Variation in Fish Community Composition, Biomass, and Harvest Relative to Environmental Parameters in Reservoirs of North and South Carolina[1]

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Abstract: Creel survey and cove rotenone data from 17 reservoirs in Piedmont North and South Carolina were subjected to correlation and regression analysis to examine environmental factors influencing fish production and taxonomic composition and to develop models for the prediction of total harvest and biomass. Summer surface chlorophyll concentration was the best univariate predictor of total harvest ($r^2 = 0.93$) and one of the best predictors of total biomass ($r^2 = 0.79$). The morphoedaphic index was a good predictor of both biomass ($r^2 = 0.79$) and harvest ($r^2 = 0.83$), but explained no more variation than conductivity alone. Mean depth was not a strong predictor of biomass ($r^2 = 0.55$) or harvest ($r^2 = 0.61$), and total phosphorus concentration was not significantly correlated with biomass or harvest. Multivariate models based on phosphorus loading and reservoir morphometry/hydrology explained up to 91% of variation in biomass and 92% of variation in harvest. Harvest composition varied along gradients of morphometry, hydrology, and productivity. Percents of harvest consisting of largemouth bass (*Micropterus salmoides*) and temperate basses (Percichthyidae) increased with reservoir retention time, while percent of harvest consisting of crappie (*Pomoxis* spp.) declined. The combined harvest of striped bass (*Morone saxatilis*) and hybrid bass (*M. saxatilis* x *M. chrysops*) declined as chlorophyll increased, possibly reflecting a loss of cool, oxygenated habitat with increasing eutrophication. Biomass composition did not vary significantly along environmental gradients, with the exception that percent of biomass consisting of common carp (*Cyprinus carpio*) declined with increasing reservoir fertility. No evidence was observed of shifts in biomass composition to undesirable species as productivity increased. The absolute abundance of most major taxa increased with increasing reservoir fertility, with the exception of percichthyids and cyprinids. Habitat preferences were evident in the negative correlations of crappie harvest and catfish biomass with mean depth and retention time.

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The development of management goals for a fishery involves consideration of relationships between the fish community and physical, chemical, and biological characteristics of the water body. When detailed ecological studies of individual water bodies are not available, empirical analyses based on groups of water bodies within a geographic region may provide a general characterization of ecological patterns. Empirical evidence of relationships among fisheries and environmental parameters provides a basis for the development of hypotheses concerning ecological influences on fish yield. In addition, models can be generated which predict or estimate fish biomass or harvest on the basis of environmental parameters. The development of predictive models allows a fisheries manager to assess the yield of existing fisheries, predict or explain changes in the biomass or harvest of a given fishery over time, and predict fish yields of reservoirs not yet constructed.

Relationships of total fish biomass and yield to environmental parameters have been extensively investigated, and a variety of predictive indices have been proposed (Ryder et al. 1974, Carline 1986). Significant relationships have been observed between fish yield and climatic factors (Schlesinger and Regier 1982), morphometric factors (Rawson 1952), nutrient concentrations (Hanson and Leggett 1982, Yurk and Ney 1989), primary production (Oglesby 1977*a*, Jones and Hoyer 1982, Downing et al. 1990), and secondary production (Matuszek 1978, Hanson and Leggett 1982). Ryder (1965) proposed that edaphic and morphometric influences on fish production be incorporated in the morphoedaphic index, which became the first widely-applied predictor of fish yield. The applicability and theoretical basis of this index have been widely investigated (e.g., Jenkins 1982, Ryder 1982, Schlesinger and Regier 1982, Downing et al. 1990). Empirical analyses have also been used to relate fish community structure to environmental variables (Tonn et al. 1983, Marshall and Ryan 1987, Dolman 1990), allowing the development of realistic management goals for lakes in specific regions despite the absence of detailed studies of individual lakes.

The objectives of this investigation were to empirically examine relationships of total fish biomass and harvest to environmental variables and predictive indices for reservoirs in Piedmont North and South Carolina; to derive models which allow the estimation of total fish biomass and harvest; to examine patterns in taxonomic composition of fish communities in relation to reservoir productivity, morphometry, and hydrology; and to identify the environmental variables most closely correlated with the abundance of individual fish taxa.

Ryder et al. (1974) and Leach et al. (1987) emphasized the need to develop models of fish production specific to geographic regions. Regional models would be expected to provide more precise predictions than global models, in that variability due to climatic, edaphic, and other ecological factors would be reduced. In addition, Kimmel and Groeger (1984) suggested caution in the application to reservoirs of empirical models developed using data from natural lakes. Characteristic differences between lakes and reservoirs in morphometry and hydrology (Kimmel and Groeger 1984) may lead to differences in the relative importance of the ecological processes influencing fish production and community structure.

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Methods

This investigation utilized cove rotenone and creel survey data from 17 mainstream reservoirs in Piedmont North and South Carolina (Table 1). Reservoirs were chosen based on availability of fisheries data. Trophic status ranged from oligotrophic to eutrophic, with sparse macrophyte development. Thermal stratification developed in spring and isothermal conditions typically persisted from late fall through winter.

Summer cove rotenone data were available for 16 reservoirs, and creel survey data for 12 reservoirs (Table 2). Total biomass and absolute and relative biomass of individual taxa were arithmetically averaged over locations within reservoirs, then over years. Total harvest and absolute and relative harvest of individual taxa were arithmetically averaged over years. Analyses utilized the most frequently reported taxonomic levels.

In 1983, Duke Power Company conducted a limnological survey of 35 reservoirs in North and South Carolina (Rodriguez 1989*a*). This survey provided the

Table 1. Selected characteristics of 17 reservoirs in Piedmont North and South Carolina.

