 1975; Rainwater and Houser 1975; Vogele and Rainwater 1975; Summerfelt and Shirley 1978; Shelton et al. 1979; Timmons, Shelton, and Davies 1980).

**Scope**

Three methods for quantifying empirical relations between reservoir hydrology and reproductive success of young black basses are described and compared in the following text, as indexed by their standing crop in August cove-roteneone samples. Space limitations narrowed the focus of the investigation, but the methods are applicable to data for other gears and species, as long as sufficient years of data acquired by consistent methods are available.

General methods of analysis are illustrated here rather than deriving regression equations specifically for predictive purposes. Predictors for Bull Shoals Lake probably would have limited utility for other impoundments, because magnitude of effects appears to vary widely among reservoirs (Ploskey, Aggus, and Nestler 1984). Bull Shoals Reservoir in northwest Arkansas is featured here because it was sampled with consistent methods for many consecutive years. Also, black bass populations were intensively studied and described in some of those years (Bryant and Houser 1971; Keith 1975; Aggus and Elliott 1975; Vogele 1975, 1981; Vogele and Rainwater 1975; Rainwater and Houser 1975; Houser and Rainwater 1975). Predictors developed in earlier assessments are compared with ones developed from a much expanded data set.
Impounded in 1950, Bull Shoals Lake is an 18,400-ha, hydropower-storage reservoir on the White River in northwest Arkansas (15,100 ha) and southwest Missouri (3,300 ha). In a very wet year, surface area can increase to about 28,000 ha or 1.5 times normal-pool area. The fluctuation zone between minimum and normal pool is inundated for part of every year and is relatively barren of vegetation except for some standing and fallen timber (Keith 1975). The flood zone, which was significantly inundated in only 8 of 39 years (21 percent) between 1955 and 1993, supports extensive deciduous woody and herbaceous vegetation. The reservoir has a drainage area of 15,672 km², mean storage ratio of 0.91 (range = 0.44-2.93) years, and maximum and mean depths of 61.3 and 20.4 m, respectively.

Total dissolved solids average 150 mg/l (Leidy and Jenkins 1977), and median concentrations of total phosphorus, total nitrogen, and chlorophyll a were 0.015, 0.530, and 3.9 mg/l, respectively, in the mid 1970s (U.S. Environmental Protection Agency 1978).
2 Methods

Reservoir hydrology data summarized as elevation-area-volume tables and daily inflows, releases, and water surface elevations for the period 1955-1993 were furnished by the U.S. Army Engineer District, Little Rock, Arkansas. Independent variables were derived from area or volume rather than elevation so that dimensions would be consistent with those for nutrient loading, reservoir productivity, and fish standing crop. Volume and area were calculated from elevation using

$$VOL = 105,747.84 - 112.45 \times ELEV - 0.03 \times ELEV^2$$

$$AREA = 326,448.88 - 351.74 \times ELEV - 0.10 \times ELEV^2$$

where

$$VOL = \text{volume in m}^3 \times 10^6$$

$$ELEV = \text{elevation in m mean sea level}$$

$$AREA = \text{surface area in ha}$$

Both equations had coefficients of determination ($r^2$) $> 0.999$, $p < 0.0001$, and $N = 40$.

The annual hydrograph was redefined as running from September through August of the next year so that the last month coincided with annual cove-rotenone sampling of fish.

In the segmented-temporal method, variables were derived based upon flow, volume, area, or select ratios thereof from time segments potentially affecting fish reproductive success (Table 1). Our concern during the variable-creation phase was completeness rather than independence (lack of intercorrelation). In the principal components method, 13 hydrologic variables were analyzed (footnoted in Table 1) to create 4 independent variables characterizing the most significant hydrologic trends (Table 2). Successive principal components prohibit intercorrelations. In the harmonic method, a cosine function was fit to each annual hydrograph of surface area (Trost
<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Multiple Season or Year</strong></td>
<td></td>
</tr>
<tr>
<td>CASUSP¹</td>
<td>Change in area, summer-spring = mean of hectares on 31 March, 30 April, and 31 May minus mean on 30 June, 31 July, and 31 August of year - 1 divided by mean on 30 June, 31 July, and 31 August of year - 1.</td>
</tr>
<tr>
<td>CASUSP2¹</td>
<td>Change in area, summer-spring = mean of hectares on 30 April, 31 May, and 30 June minus mean on 30 June, 31 July, and 31 August of year - 2 divided by mean on 30 June, 31 July, and 31 August of year - 2.</td>
</tr>
<tr>
<td>CASUSU</td>
<td>Change in area, summer-summer = mean of hectares on 30 June, 31 July, and 31 August minus mean for the same dates in year - 1 divided by mean on the same dates of year - 1.</td>
</tr>
<tr>
<td>CASUSU2</td>
<td>Change in area, summer-summer = mean of hectares on 30 June, 31 July, and 31 August minus the mean for the same dates in year - 2 divided by mean on the same dates of year - 2.</td>
</tr>
<tr>
<td>HADFLDS¹</td>
<td>Ha-days of flooding during spawning (15 April - 1 June) = ( \log_{10}(\text{sum of ha-days} \times 10^5 \text{ when elevation &gt; 654 mean sea level} + 1) ). Elevation 654 in Bull Shoals is the bottom of flood pool.</td>
</tr>
<tr>
<td>HADFLDSS¹</td>
<td>Ha-days of flooding, spawning-sampling (15 April - 15 August) = ( \log_{10}(\text{sum of ha-days} \times 10^3 \text{ at elevation &gt; 654 mean sea level} + 1) ).</td>
</tr>
<tr>
<td>HADFLDPS¹</td>
<td>Ha-days of flooding, postspawning (1 June - 15 August) = ( \log_{10}(\text{sum of ha-days} \times 10^3 \text{ when elevation &gt; 654 mean sea level} + 1) ).</td>
</tr>
<tr>
<td>XVOL1_8¹</td>
<td>Mean volume = mean of ( \log_{10}(\text{end-of-month m}^3 \times 10^6) ), January - August.</td>
</tr>
<tr>
<td>SINF1_8¹</td>
<td>Mean inflow = ( \log_{10}(\text{m}^3 \times 10^6) ), January - August.</td>
</tr>
<tr>
<td>SREL1_8¹</td>
<td>Mean release = ( \log_{10}(\text{m}^3 \times 10^6) ), January - August.</td>
</tr>
<tr>
<td>FR1_8</td>
<td>Flushing rate = sum of release volume/mean volume, January - August.</td>
</tr>
<tr>
<td>RIR1_8</td>
<td>Ratio of inflow to release = inflow/release, January - August.</td>
</tr>
<tr>
<td><strong>Fall (Year - 1)</strong></td>
<td></td>
</tr>
<tr>
<td>XVOL9_11</td>
<td>Mean volume = mean of ( \log_{10}(\text{m}^3 \times 10^6) ) on 30 September, 31 October, and 30 November.</td>
</tr>
<tr>
<td>SINF9_11¹</td>
<td>Sum of inflow = ( \log_{10}(\text{sum of m}^3 \times 10^6) ), September - November.</td>
</tr>
<tr>
<td>SREL9_11¹</td>
<td>Sum of release = ( \log_{10}(\text{sum of m}^3 \times 10^6) ), September - November.</td>
</tr>
<tr>
<td>FR9_11</td>
<td>Flushing rate = sum of release/mean volume, September - November.</td>
</tr>
<tr>
<td>RIR9_11</td>
<td>Ratio of inflow to release = inflow/release, September - November.</td>
</tr>
<tr>
<td>XA9_11¹</td>
<td>Mean area = mean of ( \log_{10}(\text{hectares}) ) on 30 September, 31 October, and 30 November.</td>
</tr>
<tr>
<td>PA9_11</td>
<td>Perimeter area = mean of ( \log_{10}(\text{hectares over depths} \leq 6 \text{ m}) ) on 30 September, 31 October, and 30 November.</td>
</tr>
<tr>
<td>CA9_11</td>
<td>Change in area = (30 November area - 30 September area)/30 November area.</td>
</tr>
</tbody>
</table>

