

COMPARATIVE RESOURCE USE BY TWO SPECIES OF BLACK BASS
IN RIVERINE AND IMPOUNDED SECTIONS OF THE NEW RIVER,
VIRGINIA

by

Mark C. Scott


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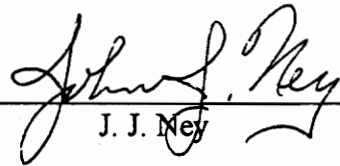
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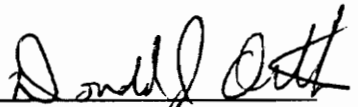
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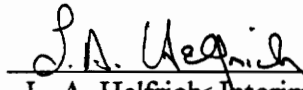
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(ABSTRACT)

Two species of black bass, smallmouth bass *Micropterus dolomieu* and spotted bass *Micropterus punctulatus*, are sympatric in both riverine and impounded sections of the New River, Virginia. Resource use (habitat and diet) by the two species was investigated to determine patterns and extent of resource partitioning between them and how those patterns might differ between lotic and lentic environments. Individual fitness indicators (i.e., growth and body condition factor) were also measured to assess performance of populations of the two species in the study areas. Fitness indicators suggested relatively good performance of both species in both river and impoundment, which implied that competitive pressures were not intense. Diet analyses indicated fairly high overlap in prey types consumed. High fitness combined with considerable diet overlap suggested that food availability was adequate, and that segregation in this impounded river system was not on a trophic basis. The two species were found to segregate spatially, with spotted bass predominant in the impoundment and smallmouth more abundant in the river. Spatial segregation was also apparent within both river and impoundment habitat types.

To Tina, who has supported me in so many ways.

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INTRODUCTION

The black basses (Centrarchidae:*Micropterus*) typically occupy the top trophic levels in eastern North American freshwater communities, and the genus is among the most important in the American freshwater sport fishery. A relatively large body of information exists on the biology and ecology of spotted bass *M. punctulatus* (Vogele 1975b; Carlander 1977), while smallmouth bass *M. dolomieu* is one of the most valued and studied fishes in North America (Coble 1975; Edwards et al. 1983; Robbins and MacCrimmon 1974; Jenkins and Burkhead 1994). Descriptions from the literature on habitat use, feeding habits, and reproduction of these two basses reflect their ecological similarity. Where resource requirements overlap extensively, experimental evidence has indicated that interspecific competition may significantly affect resource use, growth, distribution, and survival of fish populations (Nilsson 1967; Werner and Hall 1976). Accordingly, data that help identify how resources are shared in rivers and reservoirs where these two congeneric species coexist would serve an important function in aiding the management of two ecologically and economically valuable fishes. Improved understanding of the relationship between the basses would help managers better design and evaluate stocking programs involving the two species (Bennett 1970), and so avoid

increasing competitive pressure by stocking these species into a habitat where one or the other may be at a competitive advantage. Also, resource partitioning information would help in understanding and predicting effects of habitat and flow manipulations on these species (Orth 1987), because these changes may increase the intensity of competitive interactions by decreasing the availability of suitable habitats.

Species Information

Both smallmouth bass and spotted bass are native to the Gulf of Mexico drainage (Lee et al. 1980). The smallmouth bass originally was found from Minnesota and southern Quebec south to the Tennessee River system and west to eastern Oklahoma, avoiding central Mississippi River valley lowlands. Spotted bass were found throughout the central and lower Mississippi basin and along the Gulf coast from Texas to northwest Florida. The two species are naturally sympatric over a large portion of their native ranges.

In Virginia, both species are native to the Big Sandy and Tennessee river drainages (Jenkins and Burkhead 1994). Smallmouth bass were introduced into the New River and various Atlantic slope drainages by 1880, and continued to be stocked periodically in the major drainages of the state through the 1980's (MacCrimmon and Robbins 1975; Jenkins and Burkhead 1994). Spotted bass are considered introduced to the New River, but the means of stocking is unknown. The first report of a New River collection of spotted bass is from Hubbs in 1927. Stocking to James and Roanoke drainages occurred in the mid 1970's (Jenkins and Burkhead 1994).

While life histories of the two species have been studied (see reviews in Coble

1975; Vogele 1975b; Carlander 1977, Jenkins and Burkhead 1994), little study has been done on interspecific relationships involving sympatric populations. Both species are highly adaptable to environmental conditions, thriving in rivers as well as lakes and reservoirs throughout their ranges, although Hubbs and Bailey (1938) reported that the smallmouth is more often found in streams in the southern part of its range. They attributed this to temperature requirements.

Smallmouth bass habitats are generally characterized by cool-to-warm temperatures, rock and gravel substrate, clear water, with ample shelter and forage (Edwards et al. 1983). Foods of the smallmouth typically start with zooplankton and small aquatic insects (Easton and Orth 1992), then shift gradually to benthos which continue to be consumed through adulthood. As juveniles, the diet shifts from predominantly aquatic insects to crayfish and fish, which normally make up most of the food in adults (Surber 1941; Applegate et al. 1967; Roell and Orth 1993). Considerable variation exists in extent and timing of dietary shifts, depending on prey availability.

Literature on the spotted bass is considerably less comprehensive than that on smallmouth bass. Habitat use varies in different parts of its range, from small, clear, rocky streams to large, sluggish, turbid rivers (Hall 1951; Trautman 1957; Fajen 1968). Carlander (1977) called it a predominantly stream-dwelling fish that is found commonly in reservoirs. Vogele (1975a) reported that spotted bass in reservoirs appear to utilize clear and deep water, with rocky substrate. The spotted bass has been described as intermediate in habitat preference between largemouth and smallmouth bass (Trautman 1957;

Miller 1975).

Food of the spotted bass, as with the smallmouth, varies according to size of the fish, habitat, and prey availability. Fry consume zooplankton, then grow to eat insects and crayfish (Howland 1932). Fish and crayfish are the most common food of adult bass (Rosebery 1950; Applegate et al. 1967; Smith and Page 1969).

The general implications derived from these collective descriptions are that smallmouth and spotted bass are extremely similar in ecological requirements, and that both are highly adaptable to local conditions. Because the species are naturally sympatric over large portions of their respective native ranges, one would expect that mechanisms for partitioning of scarce resources would have evolved with them. Given the ecological similarity of these fishes, as well as their economic importance and present level of management, additional information is needed on their potential for competitive interactions in lotic and lentic environments.