Reservior	Surface area km^2	Mean depth m	Retention time days	Chlorophyll mg/m^3	Total phosphorus mg/m^3	MEI_{cond}	Fish biomass kg/ha	Sportfish harvest kg/ha/year
Badin	24	14	28	16.0	14	5.7	448.9	16.0
Greenwoood	46	7	82	23.8	70	13.1	333.5	31.6
Hartwell	248	14	358	3.3	9	2.0	113.4	8.4
Hickory	17	9	33	8.4	60	4.8	172.8	
James	26	14	208	3.2	37	2.6	145.0	
Jocassee	31	48	1,256	2.3	21	0.4	46.5	4.3
Keowee	74	17	422	2.1	6	1.2	40.9	5.1
John Kerr	198	11	124	24.5	16	12.9	361.2	7.0[a]
Lookout Shoals	5	8	7	5.1	19	5.1	300.2	
Mountain Island	13	5	12	6.0	11	10.2	80.2[a]	9.8
Murray	206	13	357	5.6	4	4.6	232.0	13.4
Norman	132	10	239	5.9	9	4.9	118.3	12.5
Rhodhiss	14	6	21	30.2	30	11.3	139.2[a]	
Kerr Scott	16	12	35	9.1	4	3.3	294.6	
Tuckertown	10	5	2	42.5	38	17.2		44.0
Wateree	56	7	27	31.5	52	20.6	690.1	30.9
Wylie	53	7	39	20.0	38	13.3	465.8	34.9

[a] Deleted from correlation and regression analyses (see text)

Table 2. Sources of cove rotenone and creel survey data.

	Cove rotenone		Creel survey	
Reservoir	Years sampled	Source	Years sampled	Source
Badin	1982,1984	NRRP[a]	1980	NCWRC[f]
Greenwood	1986,1987	SCWMRD[b]	1985–1987	SCWMD
Hartwell	1981,1984,1987,1990	GDNR[c]	1980–1982	NRRP
Hartwell			1988, 1989	SCWMRD
Hickory	1983	NRRP		
James	1982–1984	NRRP		
Jocassee	1987,1989,1990	DPC[d]	1980–1984,1986, 1988–1990	DPC
Keowee	1980–1982,1986–1990	DPC	1980–1982,1985, 1987,1990	DPC
John Kerr	1982	NRRP		
John Kerr	1985,1988	VDGIF[e]	1985,1988	VDGIF
Lookout Shoals	1981	NRRP		
Mountain Island	1980	NRRP	1983	DPC
Murray	1988	SCWMRD	1988	SCWMRD
Norman	1980–1985,1988–1990	DPC	1982	DPC
Kerr Scott	1980	NRRP		
Rhodhiss	1983	NRRP		
Tuckertown			1988,1989	NCWRC
Wateree	1982–1984	NRRP	1971	SCMRD
Wylie	1980–1987	DPC	1983,1986	DPC

[a] National Reservoir Research Program database (Cornelius 1989).
[b] South Carolina Wildlife and Marine Resources Department.
[c] Georgia Department of Natural Resources.
[d] Duke Power Company.
[e] Virginia Depatment of Game and Inland Fisheries.
[f] North Carolina Wildlife Resources Commission.

chemical, physical, and non-fish biological data used in this study, with the exception that total dissolved solids and shoreline development data were obtained from the National Reservoir Research Program database (Cornelius 1989). Based on reservoir size, Duke Power Company sampled 1 to 4 locations along a longitudinal gradient, including a forebay location. Data were arithmetically averaged over locations, consistent with fisheries data. The current study utilized surface values for chlorophyll, nutrients, and conductivity, and summer values for all parameters, with the exception of benthic densities which were measured in spring. Use of this database ensured consistency in analytical methods.

Zooplankton were sampled by limnetic, bottom-to-surface tows of an 80-micrometer mesh net. Littoral benthic samples were collected using a Peterson grab sampler. Secchi depth was converted to a light extinction coefficient (k_{secchi}) under the assumption that secchi depths corresponded to 10% of surface light penetration (Hutchinson 1975). Chlorophyll *a* was extracted in acetone and measured spectrophotometrically (Strickland and Parsons 1972). Light extinction due to chlorophyll (k_{chl}) was derived using the chlorophyll-secchi depth relationship of Carlson (1977), and non-algal turbidity was calculated as k_{secchi} minus k_{chl}.

Morphometric and hydraulic data were obtained from the North Carolina Department of Natural Resources and Community Development (NCDNRCD 1983), the South Carolina Department of Health and Environmental Control (Kimsey et al. 1982), and other sources (Rodriguez 1989*b*). Nutrient loading data were obtained from U.S. Environmental Protection Agency National Eutrophication Survey reports. Point source loading data represent municipal wastewater discharges. Morphoedaphic indices (MEI_{tds} and MEI_{cond}) were calculated as total dissolved solids (mg/liter) divided by mean depth (m), and as conductivity (micromho/cm) divided by mean depth, respectively.

Total fish biomass (kg/ha), total sportfish harvest (kg/ha/year), and the absolute and relative biomass and harvest of individual taxa were subjected to correlation analysis with the following environmental variables: total, areal, and volumetric loading of nitrogen, total phosphorus, and point source phosphorus; total phosphorus concentration; total and organic nitrogen concentration; chlorophyll *a*; conductivity; total dissolved solids; k_{secchi}; non-algal turbidity; reservoir surface area, volume, mean and maximum depth, retention time, and shoreline development ratio; MEI_{cond} and MEI_{tds}; mean water column temperature; areal and volumetric densities of total zooplankton, copepods, cladocerans, and rotifers; littoral benthic densities; and number of littoral benthic taxa. All fisheries and environmental variables were $\log_{10}$-transformed to obtain a normal distribution or to ensure consistency with other investigators, with the exception of mean water column temperature, k_{secchi}, non-algal turbidity, and number of benthic taxa, which were normally distributed without transformation. Only data for reservoirs from which an individual fish taxon was reported were used in analyses involving that taxon.

Empirical models to predict total biomass and harvest were developed by linear regression analysis, using as independent variables those environmental parameters most closely correlated with biomass and harvest. Regression analyses were also performed with parameters reported to be useful predictors of fish biomass and harvest, such as total phosphorus concentration and the morphoedaphic index. Regression diagnostics (Student residual) were examined to statistically identify questionable data points (SAS Inst. Inc. 1987), and as a result, final correlation and regression analyses did not utilize harvest data from John Kerr reservoir or cove rotenone data from Rhodhiss and Mountain Island reservoirs. Correlation and regression results were reported as statistically significant where $P \leq 0.01$.