¹ Temporal variables used in principal components analysis.

(Continued)
<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Spring</strong></td>
<td></td>
</tr>
<tr>
<td>XVL3.5</td>
<td>Mean volume = mean of log$_{10}$ (m$^3 \times 10^5$) on 31 March, 30 April, and 31 May.</td>
</tr>
<tr>
<td>SINF3.5</td>
<td>Sum of inflow = log$_{10}$ (sum of m$^3 \times 10^6$), March - May.</td>
</tr>
<tr>
<td>SREL3.5</td>
<td>Sum of release = log$_{10}$ (sum of m$^3 \times 10^6$), March - May.</td>
</tr>
<tr>
<td>FR3.5</td>
<td>Flushing rate = sum of release/mean volume, March - May.</td>
</tr>
<tr>
<td>RIR3.5</td>
<td>Ratio of inflow to release = inflow/release, March - May.</td>
</tr>
<tr>
<td>XA3.5$^1$</td>
<td>Mean area = mean of log$_{10}$ (hectares) on 31 March, 30 April, and 31 May.</td>
</tr>
<tr>
<td>PA3.5</td>
<td>Perimeter area = mean of log$_{10}$ (hectares over depths ≤ 6 m) on 31 March, 30 April, and 31 May.</td>
</tr>
<tr>
<td>CA3.5</td>
<td>Change in area = (31 March area - 31 May area)/30 March area.</td>
</tr>
<tr>
<td><strong>Summer</strong></td>
<td></td>
</tr>
<tr>
<td>XVL6.8</td>
<td>Mean volume = mean of log$_{10}$ (m$^3 \times 10^5$) on 30 June, 31 July, and 31 August.</td>
</tr>
<tr>
<td>SINF6.8</td>
<td>Sum of inflow = log$_{10}$ (sum of m$^3 \times 10^6$), June - August.</td>
</tr>
<tr>
<td>SREL6.8</td>
<td>Sum of release = log$_{10}$ (sum of m$^3 \times 10^6$), June - August.</td>
</tr>
<tr>
<td>FR6.8</td>
<td>Flushing rate = sum of release/mean volume, June - August.</td>
</tr>
<tr>
<td>RIR6.8</td>
<td>Ratio of inflow to release = inflow/release, June - August.</td>
</tr>
<tr>
<td>XA6.8$^1$</td>
<td>Mean area = mean of log$_{10}$ (hectares) on 30 June, 31 July, and 31 August.</td>
</tr>
<tr>
<td>PA6.8</td>
<td>Perimeter area = mean of log$_{10}$ (hectares over depths ≤ 6 m) on 30 June, 31 July, and 31 August.</td>
</tr>
<tr>
<td>CA6.8</td>
<td>Change in area = (30 June area - 31 August area)/30 June.</td>
</tr>
</tbody>
</table>

1991). Independent variables were obtained from coefficients of resulting equations. The derivation of harmonic variables is described in greater detail later in following paragraphs.

The primary advantage of harmonic analysis is its ability to describe complex patterns in time series data with relatively few, easily interpretable coefficients. Harmonic analysis is useful if underlying hydrologic processes approximate harmonic functions (Nestler 1993; Nestler and Long 1994). Harmonic analysis typically generates four coefficients: mean, period, phase, and amplitude. These coefficients can be used singly or in various combinations to generate hydrologic summary variables.

For streams, log$_{10}$-transformed discharge data can be used as a surrogate for elevation because both water depth and water velocity can usually be expressed as simple power functions of discharge at a given cross section. Harmonic analyses of the White River discharge data were based on
Table 2
Abbreviations and Correlations That Characterize Statistical Hydrologic Variables Created by Principal Components Analysis of 13 Segmented-Temporal Hydrologic Variables (footnoted in Table 1) Over 34 years

<table>
<thead>
<tr>
<th>Variable</th>
<th>Characteristics</th>
</tr>
</thead>
<tbody>
<tr>
<td>PRIN1</td>
<td>The first principal component was significantly correlated with mean volume, January - August ( (r = 0.97) ); mean area, March - May ( (r = 0.96) ); ha-days of flooding, 15 April - 15 August ( (r = 0.93) ); ha-days of flooding, 15 April - 1 June ( (r = 0.91) ); sum of releases, January - August ( (r = 0.91) ); mean summer area ( (r = 0.89) ), and ha-days of flooding, 1 June - 15 August ( (r = 0.83) ), change in area, summer-spring over 2 years ( (r = 0.71) ) and 1 year ( (r = 0.55) ).</td>
</tr>
<tr>
<td>PRIN2</td>
<td>The second principal component was significantly correlated with sum of release ( (r = 0.85) ), sum of inflow ( (r = 0.77) ), and mean area ( (r = 0.72) ) in fall of year - 1. It also was correlated with change in area from summer to spring over 1 year ( (r = -0.64) ) and 2 years ( (r = -0.37) ).</td>
</tr>
<tr>
<td>PRIN3</td>
<td>The third principal component was significantly correlated with ha-days of flooding from 1 June through 15 August ( (r = -0.42) ), and with change in area from summer to spring over 1 year ( (r = 0.38) ) and 2 years ( (r = 0.36) ).</td>
</tr>
<tr>
<td>PRIN4</td>
<td>The fourth principal component was only significantly correlated with the sum of releases in fall of year - 1 ( (r = 0.35) ) and change in mean area, summer to spring ( (r = 0.35) ) over 2 years.</td>
</tr>
</tbody>
</table>