Competitive Interactions and Segregation of Resources

The influence of competition in structuring natural communities has long been the focus of controversy and investigation among ecologists and evolutionary biologists (Connell 1983; Schoener 1982). Darwin recognized that competition is likely to be more severe between closely related forms that are similar in morphology and behavior. This concept led Gause to the formation of the competitive exclusion principle, which holds that "complete competitors cannot coexist" (Hardin 1960). Theoretically, competitive pressure is resolved by either segregation or exclusion. Segregation may result in reduced

growth and fitness of one or both competing populations, but allows reduction of competitive pressures. Exclusion indicates a loss of the less competitive population from the shared environment. Although demonstrations of segregation (e.g., resource partitioning) in nature cannot be viewed as tests of the competitive exclusion principle, study of similar coexisting species has value in illustrating mechanisms of adaptive response to competition (Winemiller and Taylor 1987). In addition, effective management of populations requires ecological information of this nature.

Competition among fishes is particularly difficult to study due to their ontogenetic size changes and considerable plasticity in growth and behavior (Weatherly 1963; Werner and Gilliam 1984). Nonetheless, effects of competition on species interactions and on the structure of fish assemblages have been demonstrated. Such evidence has included indications that food resources are limiting to growth, and experiments demonstrating shifts in resource use in allopatry and sympatry, among others (see Nilsson 1967 and Werner 1986 for reviews).

The importance of biotic interactions may not be equal between lotic and lentic systems. Shifts in resource use have been documented in lentic systems for centrarchids in sympatry and allopatry (Werner and Hall 1977). In running waters, evidence has indicated that segregation of stream salmonids occurs (Fausch and White 1981; Hearn and Kynard 1986). However, interspecific competition in lotic environments may be less important relative to lentic waters in structuring fish assemblages because unpredictable perturbations in the annual hydrologic regime of running waters may preclude establishment of

an equilibrial state in community organization (Connell 1980; Weins and Rotenberry 1980; Schlosser 1982; Schlosser and Toth 1984). This instability may prevent even strongly interacting species from excluding each other (Angermeier 1987). A gradient of the relative importance of stochastic processes in lotic systems has been hypothesized by Schlosser (1987) whereby communities in small streams are controlled largely by abiotic factors, but biotic interactions play an increasing role in larger streams (rivers). The gradient is based on increasing habitat heterogeneity, pool development, and decreasing temporal variability with increasing stream size.

For example, in the case of an impoundment on a river, one would predict based on this hypothesis that biotic interactions will be more important in the more stable impounded pool than in the more variable riverine habitat. Partitioning of habitat and food resources would thus be expected to be more pronounced in the impoundment than in the river.

Segregation is likely to be along either spatial, temporal, or trophic resource axes (Ross 1986). If overlap were low on one axis, then it may be high on the other without interference competition occurring; however, exploitation competition may still be possible with overlapping diet. By observing the extent of resource use overlap between two species and each population's fitness level in a particular habitat, certain inferences may be made concerning competitive pressure and extent of segregation (Table 1). High inter-specific overlap in habitat use and diet would demonstrate the potential for com-

Table 1. Species interactions inferred according to resource use overlap and fitness observed in two populations of different species.

| | | Resource Use Overlap | |
|---|--------------|----------------------------|-------------------------------------|
| | | High | Low |
| Both species exhibit: | High Fitness | Resources freely available | Segregation (or divergence) |
| | Low Fitness | Competition | Segregation -resources are limiting |
| One species exhibits high fitness, while the other exhibits low fitness | | Competition | Stressor from another cause |

petitive interactions. If significant overlap were coupled with high fitness levels among populations of both species, the inference would be that resources were not limited in availability. If high spatial and trophic overlap were observed with indications of low fitness for both species, low availability of resources would be likely and thus direct competition may be occurring. Given the species' evolutionary history of coexistence, this scenario was not anticipated.

High fitness for two species exhibiting low resource use overlap would imply segregation was successful for both species. Studies in allopatry would be required to discriminate between interactive segregation and evolutionary divergence as the mechanism for resource partitioning. Low overlap and low fitness observed for both species would result in the same circumstance as high fitness for both species (i.e., either segregation or divergence is responsible), except that food resources could be inferred to be scarce in the system (Table 1). Low resource use overlap coupled with low fitness indications for only one of the species would imply interactive segregation; the plastic behavior shown by both species suggests that either would shift to more available resources in the absence of interference.

Problem Statement and Objectives

A fisheries survey conducted in 1990 in the vicinity of two hydroelectric power facilities on the New River in southwestern Virginia revealed a fish community numerically dominated by smallmouth bass and spotted bass (APCO and American Electric Corp. 1991). Analysis of electrofishing data collected in 1990 showed differences in relative

abundance between the two species in riverine and impounded waters. These observations prompted questions regarding resource use and partitioning between the two species of bass, and how resource use patterns might vary between riverine and impounded habitats.

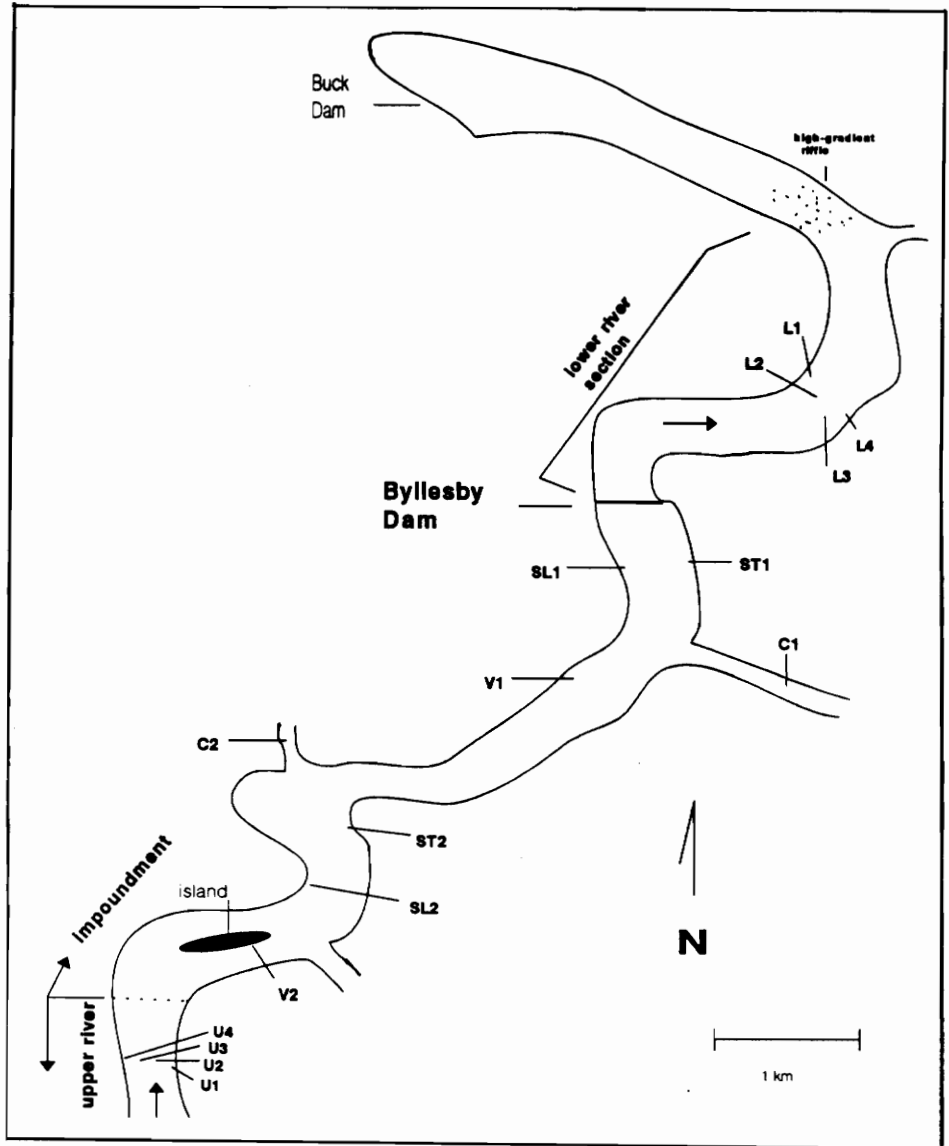
This study investigated distribution and abundance, growth, body condition, and diet of both species with respect to selected habitats in riverine and impounded environments in order to discern patterns of resource use and partitioning. Distribution, as indicated by abundance at various locations, should demonstrate any differential use of particular areas or habitats, and indicate extent of habitat use overlap. Diet analysis should demonstrate any differential use of available foods, and degree of overlap in diet. Growth and body condition of fish may be used as fitness indicators (Werner 1986) and thus reflect the relative suitability of a habitat for supporting the population. These fitness indicators assume a high degree of site fidelity in order for the information to be used as described.