Multiple regression analyses were performed to determine whether combinations of independent variables could explain more variation in total biomass or harvest than explained by individual variables. The contribution of each variable to explaining variation in biomass or harvest was defined as statistically significant where the parameter estimate associated with the variable was significantly different from zero ($P \leq 0.01$). Potential nonlinearity in relationships of total biomass and harvest to environmental factors was investigated through examination of plots, and through multiple regression analyses formatted to produce quadratic models.

Multiple regression analyses were also used to determine whether more than one environmental variable could be identified as independently influencing absolute or relative biomass or harvest of individual taxa. For this purpose, independent variables were identified as contributing significantly to explaining variation where parameter estimates were significantly different from zero ($P \leq 0.05$). All statistical analyses were performed using the SAS system (SAS Inst. Inc. 1989, 1990).

Results and Discussion

Environmental Correlates of Total Fish Biomass and Sportfish Harvest

Biomass—The strongest environmental correlates of biomass were chlorophyll, conductivity, MEI_{cond}, and total phosphorus loading (mg P/m^3/year) (Table 3). Significant, but weaker, negative correlations were observed with mean depth and retention time, possibly as a result of the interdependence of fertility, morphometry, and hydrology in these reservoirs. Total biomass was not significantly correlated with total phosphorus concentration or with densities of zooplankton or benthos.

Harvest—The strongest environmental correlates of harvest were chlorophyll, conductivity, total organic nitrogen, MEI_{cond}, total nitrogen, and point-source phosphorus loading (mg P/m^3/year) (Table 3). Harvest was negatively correlated with mean depth and retention time. No significant correlation was observed between harvest and total phosphorus concentration.

Models for the Prediction of Total Fish Biomass and Sportfish Harvest

Biomass—Chlorophyll, conductivity, and MEI_{cond} were the best individual predictors of biomass, each explaining about 80% of variation (Table 4). Biomass values predicted by chlorophyll ranged from 48 to 173% of observed values (Fig. 1a). Multiple regression analyses yielded a model based on total phosphorus

Table 3. Significant ($P = <0.01$) correlations of environmental parameters with $\log_{10}$ total fish biomass (kg/ha) and $\log_{10}$ total sportfish harvest (kg/ha/year). All environmental variables were $\log_{10}$- transformed with the exception of k_{secchi}.

	Biomass correlation			Harvest correlation		
Environmental variable	*r*	*P*	*N*	*r*	*P*	*N*
Chlorophyll, mg/m^3	0.89	0.0001	14	0.97	0.0001	11
Conductivity, micromho/cm	0.88	0.0001	14	0.93	0.0001	11
Total nitrogen, mg/m^3	0.73	0.0030	14	0.90	0.0001	11
Organic nitrogen, mg/m^3	0.72	0.0037	14	0.92	0.0001	11
Total dissolved solids, mg/liter	0.85	0.0002	13	0.85	0.0034	9
MEI_{cond}	0.89	0.0001	14	0.91	0.0001	11
MEI_{tds}	0.84	0.0003	13	0.80	0.0090	9
k_{secchi}	0.85	0.0001	14	0.89	0.0003	11
Mean depth, m	-0.74	0.0025	14	-0.78	0.0045	11
Retention time, days	-0.76	0.0016	14	-0.74	0.0093	11
Phosphorus loading, kg P/year	0.82	0.0012	12	0.86	0.0030	9
Phosphorus loading, g P/m^2/year	0.87	0.0002	12	0.80	0.0089	9
Phosphorus loading, mg P/m^3/year	0.89	0.0001	12	0.83	0.0058	9
Point-source phosphorus loading, g P/m^2/year	0.79	0.0023	12	0.88	0.0040	8
Point-source phosphorus loading, mg P/m^3/year	0.80	0.0020	12	0.91	0.0019	8
Nitrogen loading, kg N/year	0.73	0.0071	12			
Nitrogen loading, g N/m^2/year	0.75	0.0053	12			
Nitrogen loading, mg N/m^3/year	0.79	0.0023	12			
Rotifer densities, organisms/m^3				0.78	0.0045	11

loading (kg P/year) and reservoir volume which explained the highest percentage of variation in biomass (91%) of all models tested (Table 4). Biomass values predicted with this model ranged from 61% to 137% of observed biomass (Fig. 1b). A model based on point source phosphorus loading and retention time could account for 81% of variation in biomass (Table 4; Fig. 1c). Predicted values ranged from 55% to 163% of observed values. With the exception of the multivariate nutrient loading models, the use of more than one independent variable in a single model did not increase the amount of variation in biomass or harvest able to be explained. No evidence for curvilinear relationships was observed.

The relatively wide confidence and prediction intervals around the regression lines predicting biomass may be partially attributable to variability associated with the cove rotenone technique, particularly when only a few coves within a water body are sampled (Siler 1986). This factor may be especially significant in reservoirs, which tend to be characterized by longitudinal gradients in abiotic, biotic, and fisheries-related parameters (Kimmel and Groeger 1984, Siler et al. 1986, Ney et al. 1990).

Harvest—Chlorophyll concentration was the best predictor of harvest, accounting for 93% of variation (Table 4; Fig 1d). Values of harvest predicted by chlorophyll ranged from 75% to 139% of observed values. A multivariate model

Table 4. Simple and multiple regression equations to predict fish biomass (kg/ha) and harvest (kg/ha/year) based on selected environmental variables.