Stream-gauging records from the White River near Flippin, AR, from 1920 to 1949, before Bull Shoals Lake was impounded. A cosine function was fitted to monthly maximum, mean, and minimum discharges in nonlinear regression using

\[
HAR_i = AMP \times \cos((MONTH_i + PHS) \times 2.0 \times \pi)
\]

where

\[
HAR_i = \text{stage (m) or log}_{10}^{-}\text{transformed discharge (m}^3\text{s}^{-1}) \text{ standardized to a mean of 0.0 for month } I
\]

\[
AMP = \text{amplitude}
\]

\[
MONTH_i = (\text{month}^i - 0.5)/12, \text{ with } I \text{ from 1 to 12 beginning with September and ending in August}
\]

\[
PHS = \text{phase}
\]

\[
\pi = 3.142
\]

Similarly, a cosine function was fitted to end-of-month surface areas of Bull Shoals Lake using

\[
HECT_i = AMP \times \cos((MONTH_i + PHS) \times 2.0 \times \pi)
\]
where

\[ HECT_i = \log_{10} \text{(surface area, in } h < \text{ No) standardized to a mean of 0.0 for month } I \]

\[ AMP = \text{amplitude} \]

\[ MONTH_i = (\text{month}^i - 0.5)/12, \text{ with } I \text{ from 1 to 12 beginning with September and ending in August} \]

\[ PHS = \text{phase} \]

\[ \pi = 3.142 \]

Three types of variables derived from coefficients of harmonic equations and related information were used in regression analysis (Table 3). The first type described the phase shift of a cosine function fitted to end-of-month surface areas for the lake from another cosine function fitted to monthly discharge of the unregulated White River. Similar phases should be conducive to successful reproduction because native fishes in the southern United States evolved in rivers or backwaters of rivers, and their reproduction should be keyed to natural hydrographs. The second type quantified patterns of change in reservoir area each year based upon a redefined water year (September to August). The third type was based upon antecedent hydrologic conditions.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>PHS_SHFT</td>
<td>Phase Shift = absolute value of difference in phases of White River discharge and Bull Shoals surface area. It describes difference in timing between peak reservoir surface area and peak discharge in unregulated White River.</td>
</tr>
<tr>
<td>A_PHSSFT</td>
<td>Antecedent phase shift = same as PHS_SHFT above but for year - 1 evaluates effect of antecedent conditions.</td>
</tr>
<tr>
<td>AMP</td>
<td>Amplitude = difference between minimum and maximum areas as obtained from harmonic analysis - describes maximum excursion of surface area in a year as part of general annual pattern.</td>
</tr>
<tr>
<td>D_HA</td>
<td>Difference in hectares = difference in mean surface area between year of cove rotenone sample and previous year after subtraction of lowest recorded surface area - describes change in surface area from previous year proportioned to maximum possible change in surface area.</td>
</tr>
<tr>
<td>ANTCEDNT</td>
<td>Antecedent conditions = a complex variable that describes antecedent mean area change, amplitude, and phase shift, i.e., standardized estimates of D_HA plus A_AMP minus A_PHSSFT.</td>
</tr>
<tr>
<td>COR_RMSE</td>
<td>Corrected root mean square error = the sum of the residuals remaining after harmonic analysis of concurrent years surface areas divided by previous year's amplitude. It describes how well the harmonic fit the observed area data.</td>
</tr>
</tbody>
</table>
determined by harmonic analysis of surface area data in the year before collection of cove-rotenone samples (Table 3).

Rotenone samples of fish standing crop were collected annually from three coves representing the upper, middle, and lower regions of Bull Shoals Lake. Sampling was done by the State of Arkansas before 1963 and after 1982 and by the former National Reservoir Research Program, with help from State biologists, in intervening years. Fish sampled from 1960 through 1971 were not measured but were categorized as age-0, intermediates, and adults. Standing crop data were used to represent the age-0 category for these years. Standard 0.4- to 1.9-ha (mean = 1.1 ha) coves were sampled with rotenone (Grinstead et al. 1977; Davies and Shelton 1983) in August every year from 1972 through 1993. All fish were measured to the nearest 25.4-mm length class. Cove depths were sufficient to include part of the thermocline. No adjustments were made for nonrecovery of fish by length class nor for differences in distributions between cove and open-water areas because our comparisons were among years for one lake.

Standing crop variables were defined to approximate the biomass of age-0 and age-1 black basses based upon length in August of a year of maximal growth. However, classes of variables were referred to as small (<140-mm largemouth bass and <114-mm spotted and smallmouth bass) or intermediate (140- to 241-mm largemouth bass and 114- to 216-mm spotted and smallmouth bass) to show that they were based upon length rather than age. Decisions about maximum lengths of the two age groups in mid-August were easy for years when length at age data were available (e.g., Bryant and Houser 1971; Agkus and Elliott 1975; Voge and 1975). Also examined were 25.4-mm length-frequency plots for probable maximum lengths for the first two modal groups. Kilogram/hectare was used instead of numbers/hectare because weight is more sensitive to fish length than numbers within such broad length classes (25.4 mm). All dependent standing crop variables were transformed by taking the log_{10} (kilogram/hectare + 1). Within-year coefficients of variation (standard deviation/mean × 100) of geometric mean standing crops were examined to assess the relative effectiveness of cove-rotenone sampling for each species and length class.