The objectives of the study were to: 1) identify differences in habitat use as indicated by bass abundance at macro-habitat levels (i.e., lotic versus lentic environments) and meso-habitat levels (i.e., habitats within river or impoundment); 2) determine composition and relative abundance by weight of food items in the diet of each species; 3) make interspecific comparisons of the diets of similar-sized bass; 4) identify differences between river and impoundment habitats in growth and condition of the two species; 5) assess movement patterns of bass in an impounded river system to determine level of fidelity to a home range.

METHODS AND MATERIALS

Study Area

The Byllesby Hydroelectric Dam is the upper-most of a small two-dam project on the New River in southwestern Virginia, located in Carroll County (Figure 1). The 21.6 megawatt Byllesby facility creates a 97 hectare reservoir with a maximum depth of approximately 13 m; mean flow rates are estimated at 60 m³/s based on data recorded at a USGS discharge gauge 24 km upstream at Galax (APCO and American Electric Corp. 1991). The facility was operated up until the time of this study as a "peaking" power plant, meaning that at peak hours of electricity demand, the reservoir was drawn down as water was discharged through the turbines. Water quality measurements taken during the course of sampling indicated no stratification in temperature or dissolved oxygen concentration in the reservoir; the small size of the Byllesby impoundment relative to the river most likely prevented significant drops in dissolved oxygen from the river to impoundment. Likewise, temperature and other water quality parameters (e.g., pH, conductivity) were similar between river and reservoir. Secchi disk readings in the impoundment averaged 1-1.5 m for most of the year. River width in the vicinity of the study area averaged 150 m, with an approximate mean depth of 1 m. The New River dropped 2.7 m/km through the study area, the highest gradient section of the river found in Virginia. Geologic landforms are of Cambrian origin and composed of sedimentary rocks, quartzite, shale, dolomite, and limestone (Rosebery 1950).



Key to River Habitats

- U=upper river
- L=lower river
- 1=left bank (facing upstream)
- 2=40m off left bank
- 3=40m off right bank
- 4=right bank

Key to Impoundment Habitats

- ST=steep,rocky
- SL=silt flat
- C=impounded creek mouth
- V=overhanging bank vegetation
- 1=lower impoundment
- 2=upper impoundment

Figure 1. New River in the vicinity of Byllesby and Buck hydroelectric facilities. Electrofishing transects are shown.

Field Methods

Fish sampling was conducted at two free-flowing river sites, located above and below the hydroelectric facility, and in the reservoir created by the dam. At both above and below-dam river sites, four 100 m electrofishing transects were established, for a total of eight river transects. Eight 100 m shoreline transects were established in the impoundment as well, for a total of 16 study transects split evenly between river and impoundment.

Transects in the river were selected from areas accessible to a boat-mounted electrofishing unit, and were essentially pool-run habitat types. The upper site was approximately 0.5 km above the reservoir, and characterized by abundant large boulders. The lower site was located approximately 2 km below Byllesby dam, and was separated from downstream Buck reservoir by approximately 1 km and a high-gradient series of falls and riffles. Bedrock ridges were common throughout much of the lower river site. The two river sites were stratified for sampling into shoreline and mid-river transects, located on 1) the east bank, 2) 40 m off of the east bank, 3) 40 m off of the west bank, and 4) the west bank.

Sampling transects in the impoundment were stratified by the four general habitat types observed: 1) steep, rocky substrate with little or no vegetation or woody structure; 2) gradually sloping, vegetated banks with the bank vegetation overhanging the littoral zone, generally soft substrates and woody debris present as cover; 3) silt flats edged by stands of emergent vegetation (*Typha* sp.) along the shore; 4) impounded creek mouths,

which were characterized by substrates ranging from rocky to soft, and presence of woody debris. Creek mouths were sampled to assess their role as possible refuges from impoundment water quality (e.g., turbidity) or from biotic interactions that may be more prevalent in the impoundment (e.g., predation by flathead catfish *Pylodictis olivaris*). Electrofishing transects 100 m in length were randomly selected to represent each of the four impoundment habitat types. Two replicate transects per habitat type were established, one in the lower (near dam) end of the impoundment and one in the upper end, for a total of eight impoundment transects.

River and impoundment transects were characterized by physical habitat measurements: dominant substrate, water depth, and frequency occurrence of cover types. Water velocity was also recorded in the river transects. The habitat characterizations were obtained by taking measurements at 10 m intervals along each transect, for a total of 10 measurements per transect. Primary substrate was classified according to a modified Wentworth scale ranging from 1 (silt) to 7 (irregular bedrock; Table 2). Water depth was measured to the nearest 0.1 m. Cover was classified into one of several types (Table 3) and recorded as frequency of occurrence.

Transects were sampled by electrofishing between May and October 1991. Day and night samples were collected for all reservoir transects; only day samples were collected in the river due to potentially hazardous boating conditions (e.g., water currents, submerged obstacles). Six electrofishing samples collected per transect were used in comparisons among reservoir habitats, and seven samples per transect in comparisons

Table 2. Substrate scoring system places larger values on large-particle or rocky substrates.

| Substrate type | Code | Particle Size (mm) |
|-------------------|------|--------------------|
| Silt | 1 | <1 |
| Sand | 2 | 1-2 |
| Gravel | 3 | 2-16 |
| Pebble | 4 | 17-64 |
| Cobble | 5 | 65-256 |
| Boulder | 6 | >256 |
| Irregular bedrock | 7 | |

Table 3. Classes of cover type.

| |
|-----------------------------|
| Bedrock ledge |
| Undercut bank |
| Boulder |
| Woody debris |
| Overhanging bank vegetation |
| Aquatic macrophyte |

among river habitats. In comparisons between river and impoundment, four collections per transect were paired by date and time of day to equalize effort. Additional electrofishing was conducted in each habitat type to collect stomach content samples.