	R^2	P	N
Models predicting $\log_{10}$ biomass			
(1) $1.5854 + 0.8086 \log_{10} \text{Chl}$	0.79	0.0001	14
(2) $0.3515 + 1.1411 \log_{10} \text{Cond}$	0.78	0.0001	14
(3) $1.8503 + 0.7067 \log_{10} \text{MEI}_{cond}$	0.79	0.0001	14
(4) $0.0545 + 0.5966 \log_{10} L_{TP} - 0.3031 \log_{10} \text{Vol}$	0.91	0.0001	12
(5) $2.2761 + 0.2032 \log_{10} L_{PTP} - 0.4266 \log_{10} \text{RT}$	0.81	0.0006	12
Models predicting $\log_{10}$ harvest			
(6) $0.4879 + 0.7138 \log_{10} \text{Chl}$	0.93	0.0001	11
(7) $-0.9047 + 0.8834 \log_{10} \text{TON}$	0.85	0.0001	11
(8) $-0.7571 + 1.1071 \log_{10} \text{Cond}$	0.86	0.0001	11
(9) $0.7501 + 0.5858 \log_{10} \text{MEI}_{cond}$	0.83	0.0001	11
(10) $1.6077 + 0.1932 \log_{10} L_{PTP} - 0.4490 \log_{10} \text{Vol}$	0.92	0.0020	8

Chl = Chlorophyll, mg/m^3.
Cond = Conductivity, micromho/cm.
MEI_{cond} = Morphoedaphic index based on conductivity, micromho/cm/m.
LTP = Total phosphorus loading, kg P/year.
Vol = Reservoir volume, 10^6 m^3.
L_{PTP} = Municipal wastewater point-source phosphorus loading, kg P/year.
RT = Retention time, days.
TON = Total organic nitrogen, mg/m^3.

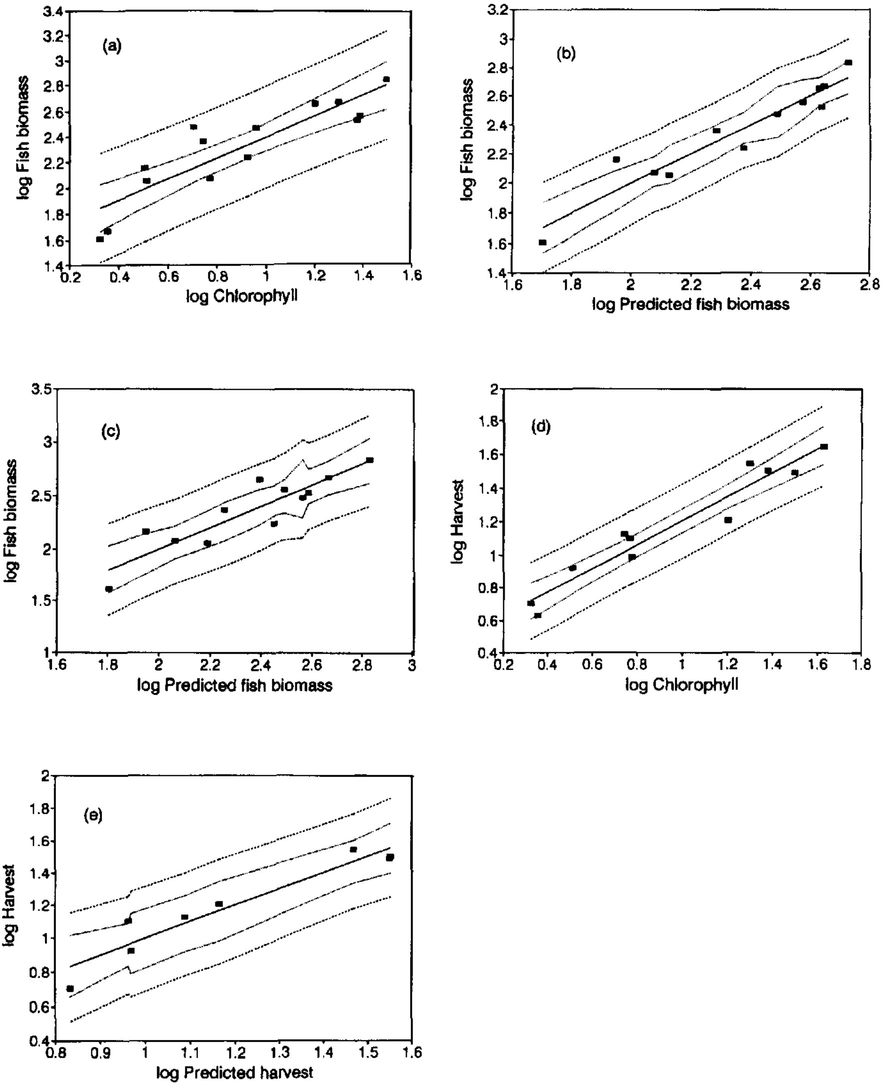


Figure 1. (a) Regression of total fish biomass on chlorophyll concentration (Equation 1, Table 4). (b) Multiple regression of total fish biomass on total phosphorus loading and reservoir volume (Equation 4, Table 4). (c) Multiple regression of total fish biomass on phosphorus loading from municipal wastewater discharges and retention time (Equation 5, Table 4). (d) Regression of sportfish harvest on chlorophyll concentration (Equation 6, Table 4). (e) Multiple regression of sportfish harvest on phosphorus loading from municipal wastewater discharges and reservoir volume (Equation 10, Table 4). Outer boundaries are 95% prediction limits; inner boundaries are 95% confidence limits.

based on point source phosphorus loading and reservoir volume could account for 92% of variation in harvest (Table 4; Fig. 1e). Predicted values ranged from 73% to 135% of observed values. No appropriate models for predicting harvest based on total phosphorus loading were obtained.

Assessment of Predictors of Total Fish Biomass and Sportfish Harvest

Chlorophyll—Chlorophyll concentration was the best predictor of harvest, and one of the best predictors of biomass, of the variables tested. These results are consistent with those of Oglesby (1977*a*), who found that summer epilimnetic chlorophyll concentrations could account for 84% of variation in fish yield in lakes worldwide. Jones and Hoyer (1982) observed that chlorophyll could explain 91% of variation in sportfish harvest in midwestern reservoirs; chlorophyll was a better predictor of harvest than were total phosphorus, alkalinity, and MEI.