Correlation, linear regression, and multiple-linear regression analyses were used to find the best single or multiple regression models for predicting standing crops of small and intermediate black bass. Independent hydrologic variables were matched by year with standing crop variables for small bass. Standing crops of intermediate black bass often are referred to as next year’s intermediates because they were matched with the previous year’s hydrology. Multiple-regression models were built from hydrologic variables with minimal intercorrelation (α < 0.05 unless specifically noted). Two years of data were withheld from the regression analysis, one high-water year (1979) and an average-water year (1993), to determine whether models would accurately forecast year-class strength in those years. Strong year classes were defined
as meeting or exceeding the 75th percentile standing crop of each species and length class over all years.
3 Results and Discussion

Intercorrelations among hydrologic variables at $\alpha = 0.05$ were very common for segmented-temporal variables, nonexistent for principal component variables, and limited in harmonic variables. An example intercorrelation among segmented-temporal variables was the correlation ($N = 35$) of January-August mean volume with 29 other variables, 13 with $r > 0.80$, 8 with $r = 0.60-0.79$, and 8 with $r = 0.40-0.59$. Only six temporal variables were independent of January-August mean volume. They included the ratio of inflow to release during three periods (September-November, January-August, and March-May) and three previous fall variables (release, flushing rate, and change in area). About 24 percent of the harmonic variables defined in Table 3 showed some intercorrelation. Amplitude was positively correlated with the difference between mean area in the present and previous year ($r = 0.54$) and with antecedent condition ($r = 0.49$), which summarizes the previous year's mean areal change, amplitude, and phase. Antecedent condition was inversely correlated with antecedent phase shift ($r = -0.72$) and positively correlated with antecedent amplitude ($r = 0.54$). Antecedent amplitude was inversely related to the difference between mean areas in the present and previous year ($r = -0.44$).

The first four principal components (Table 2) explained 91 percent of the variation in 13 segmented-temporal variables, which were identified by footnote in Table 1. Successive principal components contributed 62, 20, 5, and 4 percent to total explained variation. Unlike the first two, the third and fourth principal components were impossible to interpret. In preliminary testing, principal components were run on all 36 segmented-temporal variables (Table 1), but these components explained less of total hydrologic variation (PRIN1 = 54 percent; PRIN2 = 17 percent) and our interpretation of their meaning was the same as for 13 variables. Harmonic functions fitted to annual patterns in reservoir surface area explained 84 percent of the variation over 39 years (Figure 1). Harmonic predictions were most accurate at surface areas $\leq$ normal-pool area (18,400 ha) and less accurate for areas associated with flood-pool elevations (Figures 1 and 2).

Harmonic analysis of discharge of the unregulated White River and of end-of-month reservoir area indicated a phase shift of 4 months at low discharge, 2.5 months at mean discharge, and 1.5 months at high discharge (Figure 3). However, phase shift seldom was correlated with catches of young black
Regression plot of observed end-of-month surface areas as a function of predicted surface areas from cosine functions fit to area data of Bull Shoals Lake (1955-1993)

Exceptions include the biomass of small largemouth bass with phase shift ($r = -0.36; P = 0.0416$).

Examination of 22 years of coefficients of variation (CV) of standing crop variables revealed that largemouth and spotted bass were more effectively sampled than smallmouth bass. Average CV (followed by the percent of years with CV < 50 percent in parentheses were 48.8 (59), 39.1 (68), and 72.4 (32) percent for small largemouth bass, spotted bass, and smallmouth bass, respectively. They were 43.8 (50), 49.6 (68), and 78.5 (32) percent for intermediate largemouth, spotted, and smallmouth bass, respectively.

The biomass of intermediate largemouth bass was positively correlated with that of small largemouth bass in the previous year ($r = 0.77; P = 0.0001$);
Figure 2. End-of-month surface areas predicted by a harmonic analysis (lower curve) and residuals (upper curve) for Bull Shoals Lake, Arkansas, from 1955 through 1993.
Figure 3. Cosine functions fitted to minima (L), mean (M), and maxima (H) end-of-month, log$_{10}$-transformed surface areas of Bull Shoals Lake (top) from 1955 through 1990 and to the mean of monthly log$_{10}$-transformed discharge of the unregulated White River from 1920 through 1950 (Differences indicated phase shift)
N = 20). Comparable statistics for correlations of standing crops of intermediate length classes with small classes the previous year were r = 0.55, P = 0.0123, and N = 20 for spotted bass and r = 0.30, P = 0.2, and N = 20 for smallmouth bass.

Species composition by weight of small black bass varied significantly among years depending upon hydrologic conditions (Figure 4). Largemouth bass and spotted bass made up most of the biomass of small black bass under all conditions, with the largemouth percentage increasing in years with greater flooding of terrestrial vegetation. The proportion of spotted and smallmouth bass decreased gradually as flooding increased.

Only one significant correlation was obtained between the standing crop of young smallmouth bass and reservoir hydrologic variables. The biomass of intermediate smallmouth bass was inversely related with the January-August ratio of inflow to release in the previous year (r = -0.50; P = 0.0239). The biomass of small smallmouth bass was inversely related to the difference in mean area between consecutive years but only at P = 0.1354.

Many significant positive correlations were found for the standing crops of both length classes of largemouth and spotted bass and hydrologic variables. Small largemouth and spotted bass were significantly correlated with ha-days of flooding during each of three time periods, i.e., spawning, spawning until sampling, and postspawning (Figure 5). The fit of regression lines was slightly better (3 to 6 percent) for the postspawning period than for the spawning period.

The best single-variable models for predicting standing crop of small largemouth bass in August and next year's crop of intermediate largemouth bass were derived in the segmented-temporal method. Summer perimeter area was the most significant correlate with standing crop of both length classes. Regressions based upon perimeter area in summer has $r^2$ statistics that were at least 10 percent higher than those based upon amplitude from the harmonic method or upon the first principal component (Figure 6).

All three methods of deriving hydrologic variables produced single-variable regression models of nearly equal quality for young spotted bass (Figure 7). Amplitude from the harmonic method and the first principal component yielded regressions with $r^2$ statistics that were equal to or only 3 to 6 percent less than those of perimeter area models. Mean perimeter area was a useful predictor of small spotted bass biomass when calculated for the June-August segment of the hydrograph and of next year's intermediate spotted bass biomass when calculated for the March-May segment.

The biomass of young largemouth bass was predicted equally well by two-variable models derived from all three methods, but the best predictor of next year's intermediate largemouth bass came from the segmented temporal method (Figure 8). Regardless of approach, the first variable entered in the model had a strong positive effect—mean parameter area for June-August
Figure 4. Percent contribution by kilograms/hectare of small largemouth (LMB), spotted (SB), and smallmouth (SMB) bass to the total standing crop of small black bass predicted from ha-days of flooding from 1 June to 15 August (N = 34) (Small refers to largemouth bass <140 mm and spotted and smallmouth bass <114 mm. Regression statistics were $r^2 = 0.38$ and $P = 0.0001$ (largemouth bass), $r^2 = 0.35$ and $P = 0.0002$ (spotted bass), and $r^2 = 0.16$ and $P = 0.0158$ (smallmouth bass)