All transects were sampled using a boat-mounted electrofishing rig. A flat-bottom aluminum boat equipped with a 3500-W, 230-V gasoline-powered generator was used. Two booms suspended ring-type electrodes into the water approximately 2 m in front of the boat; the metal hull of the boat served as the cathode. Current discharge was controlled by a Smith-Root Model IV electrofisher set to deliver 440-V DC at 3-6 amps at a frequency of 60 pulses/sec. Transects were sampled by slowly moving the boat along the transect as a netter on the bow controlled output by a foot switch. Shock time (i.e., time during which electricity is discharged to the water) was standardized at around 200 sec per 100 m transect. All stunned bass were dip-netted (8-mm mesh) and placed in a live well until the transect was completely sampled.

Hoopnets and gillnets were used to sample deeper, offshore impoundment habitats, and these sampled larger fish (>150 mm). Nets were set for 24 hours and checked for catch every 12 hours. Net sampling methods were identical to those performed during a fish survey in 1990 by Virginia Tech personnel for AEP and APCO; net data from 1990 and 1991 were therefore combined for analysis.

All smallmouth and spotted bass collected were measured to the nearest 1.0 mm total length (TL). Weight for specimens under 10 g was measured to the nearest 0.1 g; for specimens between 10 g and 1 kg, weight was measured to the nearest 1.0 g; any

specimens over 1 kg were weighed to the nearest 10 g. Scales for age determination were taken from the mid-side, just below the lateral line, of all sizes of fish collected, or a subsample thereof (excluding young-of-year). Scales were sealed in a labeled envelope for lab analysis.

A bass tagging program begun in 1990 was continued in this study. All bass >200 mm TL were dorsally tagged with an anchor tag marked with an individual number which was recorded. Any previously tagged fish that were recaptured were noted during the work-up procedure described above.

Stomach contents were obtained from specimens over 130 mm TL by the stomach-tube method described by Van den Avyle and Roussel (1980) for obtaining stomach contents without sacrificing fish; clear acrylic tubes provided for visual confirmation that stomachs were completely emptied. Stomach contents were placed in individually labeled plastic bags with 10% buffered formalin and returned to the laboratory for analysis. Due to size limitations of the tube method, a sample of specimens under 130 mm TL was collected each month outside of the transect but within the same habitat type. These specimens were placed in formalin and returned to the lab for stomach content removal and analysis.

Laboratory Methods

Fish were assigned to three size classes for analysis of stomach contents: 40-80 mm TL, 81-150 mm TL, and >150mm TL; no bass less than 40 mm in length were included in this study. The size classes were selected to account for ontogenetic diet

shifts. By approximately 80 mm, both species are reported to convert from preying mainly on insects to including fish and crayfish (Coble 1975; Voegelé 1975b). The middle size class corresponds roughly to age 1+ bass, and older fish were grouped into the large class. Each stomach's contents were rinsed in several changes of water, separated according to food category, and weighed after blotting dry to the nearest 0.01 gram. The following food categories were used: microcrustaceans identified to order, terrestrial insects, aquatic insects to order, crayfish, and fish to family. When very small food items such as zooplankton and immature insects weighed less than 0.01 g, that item's proportion of total stomach content volume was estimated visually and recorded. Weights of food categories were also converted to proportions of the total stomach content weight for statistical analysis.

To compare growth rates, mean length-at-age was back-calculated from scale annuli measurements of all sizes of fish. Impressions of scales were formed on a plastic slide using a manual roller press, and examined by microprojector at 40x magnification. Lengths from focus to successive annuli were measured using criteria presented in Jearld (1983). Length at younger ages was back-calculated using the DisBCal computer program (Missouri Dept of Conservation 1989), which employs the Fraser-Lee relationship between scale growth and body length:

$$L_n = a + \left(\frac{S_n}{S_c}\right)(L_c - a)$$

where:

L_n = the total length of the fish at the time of formation of annulus n ;

a = the intercept value of a body-scale length regression (species-specific);

S_n = the scale measurement from focus to annulus n ;

S_c = the distance from the scale focus to the anterior margin; and

L_c = the total length of the fish at capture.

Assessment of growth allows for comparisons of fitness among populations, assuming that the measured growth occurred in the habitat where the fish was captured. This assumption was gauged by examining mark-recapture data for site fidelity, as addressed in the Results section.

Statistical Analyses

To identify interspecific associations with particular habitats, chi-square tests of independence were used to compare the relative abundance of each species in selected habitats: 1) river versus impoundment; 2) between river sites (below-dam versus above-impoundment); 3) midriver versus river margin habitats; 4) among impoundment habitat types. The chi-square tests whether the two species' respective proportion of total bass catch shifts significantly between the habitats of interest, the null hypothesis being that the catch proportions of the two species are equal among habitat types and independent of habitat. Where sample size allowed, the chi-square test was run on each of the three size classes (40-80, 81-150, >150 mm TL) to determine ontogenetic effects on habitat use. This statistic required that equal effort was applied toward collection of each species in the habitats being compared. Because the anatomy and behavior of the two closely-related

basses are so similar, electrofishing techniques were considered equally effective in collecting either species located within the electric field. Sampling among habitats was paired by date and time of day when required to equalize sampling effort spatio-temporally. Because river electrofishing samples were collected only during the day, the night samples collected in the impoundment were omitted from analyses involving both locations to avoid diel sampling bias (Paragamian 1989). Species distribution was not associated with position in the reservoir, with 72 % spotted bass vs. 28 % smallmouth bass in the lower end of the impoundment and 68 % spotted bass vs. 32 % smallmouth bass in the upper end ($\chi^2=1.4$; $P>0.20$). Therefore, replicates from the upper and lower impoundment were pooled among the four habitat types for analysis. All statistical analyses were performed using SAS[®] software (SAS Institute Inc. 1987).

While the chi-square test compared the proportional collection of the two species among habitat types, intraspecific differences in abundance among habitats were also evaluated to determine if one species or both were responsible for any changes in species predominance. To quantify abundance, catch per unit effort (CPUE) values were calculated as number of fish per one hundred meter transect for each species. Netting CPUE was expressed as number per netday (12 hours). Comparisons of abundance among pairs of locations were made using the Wilcoxon rank sum test (non-parametric statistical analog to the t-test). Comparisons among multiple locations were performed using a non-parametric analog to the one-way analysis of variance, the Kruskal-Wallis test on ranks.