Strong empirical relationships between chlorophyll and fish abundance suggest that fish production was limited by production at the base of the food web. This is consistent with Downing et al.'s (1990) observation that phytoplankton production and fish production were strongly related, and with the conclusion of Jenkins and Morais (1978) that food availability was the most significant factor limiting predatory fish production in reservoirs.

Environmental factors which affect the conversion of nutrients and energy to biomass represent a source of uncertainty associated with the prediction of fish production on the basis of abiotic parameters. Models based on nutrient concentrations, for example, are subject to uncertainty associated with variability in phosphorus bioavailability (Peters 1986), and are subject to error when phytoplankton production is limited by factors other than nutrients, as in very turbid reservoirs or those with very short retention times. Because surface chlorophyll concentration is a manifestation of the realized productivity of a water body, use of chlorophyll as an index of fertility eliminates some of the uncertainty associated with predictions based on abiotic variables.

Application of these models should be restricted to reservoirs which fall within the geographic, morphologic, and hydrologic boundaries of the data used to produce the model (Ryder et al. 1974, Leach et al. 1987). In addition, the models may not be appropriate for reservoirs with trophic structures unlike those characteristic of these reservoirs; chlorophyll-based models may underpredict fish abundance where macrophytes or allochthonous organic material contribute significantly to the food web. Similarly, these models may not apply to reservoirs in which phytoplankton standing crop is limited by zooplankton grazing rather than by nutrients; in this study, the effect of grazing on phytoplankton was minimized due to the severe limitation of zooplankton densities by clupeid fish predation (Rodriguez 1989*b*).

Phosphorus—Total phosphorus concentrations have been found to be significantly related to total fish biomass in southern Appalachian reservoirs (Yurk and Ney 1989) and to fish yield in north temperate lakes (Hanson and Leggett 1982). In this study, total phosphorus concentration was not a good predictor of fish biomass or harvest.

The theoretical basis for relationships between phosphorus and fish parameters is the status of phosphorus as the nutrient limiting primary production. Kimsey et al. (1982) found that nitrogen, rather than phosphorus, may at times have limited primary production in some of these reservoirs. In addition, total phosphorus concentrations may not have provided good estimates of bioavailable phosphorus, due to variability in sources of phosphorus. The percent of total phosphorus load originating from point sources varied widely among reservoirs, ranging from 0% to 86%. Phosphorus in municipal wastewater is generally more bioavailable than phosphorus from non-point sources (Huettl et al. 1979, Young et al. 1982). This may be particularly true in Piedmont North and South Carolina, where clays, which have the capacity to absorb phosphorus and reduce its bioavailability (Edzwald et al. 1976, Golterman 1977), are a predominant soil type (Kimsey et al. 1982, Simmons 1988).

Conductivity—Conductivity was a very good predictor of both biomass and harvest, presumably due to proportionality between conductivity and ionic concentrations of limiting nutrients (Ryder et al. 1974). However, Oglesby (1977*b*) observed that edaphic and cultural factors could significantly affect that proportionality. Chlorophyll is less likely than conductivity or measures of nutrient concentrations to be "uncoupled" from fish production due to environmental or anthropogenic influences.

Physical parameters—Both mean depth and retention time were significantly correlated with total biomass and harvest, but explained less than 62% of variation in biomass and harvest. Both mean depth and retention time were significantly correlated with chlorophyll ($r = 0.65$; $P = 0.0063$; $N = 16$, and $r = 0.62$; $P = 0.0094$; $N = 16$, respectively), suggesting that the relationships observed between fish abundance and physical parameters may have been attributable to the influence of these parameters on reservoir productivity. Aggus and Lewis (1978) found that retention time and total annual discharge were significantly correlated with total standing crop in southern reservoirs. However, these parameters each explained less than 35% of variation in fish crop, and relationships of standing crop to chlorophyll, nutrients, and conductivity were not analyzed.

Morphoedaphic index—MEI_{cond} was a good predictor of both biomass and harvest in this study, but accounted for no more variation in fish parameters than was explained by conductivity alone. Multiple regression analyses indicated that mean depth did not account for variation beyond that attributable to conductivity. Ryder (1982) described productivity as being affected primarily by "energy and nutrient inputs constrained by the morphology of the lake basin." In this study, conductivity did not represent a surrogate for nutrient inputs, but rather a surrogate for nutrient concentrations. Correlations between conductivity and nutrient concentrations were much stronger than those between conductivity and nutrient inputs. Reckhow and Clements (1984) observed that nutrient inputs and concentrations were not linearly related in southeastern lakes. Because in-lake concentrations incorporate the influences of morphometry and hydrology on the distribution of nutrient inputs, mean depth did not represent an independent source of variation in fish parameters in these reservoirs.

Jenkins (1982) described a curvilinear relationship of MEI_{tds} to biomass and harvest, and produced quadratic equations accounting for 8% of variability in sportfish harvest and as much as 72% of variability in total biomass. In this study, the addition of a quadratic term to predictive equations based on MEI_{tds} and MEI_{cond} did not significantly improve the amount of variance explained. However, Jenkins' regressions were based on larger numbers of reservoirs, with a wider range of MEI_{tds}. The range of MEI_{tds} values in this study would confine the data to virtually linear portions of Jenkins' curves.

Phosphorus loading—Phosphorus loading, in conjunction with morphometry/hydrology, could explain over 90% of variation in fish biomass and harvest. Although it is generally acknowledged that fish production is influenced by nutrient inputs, empirical models using nutrient loading to predict biomass and harvest have not been commonly developed (Carline 1986). This may be due to the relative difficulty of obtaining nutrient loading data, in comparison to measuring in-lake parameters. In addition, empirical models based on nutrient loading are subject to error due to temporal and spatial variability in limiting factors and to differences in bioavailability of nutrients from various sources. However, such models provide a means of predicting fish biomass and yield in reservoirs not yet constructed and of predicting changes in fish production associated with proposed changes in nutrient loading rates. The strength of point source phosphorus loading as a predictor of fish production may be attributed to the greater bioavailability of phosphorus from municipal wastewater facilities, as compared to phosphorus from non-point sources.