(segmented temporal), first principal component, and amplitude (harmonic). The second variable entered had a less significant negative coefficient in regressions for small largemouth bass (all methods) and for next year's intermediate largemouth bass from the principal-component method. The best model for forecasting next year's standing crop of intermediate largemouth bass included perimeter area in summer and the ratio of inflow to release in spring (Table 4). This model had an $r^2$ statistic that was 5 and 11 percent
Figure 5. Scatter plots of the standing crop of (a) small largemouth and (b) spotted bass in August as a function of ha-days of flooding during three time periods: post-spawning (HADFLDPS), spawning until sampling (HADFLDSS), and spawning (HADFLDS).

higher than that from the best models based upon harmonics and principal components, respectively. It also had no intercorrelation ($r^2 = 0.03$; $P = 0.2873$) unlike the harmonic model ($r^2 = 0.24$; $P = 0.0016$). For spotted bass, the $r^2$ statistics of 2-variable models from the segmented temporal method were only 3 to 4 percent higher than those from the harmonic method but were 9 to 15 percent higher than those from the principal component method (Figure 9; Table 4). The second principal component entered
Figure 6. Scatter plots of the standing crop of two size classes of largemouth bass in August as a function of June-August mean perimeter area (PA6_8), amplitude of a cosine function (AMP) fitted to end-of-month surface areas, or first principal component (PRIN1) describing 13 hydrologic variables for Bull Shoals Lake into models for both small and intermediate spotted bass with negative coefficients. By contrast, coefficients for second entries for segmented-temporal and harmonic models were positive. Intercorrelations were minimal between (a) January-August mean volume and March-May ratio of inflow to release ($r^2 = 0.00; P = 0.93$), (b) change in area from summer to spring and previous fall mean volume ($r^2 = 0.05; P = 0.19$), (c) amplitude and the corrected
Figure 7. Scatter plots of standing crop of two size classes of spotted bass in August as a function of June-August mean perimeter area (PA6_8), March-May perimeter area (PA3_5), amplitude of a cosine function (AMP) fitted to end-of-month surface areas, or first principal component (PRIN1) describing 13 hydrologic variables for Bull Shoals Lake.

root mean square error ($r^2 = 0.05; P = 0.18$), and (d) amplitude and antecedent phase shift ($r^2 = 0.00; P = 0.57$).

Some significant three- and four-variable models were found for predicting the biomass of small and intermediate black basses (Table 4), but rarely was there substantial improvement in fit over the two-variable models. Surprisingly, one three-variable model emerged for predicting the biomass of next
Figure 8. Surface plots of two-variable models predicting standing crop of two size classes of largemouth bass in August for Bull Shoals Lake, Arkansas (Abbreviations include PA6.8 = June-August mean perimeter area; September-November change in area (previous year); RIR3.5 = March-May ratio of inflow to release; CASUSP = summer to spring change in mean area; PRIN1 = first principal component; PRIN2 = second principal component; AMP = amplitude of a harmonic cosine function; D_HA = difference in mean annual surface area in consecutive years; and ANTCEEDNT = complex variable related to mean areal change, amplitude, and phase shift)
<table>
<thead>
<tr>
<th>Length</th>
<th>Species, Equation, and Statistics</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;140-mm</td>
<td>Largemouth bass</td>
</tr>
<tr>
<td></td>
<td>$-26.01 + 7.39(\text{PA6}<em>{8}) - 0.07(\text{CA9}</em>{11})$</td>
</tr>
<tr>
<td></td>
<td>$R^2 = 0.61; P = 0.0001; N = 32; \text{Method: Segmented Temporal}$</td>
</tr>
<tr>
<td></td>
<td>$0.37 + 0.06(\text{PRIN1}) - 0.07(\text{PRIN2})$</td>
</tr>
<tr>
<td></td>
<td>$R^2 = 0.60; P = 0.0001; N = 32; \text{Method: Principal Components}$</td>
</tr>
<tr>
<td></td>
<td>$0.10 + 10.07(\text{AMP}) + 0.17(\text{D_HA})$</td>
</tr>
<tr>
<td></td>
<td>$R^2 = 0.57; P = 0.0001; N = 32; \text{Method: Harmonic}$</td>
</tr>
<tr>
<td>140- to 241-mm</td>
<td>-18.7 + 4.90(\text{PA6}<em>{8}) + 1.39(\text{RIR3}</em>{5})</td>
</tr>
<tr>
<td></td>
<td>$R^2 = 0.86; P = 0.0001; N = 20; \text{Method: Segmented Temporal}$</td>
</tr>
<tr>
<td></td>
<td>$0.12 + 8.60(\text{AMP}) + 0.09(\text{ANTCEDNT})$</td>
</tr>
<tr>
<td></td>
<td>$R^2 = 0.81; P = 0.0001; N = 20; \text{Method: Harmonic}$</td>
</tr>
<tr>
<td></td>
<td>$0.29 + 0.04(\text{PRIN1}) - 0.04(\text{PRIN2})$</td>
</tr>
<tr>
<td></td>
<td>$R^2 = 0.75; P = 0.0001; N = 20; \text{Method: Principal Components}$</td>
</tr>
<tr>
<td></td>
<td>$-3.89 + 5.85(\text{PA6}<em>{8}) - 3.18(\text{X9A}</em>{11}) + 0.43(\text{CA9}_{11})$</td>
</tr>
<tr>
<td></td>
<td>$R^2 = 0.90; P = 0.0001; N = 20; \text{Method: Segmented Temporal}$</td>
</tr>
<tr>
<td></td>
<td>$0.30 + 0.04(\text{PRIN1}) - 0.04(\text{PRIN2}) - 0.03(\text{PRIN3})$</td>
</tr>
<tr>
<td></td>
<td>$R^2 = 0.80; P = 0.0001; N = 20; \text{Method: Principal Components}$</td>
</tr>
<tr>
<td></td>
<td>$0.16 + 8.65(\text{AMP}) - 0.50(\text{PHS}_\text{SHIFT}) + 0.06(\text{ANTCEDNT}) + 3.44(\text{COR_RMSE})$</td>
</tr>
<tr>
<td></td>
<td>$R^2 = 0.87; P = 0.0001; N = 20; \text{Method: Harmonic}$</td>
</tr>
<tr>
<td>&lt;114-mm</td>
<td>Spotted bass</td>
</tr>
<tr>
<td></td>
<td>$-6.85 + 1.86(\text{XVOL1}<em>{8}) + 0.44(\text{RIR3}</em>{5})$</td>
</tr>
<tr>
<td></td>
<td>$R^2 = 0.68; P = 0.0001; N = 32; \text{Method: Segmented Temporal}$</td>
</tr>
<tr>
<td></td>
<td>$0.12 + 3.83(\text{AMP}) - 26.31(\text{COR_RMSE})$</td>
</tr>
<tr>
<td></td>
<td>$R^2 = 0.65; P = 0.0001; N = 32; \text{Method: Harmonic}$</td>
</tr>
<tr>
<td></td>
<td>$0.24 + 0.02(\text{PRIN1}) - 0.01(\text{PRIN2})$</td>
</tr>
<tr>
<td></td>
<td>$R^2 = 0.59; P = 0.0001; N = 32; \text{Method: Principal Components}$</td>
</tr>
</tbody>
</table>
### Table 4 (Concluded)