Habitat data for each transect was represented by either a mean value for

continuous variables (depth, substrate score, current velocity) or a total frequency occurrence for the discrete variables (i.e., cover types, see Table 3). Because transects were selected to be fairly homogeneous representatives of a particular habitat type, use of mean values was considered indicative of characteristics at a meso-habitat scale. Principal components analysis (PCA) was used to ordinate electrofishing transects using a correlation matrix of the measured habitat variables; this helped identify features that contributed the most to variation in habitat. PCA derives a small number of linear combinations of variables that can help describe variation in the data. River and impoundment data were analyzed separately to show habitat characteristics of transects relative to each other. The physical characteristics of sites could then be compared to differences in bass abundance among the sites.

Mean length-at-age was used as the statistic for growth comparisons, and may serve as an indication of relative fitness among populations. Intraspecific comparisons were made by year class between three locations: lower river, upper river, and impoundment. Data from within each of the three locations were pooled and, since they met normality and equal variance assumptions, tested for significant differences among locations using analysis of variance (ANOVA). Duncan's multiple range test was used to indicate which sites were different.

Another measure of individual fitness is the length-weight index, which provides an assessment of physiological condition of larger (>150 mm TL) fish. Relative weight (W_r) was used because it allows for comparison among variable sizes of fish, and among

populations and/or species (Murphy et al. 1991). Relative weight is quantified as:

$$W_r = \left(\frac{W}{W_s} \right) \times 100$$

where: W = weight of the fish in grams; and

W_s = standard weight for the species from a length-weight regression equation. The W_s equation employed for smallmouth bass was from Kolander et al. (1993):

$$\log_{10} W_s = -5.329 + 3.200 \log_{10} L$$

and that used for spotted bass was developed by Gabelhouse (Murphy et al. 1991):

$$\log_{10} W_s = -4.960 + 3.055 \log_{10} L$$

with L being total length in mm. Comparisons of large size class were made intra-specifically among upper river, lower river, and reservoir locations; bass less than 150 mm TL exhibit considerably greater variance in W_r and were omitted from analysis (Kolander et al. 1993). Because data met the normality and equal variance assumptions, ANOVA was used to detect significant differences among locations, with Duncan's multiple range test used to indicate which are different.

Diet similarity between the species was quantified using a diet overlap index. Substantial diet overlap indicates a potential for competitive interactions if food resources are limiting. Schoener's (1970) index of overlap (α) was employed, as recommended by

Wallace (1981) for use when food availability data are lacking, and is computed as:

$$\alpha = 1 - 0.5 \left(\sum_{i=1}^n |p_{xi} - p_{yi}| \right)$$

where p_{xi} = proportion of food category i in the diet of species x ;

p_{yi} = proportion of food category i in the diet of species y ;

n = number of food categories.

Overlap indexes were calculated for the three size classes in 1) overall Byllesby impoundment-New River system; 2) pooled river sites; and 3) pooled impoundment sites. Index values range from 0 (completely different) to 1.0 (complete overlap). Overlap values exceeding 0.6 have been designated as indicating potential interspecific competition if resources are limited (Zaret and Rand 1971). Values less than 0.4 were considered by Ross (1986) to indicate substantially different resource use. These conventions were followed in this study.

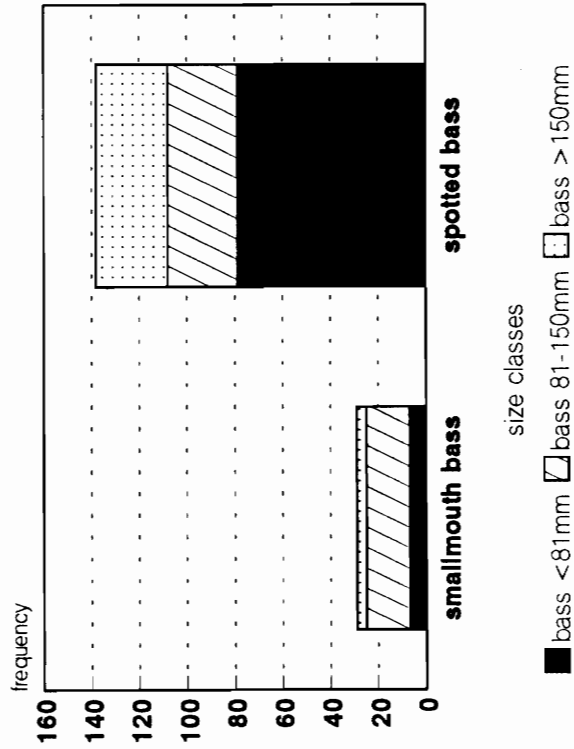
RESULTS

Abundance and distribution

Abundance of bass differed significantly by habitat. The total summer electro-fishing catch from the pooled river versus reservoir sites yielded contrasting proportions of bass species with all size classes pooled. The smallmouth bass dominated the bass catch in the river, while the majority of bass collected in the reservoir were spotted bass ($\chi^2=64.3$; $P<0.001$; Figure 2). The chi-square test was run on each of the three size classes separately, and results for each also showed that catch proportion depended on whether the collection site was river or impoundment ($P<0.01$ for all size classes), demonstrating agreement with the overall result. Intraspecific catch rate comparisons showed that abundance of both species shifted significantly, with greater smallmouth bass abundance in the river locations (Wilcoxon test; $P=0.0003$; Table 4) and greater abundance of spotted bass in the reservoir ($P=0.0017$).

Within the river sites, predominance of a species was found to be associated with location relative to the reservoir. The smallmouth bass was overall the predominant bass in the river site above the reservoir, while the spotted bass dominated the catch at the below-dam river site ($\chi^2=27.5$; $P<0.001$; Figure 3). Small bass were the only size class not to show this trend, with young of both species more abundant below the dam and with spotted bass young predominant in both areas. Smallmouth bass abundance was significantly greater at the upper river site ($P=0.007$) compared to the lower river (Table 5). Spotted bass catch rate was too variable to show a significant difference between