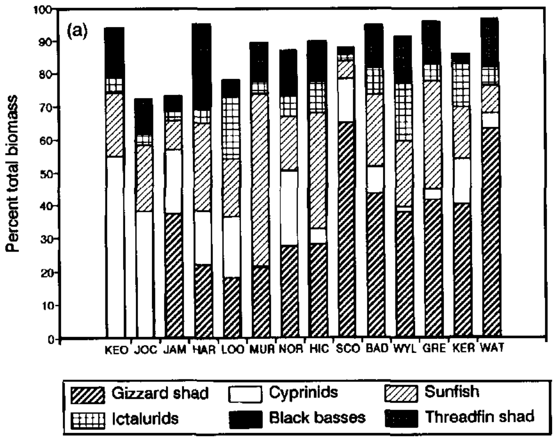
Variation in Taxonomic Composition Along Environmental Gradients

Biomass—Fish biomass in cove rotenone samples was dominated on average by gizzard shad (*Dorosoma cepedianum*), bluegill (*Lepomis macrochirus*), and common carp, which comprised 32%, 15%, and 15% of total biomass, respectively. Threadfin shad (*Dorosoma petenense*) comprised 6% of total biomass, largemouth bass 5%, channel catfish (*Ictalurus punctatus*) 4%, redbreast sunfish (*Lepomis auritus*) 3%, yellow perch (*Perca flavescens*) 2%, and white catfish (*Ictalurus catus*) 2%. Although relative biomass composition varied substantially among reservoirs (Table 5), discrete community types were not apparent based on examination of the major taxonomic components of biomass (Fig. 2a), with one exception. Gizzard shad, abundant in all other reservoirs, were not observed in Lakes Jocassee and Keowee, very long-retention-time, unproductive reservoirs located in series in the upper Savannah River watershed. Reasons for the absence of gizzard shad are unknown.

The general lack of discrete community types can be attributed in part to the fact that cove rotenone samples measured only littoral biomass, eliminating pelagic species from characterizations of biomass composition. In addition, the averaging of biomass data over locations within reservoirs may have obscured the existence of discrete community types associated with particular habitats. Intra-reservoir dif-

Table 5. Mean taxonomic composition of biomass and harvest for reservoirs in Piedmont North and South Carolina, expressed as percent of total. Species belonging to the families Esocidae, Lepisosteidae, Poeciliidae, and Atherinidae were also present in small numbers in cove rotenone samples. Catfish harvest data were not available for Lakes Greenwood and Murray. Key to biomass taxa: CLU = Clupeidae, CEN = Centrarchidae, CYP = Cyprindae, ICT = Ictaluridae, CAT = Catostomidae, PER = Percidae, PRC = Percicthyidae. Key to harvest taxa: CRA = crappie, LMB = largemouth bass, CTF = catfishes, SUN = sunfishes, STB = striped bass, HYB = striped x white bass hybrid, WTB = white bass, WTP = white perch, SAL = salmonids.

	Biomass							Harvest								
Reservoir	CLU	CEN	CYP	ICT	CAT	PER	PRC	CRA	LMB	CTF	SUN	STB	HYB	WTB	WTP	SAL
Badin	53	26	8	8	1	1	2	40	24	8	11	6	0	7	2	0
Greenwood	51	37	3	5	1	2	1	21	47		8	2	0	0	18	0
Hartwell	40	35	16	4	1	2	<1	12	37	2	2	4	37	2	0	0
Hickory	28	49	5	9	0	7	2									
James	37	21	20	3	12	6	1									
Jocassee	23	30	38	4	5	1	<1	3	44	0	3	0	0	0	0	42
Keowee	6	30	55	5	4	1	0	28	67	1	2	0	0	0	0	<1
John Kerr	42	21	6	14	15	2	1									
Lookout Shoals	18	25	18	19	15	4	<1									
Mtn. Island								46	11	17	13	10	0	<1	0	0
Murray	28	58	<1	4	2	6	1	13	28		29	13	0	0	6	0
Norman	37	27	23	6	2	3	1	49	17	5	3	12	0	5	0	0
Kerr Scott	67	9	13	2	8	0	1									
Tuckertown								60	6	25	3	<1	0	5	<1	0
Wateree	75	12	5	6	2	1	<1	45	26	7	6	0	0	14	0	0
Wylie	47	25	2	17	6	1	2	21	24	36	9	<1	0	9	0	0
Mean	39	29	15	8	5	3	1	31	30		8	4	3	4	2	4



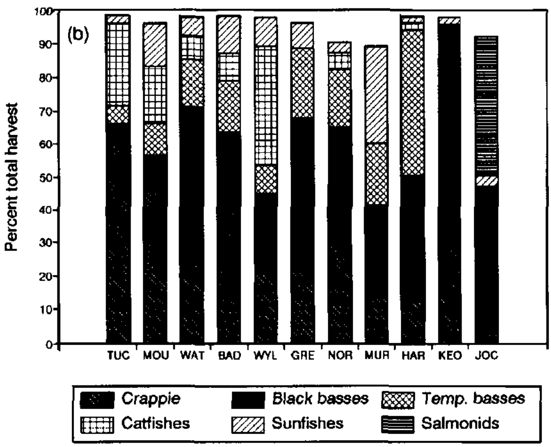


Figure 2. (a) Percentages which selected taxa comprised of total fish biomass. Reservoirs are sorted from least (KEO) to most (WAT) productive, as measured by chlorophyll. (b) Percentages which selected taxa comprised of total harvest. Reservoirs are sorted from shortest (TUC) to longest (JOC) retention time. Reservoirs are identified by first 3 letters of reservoir name.

ferences in fish community composition along headwaters-to-forebay gradients have been documented for 2 large southeastern reservoirs by Siler et al. (1986) and Ney et al. (1990). Finally, environmental variables generally did not exhibit discontinuities, as all reservoirs were located within 1 geographic/climatic region.