<table>
<thead>
<tr>
<th>Length</th>
<th>Species, Equation, and Statistics</th>
</tr>
</thead>
</table>
| 114- to 216-mm | Spotted bass (continued)  
  
-8.01 + 6.40(CASUSP) + 2.34(XVOL9_11)  
  
$R^2 = 0.54$; $P = 0.0001$; $N = 20$; Method: Segmented Temporal  
  
$0.17 + 3.28(AMP) + 0.07(A\_PHSSF)$  
  
$R^2 = 0.50$; $P = 0.0001$; $N = 20$; Method: Harmonic  
  
$0.27 + 0.02(PRIN1) - 0.01(PRIN2)$  
  
$R^2 = 0.38$; $P = 0.0001$; $N = 20$; Method: Principal Components |
| 114- to 216-mm | Smallmouth bass  
  
$3.52 - 3.33(RIR1_8) + 3.18(CASUSP) - 0.07(HADFLDSS)$  
  
$R^2 = 0.56$; $P = 0.0038$; $N = 20$; Method: Segmented Temporal |

year's intermediate smallmouth bass, after only one significant one-variable had been found previously. This model indicated significant negative effects of January-August ratio of inflow to release and of ha-days of flooding from spawning until sampling. It suggested a positive effect of summer to spring change in area. However, the model contained one significant intercorrelation between summer-to-spring change in area and ha-days of flooding from spawning until sampling in August ($r^2 = 0.27; P = 0.0015$).

Predictions of small largemouth and spotted bass biomass by two-variable models from the segmented-temporal method (Table 4) for 1979 and 1993 were slightly higher than observed catches. Predicted standing crops of both species and length classes exceeded the 75th percentile standing crop in 1979 but were less than the 75th percentile in 1993.
Figure 9. Surface plots of two-variable models predicting standing crop of two size classes of spotted bass in August for Bull Shoals Lake, Arkansas (Abbreviations include XVL01_8 = January-August mean volume; RIR3_5 = March-May ratio of inflow to release; CASUSP = summer to spring change in mean area; XVL02_11 = September-November volume (previous year); AMP = amplitude of a cosine function; COR_RMSE = corrected root mean square error for the fit of a cosine function; A_PHSSFT = antecedent phase shift; PRIN1 = first principal component; PRIN2 = second principal component)
4 Conclusions and Recommendations

Intercorrelations between segmented-temporal hydrologic variables were common because of the way variables were defined or because events in time series were autocorrelated. In the definition case, correlations between area and volume variables result because reservoir area and volume are highly correlated, or a time segment such as January-August includes segments for March-May and June-August. Autocorrelation of hydrologic events result when an event in one time segment affects variables in adjacent time segments. For example, very high inflow in spring may result in above-average surface area in spring and summer periods because operators cannot follow the typical rule curve for managing capacity.

Intercorrelation among "independent" variables is not a serious problem for multiple regression if the primary goal is inference (as in this report) or for prediction, as long as highly intercorrelated variables are excluded from the same multiple-regression model. For example, correlated variables were excluded in the segmented temporal method. When independent variables are correlated, regression coefficients and sums of squares are not unique but depend on other variables in the model (Neter and Wasserman 1974). The reduction in total variation ascribed to an independent variable must be viewed in the context of other independent variables in the model. A regression coefficient for a variable in a two-variable model with intercorrelation likely will differ from what it was for the same variable in a single-variable model.

Some intercorrelation within harmonic variables may be accepted if one of a pair of intercorrelated variables provided substantially different information. An example was the retention of change in mean area among years in a 2-variable model with amplitude, although they were correlated ($r = 0.54$; $P = 0.0004$). Change in mean area measures differences in the baselines about which two consecutive harmonics cycle, whereas amplitude is a function of within year variation in surface area.

The principal components method was foolproof, easy, and fast, but did not necessarily produce the best regression models.
Principal components analysis is an excellent way to reduce the number of independent variables and avoid intercorrelation (SAS Institute, Incorporated 1989). In the latter sense, it is foolproof. The first and second principal components derived explained 82 percent of hydrologic variation and could be broadly associated with positive effects of the wetness of a year (first component) and negative effects of high flow and area the previous fall (second component). The meaning of the third and fourth principal components (Table 2) did not lend themselves to as ready an interpretation, but they did not show up in multiple regression models anyway. Principal components may not produce the best regression models because the most significant effects on young bass occur within specific time segments not optimally described by this method. Also, a few of the hydrologic variables from which principal components were derived may have little or no effect on year-class strength (e.g., previous fall release) and yet still influence resulting principal components.

The harmonic method was initially time-consuming, but it provided good explanation of variation in surface area patterns (Figures 1 and 2) and of standing crops of young largemouth and spotted bass (Figures 6-9 and Table 4) with relatively few variables. It is much like principal components in variable-reduction capability, but its coefficients were relatively easy to interpret. From a modeling standpoint, the harmonic method has two major advantages. First, it can accurately describe complex hydrologic patterns with a few coefficients, which facilitates comparisons of operating alternatives. Second, harmonic variables can be derived in a few programming steps including a relatively simple nonlinear regression routine. In contrast, programming models based upon principal components would have to include a principal-components routine and verification of its consistency with alternative simulations. If the harmonic method has a weakness, it may be its lack of specificity for critical segments of the hydrograph such as postspawning.

Phase shift, as identified by harmonic analysis (Figure 3), was unrelated to reproductive success of spotted and smallmouth bass, and only a weak negative correlate with biomass of small largemouth bass ($r = -0.36; P = 0.0416)$. This correlation may be coincidental because phase shift tended to be lower in wet years with high perimeter area than in dry years, and perimeter area had a strong positive effect (Figure 6). Also, we would expect all species to be affected the same by a phase shift that might disrupt spawning or food availability for age-0 black bass at critical times. Effect of phase shift probably is moderated by comparable shifts in temperature cycles because seasonal temperature changes occur more slowly in the reservoir than in the river.