Reservoir Bass



River Bass

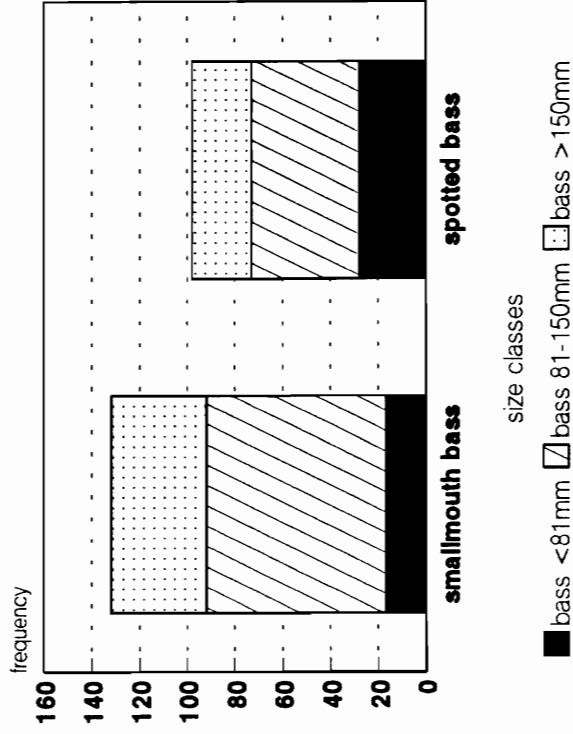
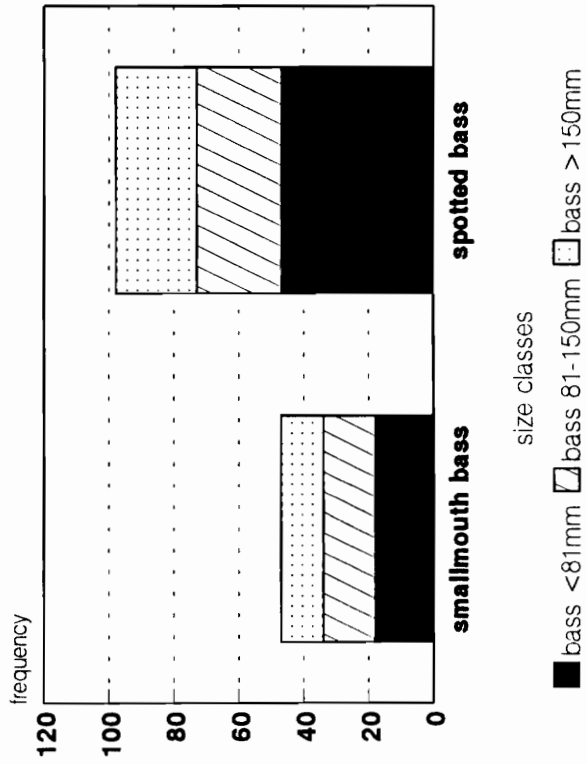


Figure 2. Comparison of the number of bass collected by electrofishing from river versus impoundment. All river habitats were pooled to compare to pooled impoundment sites. Collections were paired by date to provide equal sampling effort between locations.

Table 4. Intraspecific bass electrofishing catch compared between pooled river and pooled impoundment collections using Wilcoxon rank sum test. Because only day samples were collected in the river, night collections from the impoundment were omitted to avoid potential diel bias. Riverine samples were paired with impoundment samples by date. Samples on four different occasions in summer 1991 from eight sampling transects per location (total of 32 samples per location) were included in the analysis. Means and standard deviations (SD) are shown.

| Species | Location | Mean no. fish per 100m | SD | <i>P</i> -value |
|------------|-------------|------------------------------|-----|-----------------|
| smallmouth | river | 3.69 | 3.5 | 0.003 |
| | impoundment | 1.31 | 1.6 | |
| spotted | river | 3.03 | 4.3 | 0.0017 |
| | impoundment | 6.00 | 4.8 | |

New River below Bylesby



New River above Bylesby

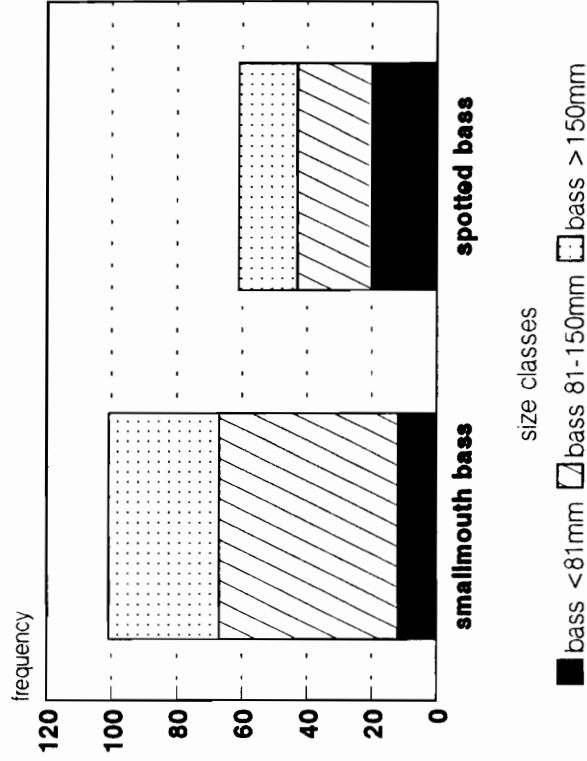


Figure 3. Comparison of the number of bass collected by electrofishing from the river downstream of Bylesby dam versus upstream of the impoundment. All collections from habitats within these locations were pooled. Collections were paired by date to provide equal sampling effort between locations.

Table 5. Intraspecific bass electrofishing catch compared between pooled upper river and pooled lower river collections using Wilcoxon rank sum test. Samples on seven different occasions in summer 1991 from four sampling transects per location (total of 28 samples per location) were included in the analysis. Means and standard deviations (SD) are shown.

| Species | Location | Mean no. fish per 100m | SD | <i>P</i> -value |
|------------|-------------|------------------------------|-----|-----------------|
| smallmouth | upper river | 3.39 | 2.5 | 0.007 |
| | lower river | 1.68 | 1.7 | |
| spotted | upper river | 2.11 | 3.2 | >0.5 |
| | lower river | 3.46 | 5.8 | |

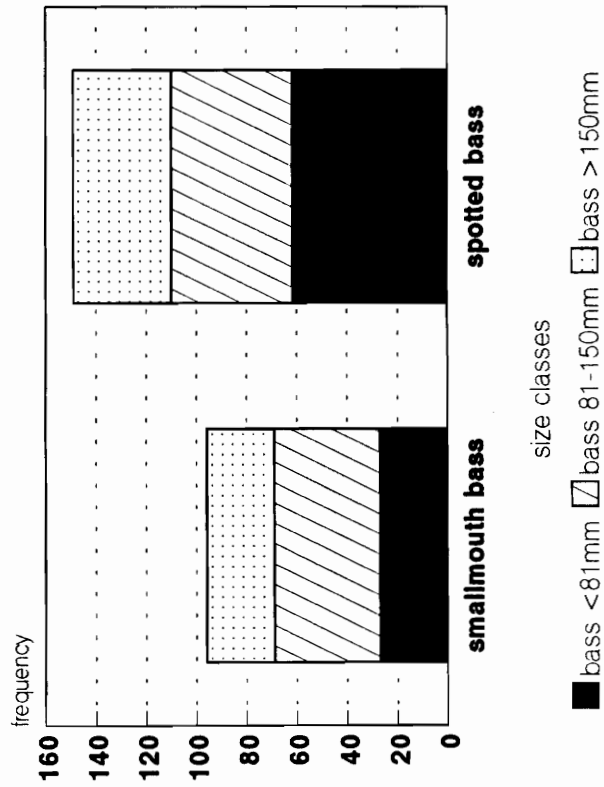
upper and lower river sites (Table 5).