Variation in biomass composition along environmental gradients was not evident in correlation analyses, with one exception. The percent of biomass consisting of common carp was negatively correlated with chlorophyll (r = –0.88; P = 0.0001; N = 13) and total fish biomass (r = –0.81; P = 0.0009; N = 13). Eutrophication has been cited as leading to increased dominance of rough fish such as carp (Lee and Jones 1991). In this study, however, the relative biomass of common carp declined with increasing fertility (Fig. 2a).

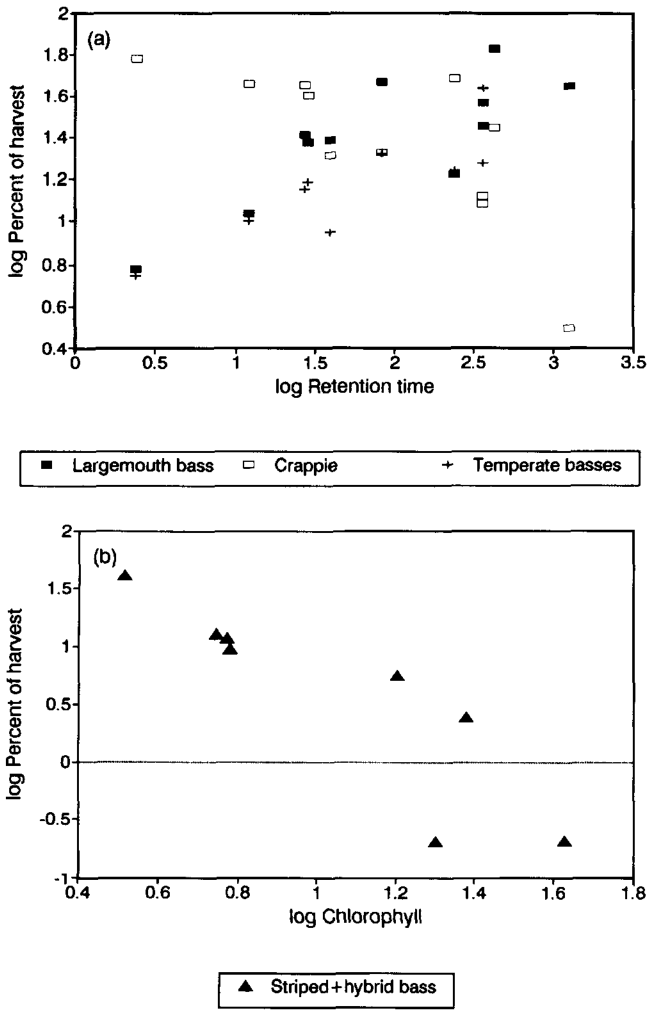


Figure 3.
(a) Percent of total harvest consisting of largemouth bass, crappie, and temperate basses, vs. retention time (days). (b) Percent of total harvest consisting of striped plus hybrid bass, vs. chlorophyll. Only those reservoirs from which harvest of taxon was reported are included.

Harvest—Sportfish harvest was generally dominated by crappie and largemouth bass, although substantial variability in harvest composition was evident (Table 5; Fig. 2b). Much of the variability could be attributed to the influence of stocking, in that striped bass, hybrid bass, and salmonids existed primarily as "put-and-take" fisheries. Despite the importance of stocking, however, correlation analyses did provide evidence of variation in harvest composition along environmental gradients.

Harvest composition varied primarily along morphometric/hydrologic gradients. The percent of harvest consisting of largemouth bass tended to increase with increasing retention time. ($r = 0.79$; $P = 0.0036$; $N = 11$) (Fig. 3a). Similarly, the percent consisting of temperate basses increased with retention time ($r = 0.85$; $P = 0.0037$; $N = 9$) and reservoir volume ($r = 0.83$; $P = 0.006$; $N = 9$). In contrast, the percent of harvest consisting of crappie declined as retention time ($r = -0.75$; $P = 0.008$; $N = 11$) and mean depth ($r = -0.79$; $P = 0.0036$; $N = 11$) increased. No significant relationships were detected between environmental gradients and percents of harvest consisting of sunfishes or catfishes.

The relationship of harvest composition to morphometry and hydrology was most likely due to the influence of these factors on the extent to which pelagic habitat was developed. Mean depth influences thermal structure of lakes (Marshall and Ryan 1987) and the percentage of lake area consisting of littoral habitat (Hanson and Leggett 1982). In these reservoirs, the development of a lacustrine region was associated with long retention time (Rodriguez 1989*b*).

Correlation analysis also revealed a shift in harvest composition along a gradient of productivity. The percent of harvest consisting of striped plus hybrid bass declined with increasing chlorophyll ($r = -0.89$; $P = 0.0033$; $N = 8$) (Fig. 3b). Greater algal productivity may be associated with a loss of the cool, oxygenated habitat preferred by striped bass (Lee and Jones 1991).

Factors Affecting Absolute Biomass and Harvest of Individual Taxa

Largemouth bass—Largemouth bass biomass tended to increase as reservoir productivity increased, as evidenced by positive correlations with total organic nitrogen ($r = 0.83$; $P = 0.0002$; $N = 14$), phosphorus loading (mg P/m^3/year) ($r = 0.84$; $P = 0.0006$; $N = 12$), and chlorophyll ($r = 0.70$; $P = 0.0053$; $N = 14$). Negative correlations with mean depth ($r = -0.71$; $P = 0.0042$; $N = 14$) and retention time ($r = -0.70$; $P = 0.0052$; $N = 14$) were probably attributable to the interdependence of productivity, morphometry, and hydrology in these reservoirs, since multiple regression analysis revealed that mean depth did not explain variation in largemouth bass biomass independent of that explained by total organic nitrogen.