Perimeter area from June through August ($PA6_{-8}$) from the segmented-temporal method often was the most significant variable in models for largemouth and spotted bass (Figures 6-8). Hectare-days of flooding during the postspawning period also explained slightly more of the variation in standing crops of small largemouth and spotted bass than flooding during the spawning season (Figure 5). This is consistent with findings of Aggus and Elliott...
(1975) for the same lake and species, though less robust. They found correlation coefficients and probabilities $r = 0.72$ and $P = 0.1$ for the spawning period, $r = 0.83$ and $P = 0.05$ for the spawning to sampling period, and $r = 0.91$ and $P = 0.01$ for the postspawning period. Difference in robustness may be a function of differences in sample size (32 years in this study versus 7 in the 1975 study) or in the accuracy of identifying age-0 fish. Our use of maximum length in rapid growth years obviously is inferior to obtaining ages from scales.

The importance of postspawning survival of age-0 largemouth may be deduced from observations of hatching success versus year-class strength of Kohler, Sheenan, and Sweatman (1993). They observed that hatching success was disrupted by rapidly rising or declining water levels in two Illinois reservoirs. However, recruitment was considerably higher in high-water years than in low-water years and apparently unrelated to hatching success. These results seem intuitive for r-selected organisms (Odum 1971) that flood the environment with eggs and fry every year, but succeed in producing strong year classes only when environmental conditions and carrying capacity permit.

The number of years of data required to establish reliable relations between catches of young fish and reservoir hydrology probably depends more upon the quality of the data than upon sample size.

Only 7 years of data used by Aggus and Elliott (1975), 8 years by Rainwater and Houser (1975), and 9 years by Aggus (1979) were needed to quantify important empirical relations for young black basses in Bull Shoals Lake. Relations between the species composition of small black bass in August and ha-days of flooding depicted in Figure 4 ($N = 34$) are virtually identical to those ($N = 9$) presented by Aggus (1979). However, trends in species composition do not necessarily parallel trends in the biomass of small black basses. For example, the biomass of small spotted bass increased in years of high water but was so dwarfed by increases in largemouth bass biomass that its percent composition declined. Using 32 years of data (2 were withheld for testing predictors), relations were confirmed for largemouth bass that were first obtained with seven points by Aggus and Elliott (1975). Relations in earlier studies are consistent with those obtained after more than quadrupling sample size, although coefficients of determination have declined. Reduced explained variation could be a function of sample size, wherein we are now approaching the true explained variability, or it may be related to how age-0 and age-1 bass were defined, or both. Aggus and Elliott's assignment of young bass to the age-0 category every year based upon scale readings was far superior to our assignments of biomass according to maximum length at age. Varying maximum length at age assignments could not be done legitimately among years without age data, most of which were lost after the demise of the former National Reservoir Research Program. Nevertheless, there were obvious differences in length frequency distributions among years. Species-specific correlations of the biomass of intermediate black bass with that of small black bass the previous year indicate that the abundance of age-0 largemouth and spotted bass in August is a fairly reliable indicator of future
year-class strength in Bull Shoals Lake. Relations also suggest that our maximum length at age definitions were best for largemouth bass, next for spotted bass, and worst for smallmouth bass. The most likely classification errors are those that would inflate standing crop variables by erroneously including weights of bass of next age class. These errors should be worst in years of slow growth, which typically coincided with years of below average water levels. They should reduce the likelihood of finding significant positive correlations with water-level variables by increasing standing crop in dry years.

A paucity of age information in historical data sets is common, but it does not preclude a search for empirical relations, although it may hinder detection of less robust effects. A stunted population of older fish in a reservoir could suggest exceptional reproduction every year if examined solely by length-frequency data. A few years of length-at-age data or a single study of age and growth may be sufficient to identify this problem. Chances of finding significant empirical relations for reservoirs where effects are less pronounced than those at Bull Shoals Lake would be greatly enhanced by accurately estimating age-0 and age-1 catches every year. Future studies designed to quantitatively monitor effects on reproductive success would be amiss not to collect age data routinely.

Although time-consuming, the temporal-segmented approach usually produced the best, most easily interpreted predictive models (Table 4). These variables were the easiest and most intuitive variables to create and therefore would be particularly amenable for use in multipurpose evaluation models. Model building was the most time-consuming part of this method because including correlated independent variables had to be avoided in multiple regression models. Predictions of biomass of young largemouth and spotted bass by two-variable models accurately classified the strength of 1979 and 1993 year classes relative to the 75th percentile catch (Table 5).

Why do the empirical relations occur in Bull Shoals Lake? Most fishery biologists that have studied recruitment of largemouth and spotted bass in this reservoir attribute strong year classes to high inflow and resultant flooding of terrestrial vegetation (Keith 1975; Aggus and Elliott 1975; Aggus 1979; Bryant and Houser 1971; Rainwater and Houser 1975; and Houser and Rainwater 1975). Flooding of vegetation apparently alters the trophic base because age-0 largemouth and spotted bass grow faster in spite of high densities and switch to a more productive diet of fish earlier than they do in drier years. An abundance of suitable forage apparently is critical. Accelerated growth and an increased complexity of habitat as refuge from predation are apparently important factors increasing survival especially during the first summer of life. Also, predation was considered to be a major factor affecting year-class-strength with higher over-winter survival for larger age-0 largemouth bass than for their smaller siblings (Aggus and Elliott 1975).

If the most important variable affecting production of strong year classes is postspawning mortality, a productive strategy of water-level management
Table 5
Predicted and Observed Catches for a High-Water Year in 1979 and an Average Water Year in 1993 and the 75th Percentile Observed Catch for All 34 Years (catch is expressed as $\log_{10}(\text{kg/ha} + 1)$)

<table>
<thead>
<tr>
<th>Size, Species, and Catch</th>
<th>1979 (high water)</th>
<th>1993 (average)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>&lt;140-mm Largemouth Bass</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predicted</td>
<td>0.86</td>
<td>0.35</td>
</tr>
<tr>
<td>Observed</td>
<td>0.64</td>
<td>0.15</td>
</tr>
<tr>
<td>75th percentile</td>
<td>0.64</td>
<td>0.64</td>
</tr>
<tr>
<td><strong>&lt;114-mm Spotted Bass</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predicted</td>
<td>0.38</td>
<td>0.23</td>
</tr>
<tr>
<td>Observed</td>
<td>0.23</td>
<td>0.13</td>
</tr>
<tr>
<td>75th percentile</td>
<td>0.27</td>
<td>0.27</td>
</tr>
<tr>
<td><strong>Next Year's 140- to 241-mm Largemouth Bass</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predicted</td>
<td>0.64</td>
<td>0.21</td>
</tr>
<tr>
<td>Observed$^1$</td>
<td>0.61</td>
<td></td>
</tr>
<tr>
<td>75th percentile</td>
<td>0.43</td>
<td>0.43</td>
</tr>
<tr>
<td><strong>Next Year's 114- to 216-mm Spotted Bass</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Predicted</td>
<td>0.45</td>
<td>0.32</td>
</tr>
<tr>
<td>Observed$^1$</td>
<td>0.33</td>
<td></td>
</tr>
<tr>
<td>75th percentile</td>
<td>0.33</td>
<td>0.33</td>
</tr>
</tbody>
</table>