A comparison of river margin habitats with mid-channel habitats also revealed a significant association with bass abundance. The majority of bass caught in margin habitats were spotted bass while smallmouth were dominant in mid-river ($\chi^2=39.6$; $P<0.001$; Figure 4). Young-of-year of both species were more likely to be found in river margins, however. Analysis of catch-per-effort data indicated that spotted bass were driving this interspecific shift of dominance (Table 6). Both species were found in greater abundance along the banks compared to midriver but the shift was much more pronounced for spotted bass.

Within the reservoir, spotted bass predominated in all habitat types except steep, rocky shoreline. Bass catch-per-effort differences were observed in shoreline habitat types for both species (Table 7). Smallmouth bass were caught at a greater rate in the steep, rocky habitats than in any other habitat type ($P<0.0001$), while spotted bass were collected in significantly greater numbers in the vegetated bank transects compared to the others ($P=0.0156$). Catch rates for neither species differed significantly among remaining habitat types. Adult bass collected offshore by netting were caught in similar interspecific proportions as shoreline electrofishing collections (spotted:smallmouth ratio of 79:21 offshore and 69:31 onshore; $\chi^2=2.67$; $P>0.10$), demonstrating agreement between sampling techniques regarding the prevalence of spotted bass in the impoundment.

A principal components analysis (PCA) of habitat data permitted physical characterization of the transects, which can then be related to bass abundance. While the

Margin Habitat



Midriver Habitat

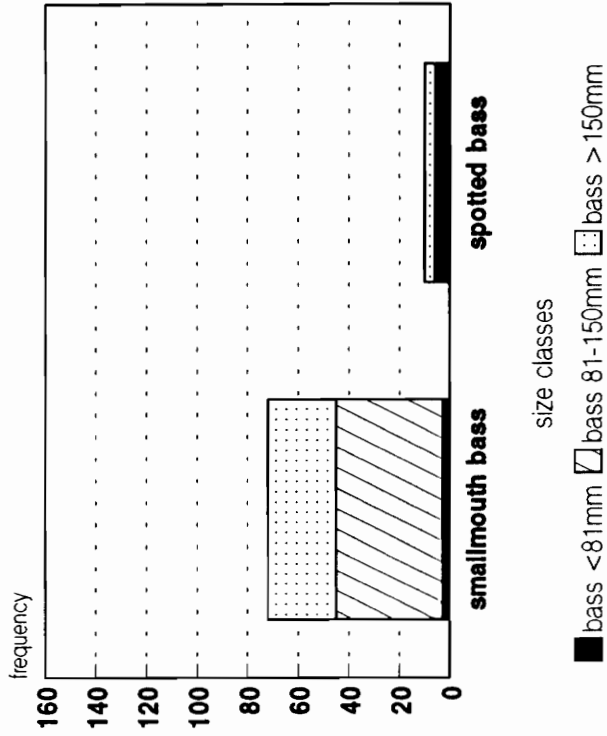


Figure 4. Comparison of the number of bass collected by electrofishing from the river bank transects versus midriver transects, upper and lower river sections pooled. Collections were paired by date to provide equal sampling effort between locations.

Table 6. Intraspecific bass electrofishing catch compared between pooled mid-river and pooled river bank collections using Wilcoxon rank sum test. Samples on seven different occasions in summer 1991 from four sampling transects per location (total of 28 samples per location) were included in the analysis. Means and standard deviations (SD) are shown.

| Species | Location | Mean no. fish per 100m | SD | <i>P</i> -value |
|------------|------------|------------------------------|-----|-----------------|
| smallmouth | mid river | 1.79 | 1.8 | 0.015 |
| | river bank | 3.29 | 2.5 | |
| spotted | mid river | 0.32 | 0.9 | <0.0001 |
| | river bank | 5.25 | 5.6 | |

Table 7. Impoundment bass shoreline electrofishing catch-per-effort: intraspecific comparison among Byllesby Reservoir habitats (Kruskal-Wallis ANOVA on ranks; 12 samples per habitat). Means with continuous bars are not significantly different (Duncan's multiple range test).

| Species | Habitat type | Mean no. fish per 100m | SD | <i>P</i> -value |
|------------|--------------|---------------------------|------|-----------------|
| smallmouth | ST | 6.25 | 5.56 | 0.0001 |
| | VG | 2.17 | 2.55 | |
| | CR | 0.42 | 0.67 | |
| | SL | 0.42 | 0.79 | |
| spotted | VG | 10.5 | 6.0 | 0.0156 |
| | SL | 4.67 | 4.1 | |
| | ST | 4.58 | 2.5 | |
| | CR | 4.17 | 3.0 | |

ST = steep, rocky

VG = undercut banks with overhanging vegetation

SL = silt flats

CR = impounded creek mouths

analysis of all 16 transects from both reservoir and river together did not separate out the two environments meaningfully, analysis of river and reservoir transects separately did generate some results useful for visualizing differences in habitat characteristics. Table 8 gives the eigenvalues and associated amount of variance in the habitat data explained by the first three principal components. Variable loadings on the first three principal components of river habitat data are shown in Table 9; no other principal components explained more than 10% of habitat variance.

Presentation of river transects in principal component space allows visualization of their similarities and differences in terms of primary riverine habitat variables. The best separation was achieved when transects were plotted against the first two principal components, which accounted for 71% of the variation in measured habitat variables of river transects (Figure 5). Transects where smallmouth bass predominated over spotted bass, found in Table 10, separated out generally to the top and left of the figure, corresponding to habitat characteristics such as large-particle (rocky) substrates, lack of woody cover and overhanging bank vegetation, presence of aquatic macrophytes and bedrock ledges, and higher current velocities. In contrast, transects that produced predominantly spotted bass separate out to the bottom and right of Figure 5. These areas correspond to presence of woody cover, bank vegetation, boulder cover, small-particle substrates, and slower current. The other river comparisons also hold generally to this placement in component space: river margins versus river banks, upper river versus lower river.