Largemouth bass harvest was positively correlated with point-source phosphorus loading (mg P/m^3/year) ($r = 0.86$; $P = 0.0057$; $N = 8$), and negatively correlated with non-algal turbidity ($r = -0.75$; $P = 0.008$; $N = 11$), consistent with a preference for clear water (Carlander 1969). These correlations suggest that largemouth bass responded positively to increased productivity in waters with low levels of non-algal turbidity, conditions likely to occur when nutrient inputs are not strongly associated with turbidity.

As with all taxa examined, a significant amount of variability in the relationships of largemouth bass abundance to environmental parameters may have been attributable to competition, and to the effects of "top-down" forces such as predation and angling. It was not possible to account for these factors in the correlation and regression analyses.

Crappie—Crappie harvest increased with increasing fertility, as evidenced by strong correlations with chlorophyll concentration ($r = 0.85$; $P = 0.0009$; $N = 11$); nitrogen concentration ($r = 0.89$; $P = 0.0002$; $N = 11$); and conductivity ($r = 0.85$; $P = 0.0008$; $N = 11$). Crappie harvest was also strongly negatively correlated with mean depth ($r = -0.89$; $P = 0.0002$; $N = 11$), and retention time ($r = -0.85$; $P = 0.001$; $N = 11$). Multiple regression analyses indicated that both chlorophyll and mean depth contributed significantly to explaining variation in crappie harvest (R^2

= 0.88; $P = 0.0002$; $N = 11$), indicating that both habitat-related factors and food supply influenced crappie harvest.

Percichthyids—The temperate bass community consisted of striped, white, and hybrid bass, and white perch. Striped bass reproduction is rare in these reservoirs, and the fishery is generally dependent on stocking. The influence of stocking and the small number of reservoirs in which individual taxa were observed (Table 5) resulted in the detection of few significant relationships between percichthyid harvest and environmental parameters.

Total percichthyid harvest was not significantly correlated with any environmental parameters. White bass harvest was inversely related to non-algal turbidity ($r = -0.92$; $P = 0.0033$; $N = 7$), suggesting a preference for waters low in inorganic particulate material. The sum of striped and hybrid bass harvest was negatively correlated with chlorophyll concentration ($r = -0.84$; $P = 0.0088$; $N = 8$), probably reflecting a decline, with increasing eutrophication, in cool, oxygenated habitat.

Ictalurids—Biomass of catfishes (*Ictalurus catus*, *I. furcatus*, *I. punctatus*, *Pylodictis olivaris*) increased with reservoir productivity, as evidenced by positive correlations with conductivity ($r = 0.84$; $P = 0.0002$; $N = 14$), phosphorus loading (mg P/m^3/year) ($r = 0.82$; $P = 0.001$; $N = 12$), and chlorophyll concentration ($r = 0.79$; $P = 0.0007$; $N = 14$). Catfish harvest also increased with increasing fertility, as evidenced by strong correlations with phosphorus loading (mg P/m^3/year) ($r = 0.89$; $P = 0.0071$; $N = 7$) and chlorophyll concentration ($r = 0.88$; $P = 0.0037$; $N = 8$). Habitat preference was apparent in that catfish biomass declined as reservoir mean depth ($r = -0.76$; $P = 0.0016$; $N = 14$) and retention time ($r = -0.74$; $P = 0.0023$; $N = 14$) increased. Multiple regression analyses indicated that both fertility and habitat-related factors contributed significantly to explaining variation in catfish biomass.

Gizzard shad—Gizzard shad biomass was strongly correlated with chlorophyll concentration ($r = 0.86$; $P = 0.0004$; $N = 12$), consistent with the planktivorous habit of this species. No significant relationships with morphometric or hydrologic parameters were observed, suggesting that food supply was a limiting factor for this taxon. Gizzard shad in these reservoirs frequently attain sizes too large to serve as prey (Noble 1981), reducing the potential impact of predation as a limiting factor.

Threadfin shad—Threadfin shad biomass was not significantly correlated with chlorophyll, nutrient concentrations, or morphometric/hydrologic parameters. Densities of this species may have been affected by stocking rates, predation, and sensitivity to temperature, all of which can cause large fluctuations in biomass from year to year (Carlander 1969, Harper and Namminga 1986). A strong negative correlation with areal copepod densities ($r = -0.86$; $P = 0.0007$; $N = 11$) may reflect the impact of clupeid predation on zooplankton.

Conclusions and Management Implications

Results of this study suggest that total fish biomass and total sportfish harvest in Piedmont Carolina reservoirs are largely controlled by reservoir fertility. The limiting effect of primary production on fish production has been established for other geographic regions as well (e.g., Oglesby 1977*a*, Jones and Hoyer 1982, Downing et al. 1990). The predictive models developed in this study will allow fisheries managers to estimate the upper boundaries of potential sportfish harvest in individual reservoirs, providing a means of assessing the yield of the fishery and of developing realistic management goals.

While overall yield increased with increasing primary production, the composition of the harvest was primarily dependent on reservoir morphometry, hydrology, and stocking practices. Harvest in shallower, shorter-retention-time reservoirs was dominated by crappie. Largemouth and temperate basses comprised an increasing percentage of harvest as retention time increased. The influence of fertility on harvest composition was evident in a decline in the combined harvest of striped and hybrid bass as reservoir fertility increased, most likely attributable to a decline in cool-water, oxygenated habitat. Other major harvest taxa tended to respond positively to increased reservoir fertility. Generally, the development of realistic fisheries management goals requires consideration of reservoir morphometry, hydrology, and fertility; assessment of available habitat should include consideration of the impact of fertility on habitat characteristics.

Likewise, assessment of the impact of environmental perturbations on fisheries necessarily includes consideration of the effects on both overall fish production and on taxonomic composition. Point source phosphorus loading, for example, was positively correlated with total harvest and harvests of crappie, catfish, and largemouth bass. No increases in the biomass of rough fish such as carp occurred in conjunction with increased phosphorus loading. However, as noted above, the harvest of striped plus hybrid bass declined as reservoir fertility increased. Consideration of these specific responses by the fish community should aid in the assessment of environmental impacts and in setting attainable management goals.

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