$^1$ Unavailable for 1994.

would consist of ensuring high water and acceptable habitat after an acceptably wet spring. Correlations did not indicate the relative importance of high inflow versus inundation of terrestrial vegetation for producing strong year classes of largemouth and spotted bass. Both factors probably are critical. Flooding of terrestrial vegetation in a year of average inflow probably does not provide as robust a basis for increasing largemouth bass growth and recruitment as inundating vegetation in a year of naturally high inflow and nutrient loading (Strange, Kittrell, and Broadbent 1982).

Smallmouth bass responded differently to hydrologic changes than did largemouth and spotted bass. The biomass of intermediate smallmouth bass was inversely related to January-August inflow in the previous year. Lower and more variable standing crops of smallmouth bass than those of the other species may account for correlation with a single hydrologic variable.
Differences in responses among species may be related to differences in habitat selection and predator-avoidance responses of age-0 black basses. Large-mouth and especially spotted bass prefer to nest near brush shelters or in flooded terrestrial vegetation, while smallmouth bass show no preference for brush areas but prefer gravel or broken rock (Vogele and Rainwater 1975). Smallmouth bass fry schools usually disperse much more rapidly than schools of largemouth and spotted bass (Vogele 1975, 1981). Adult spotted bass have been observed apparently conducting schools of fry into areas of heavy cover (Vogele 1975). Two other observations can be made based upon 18 years of observing the behavior of age-0 black basses in Bull Shoals Lake.\(^1\) Age-0 smallmouth bass prefer rocky areas near the bottom (Vogele 1981) and will hide in rocky crevices when threatened.\(^1\) By contrast, age-0 spotted and largemouth bass school in or near heavy cover when it is available.

All three empirical methods in this report provide concordant results for spotted and largemouth bass in Bull Shoals Reservoir and would be useful for identifying potential relations in other reservoirs. The use of principal components is a logical preliminary step in the search for relations between fish reproductive success and hydrology. It would indicate whether a closer examination was warranted with the segmented-temporal or harmonic method. The latter, more detailed methods, would be preferred if regression models will be incorporated in a large multiple-use model (e.g., Ploskey et al. 1993).

There are several advantages to having empirical models for a specific reservoir. First, many Federal agencies will be evaluating multipurpose uses of reservoirs and river systems in the next decade. This was done in 1992-94 for the Missouri River system and in 1993-95 for major river basins in Alabama, Georgia, and Florida. Effects of alternative reservoir operations on fish populations must be modeled qualitatively or preferably quantitatively for adequate representation in trade-off analyses. Second, fishery managers will find resource-development agencies more receptive of water-level plans that have a quantitative basis and predictive ability.

An incomplete understanding of intricate details in biological responses does not and should not inhibit managers from exploring and using empirical relations to improve reservoir fisheries. Empirical ecological relations have proven very useful for assessing reservoir fisheries potential (Jenkins 1967; Jenkins and Morais 1971; Oglesby 1982). Increasing demands for hydropower, flood control, water supply, irrigation, navigation, instream flow, and recreation (including fisheries), require equitable evaluations that will not wait for comprehensive understanding.

In defense of our approach, we quote Rigler (1982), who offered empiricism as a unifying approach for fishery biologists and limnologists:

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1 Personal Communication, L. E. Vogele, National Reservoir Research Program.
Because empirical ecology produces and tests theories, it is science in its purest form. It provides the basis for ecological engineering, but this is the application of empirical theory by managers, not the production of theories. If empirical ecology has done anything to justify the appellation "engineering," it is that it has produced theories that can be applied, whereas paradigmal ecology has proliferated generalizations that are entertaining to teach but that cannot be applied by managers because they are not predictive.

Methods described in this paper should help fishery managers identify useful empirical predictors for specific reservoirs and hopefully will stimulate future research. Good predictors can improve water-resource decisions to benefit fisheries, but are not a substitute for careful biological studies of proximate causes and effects. Our methods are empirical in that concurrent biological information that might help explain relations was not collected every year. Numerous biological observations published by the former National Reservoir Research Program aided significantly in helping to identify probable causes and effects.
References


Three methods are described for relating reproductive success of fish to reservoir hydrology with an example of responses of young black bass in Bull Shoals Reservoir, Arkansas. Reproductive success was indexed by standing crops of one or two length classes of young largemouth bass (Micropterus salmoides), spotted bass (M. punctulatus), and smallmouth bass (M. dolomieu) in 34 years of August cove-rotenone samples.

First, hydrologic variables were calculated based upon inflow, release, volume, mean area, change in area, or selected ratios thereof from time segments ranging from one season to 2 years before fish sampling in August. This segmented temporal approach produced 36 variables, many of which were intercorrelated. Standing crops were regressed on subsets of variables lacking intercorrelation at $\alpha = 0.05$. Although time-consuming, this approach usually provided the best, most easily interpreted predictive models.

Second, intercorrelation problems were avoided by using principal components as independent variables in regression analyses. Four components explained 91 percent of the variation in 13 segmented-temporal hydrologic variables, but only the first two (explaining 82 percent) were possible to interpret and were significant in regression models. This method was foolproof, easy, and fast but did not necessarily produce the best (most useful) models.

(Continued)
Third, cosine functions were fit to monthly discharge of the unregulated White River (1920-49) and to end-of-month area of Bull Shoals Reservoir (1955-93). Eight independent variables were derived related to amplitude, phase, differences in the phase of the reservoir from the preproject river, and error in fit of the harmonic function to reservoir hydrology. This harmonic approach was initially time-consuming, but provided good explanation of variations in surface area \( (r^2 = 0.84, N = 465) \) and in largemouth bass and spotted bass standing crop, with minimal intercorrelation.

All three methods would be useful for quantifying effects of operations and hydrology on fish populations in multiple-use or basinwide assessments of water resources.