Proportional and cumulative variance explained by the first three principal

Table 8. Results of principal components analysis of habitat variables from the 8 New River sites, showing the relative amount of variation between sites explained by the first three principal components. The three components accounted for 86% of the variation in the river habitat data. No other component had an eigenvalue greater than 1.0.

| Principal Component | Eigenvalue | Variance explained | |
|---------------------|------------|--------------------|------------|
| | | Proportion | Cumulative |
| PC1 | 3.895 | 48.7% | 48.7% |
| PC2 | 1.808 | 22.6% | 71.3% |
| PC3 | 1.215 | 15.2% | 86.5% |

Table 9. New River habitat variable loadings on the first three principal components, based on data from 8 river sites.

| River Habitat Variable | Eigenvectors | | |
|-----------------------------|--------------|-------|-------|
| | PC1 | PC2 | PC3 |
| water depth | 0.44 | 0.30 | 0.16 |
| substrate* | -0.37 | 0.35 | 0.08 |
| current velocity | -0.45 | -0.25 | -0.09 |
| bedrock ledges | -0.33 | 0.28 | -0.47 |
| undercut banks | 0.00 | 0.00 | 0.00 |
| boulders | 0.39 | 0.21 | -0.19 |
| woody debris | 0.08 | -0.68 | 0.30 |
| overhanging bank vegetation | 0.43 | -0.02 | -0.28 |
| aquatic macrophytes | -0.09 | 0.37 | 0.73 |

* substrate scale ascribes low values for small particles (i.e., silt) and increasingly higher values for larger particles.

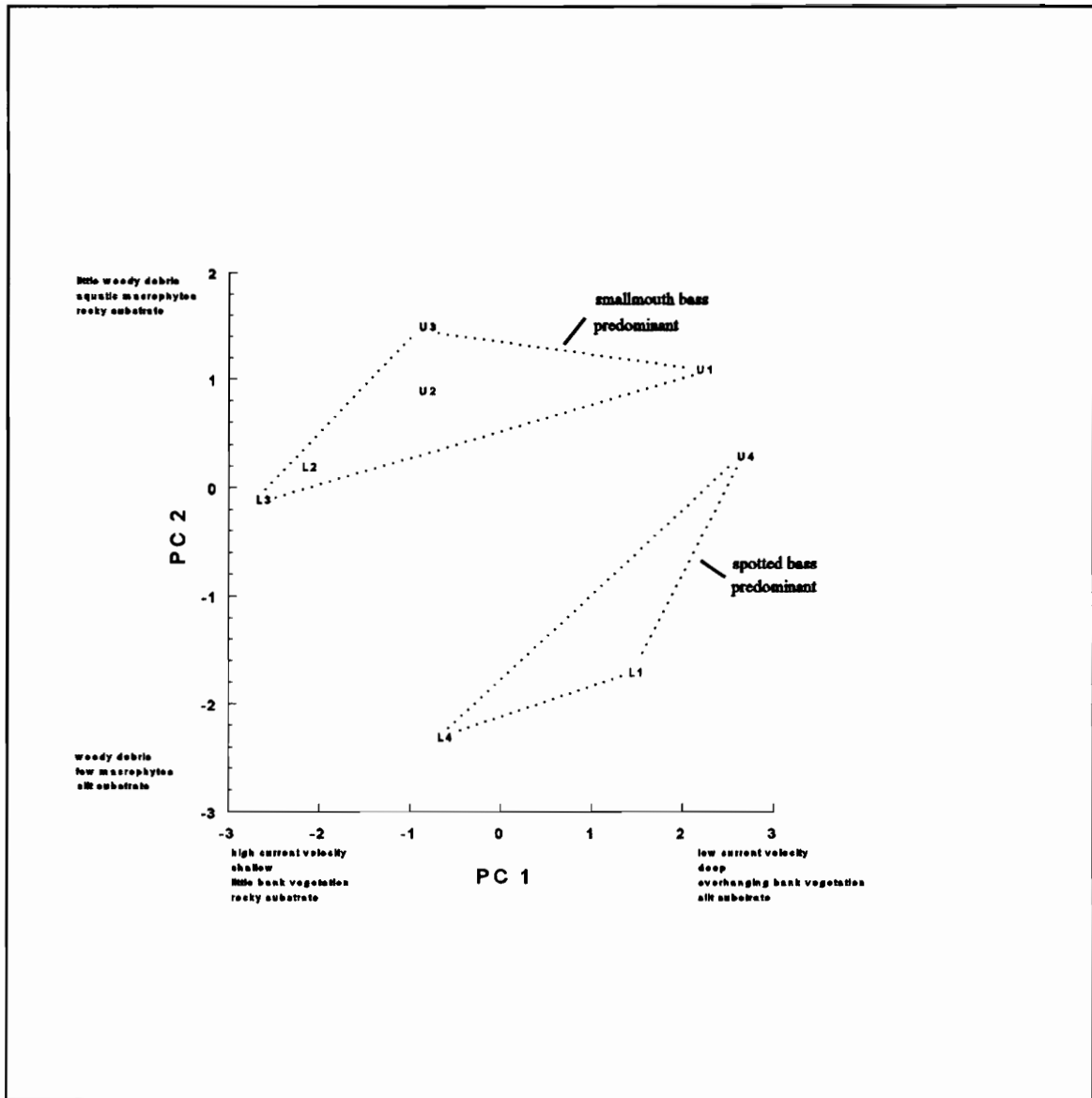


Figure 5. Plot of river transects on the first two principal components of river habitat data. See Table 9 for variable loadings on the components, and Table 10 for legend of transects and their ranking in terms of bass abundance.

Table 10. Bass catch per unit effort in New River electrofishing transects (CPUE=number of fish/100m; each transect sampled 7 times).

| smallmouth bass | | spotted bass | |
|-----------------|----------------|--------------|----------------|
| Transect | Mean CPUE (SD) | Transect | Mean CPUE (SD) |
| U1 | 5.86 (2.6) | L4 | 8.29 (9.4) |
| U4 | 3.14 (1.8) | U4 | 5.71 (4.2) |
| U3 | 2.86 (2.2) | L1 | 4.86 (3.0) |
| L1 | 2.14 (1.5) | U1 | 2.14 (2.4) |
| L4 | 2.00 (2.2) | U3 | 0.57 (1.1) |
| L3 | 1.86 (1.8) | L3 | 0.43 (1.1) |
| U2 | 1.71 (1.5) | L2 | 0.29 (0.8) |
| L2 | 0.71 (1.3) | U2 | n/a |

U=upriver site (above Byllesby impoundment).

L=lower river site (below Byllesby dam).

1=left shoreline facing upstream.

2=mid river 40m off left bank.

3=mid river 40m off right bank.

4=right shoreline.

components in Byllesby impoundment habitat data are shown in Table 11. Loadings for impoundment habitat variables on the first three principal components are presented in Table 12. As with river data, the best separation of transects occurs when they are plotted against the first two principal components, which account for 56% of habitat variability in the impoundment data (Figure 6). The steep, rocky transects were the sites of greater smallmouth bass abundance (Table 13), and these sites were placed by the PCA to the left and center of the figure. Habitat variables associated with this placement are occurrence of bedrock ledges and rocky substrate, and lack of woody debris. In contrast, the sites with greatest spotted bass abundance (i.e., vegetated bank transects) are placed generally to the right of the graph, corresponding to presence of woody cover, undercut banks, small-particle substrates, and overhanging bank vegetation. The placement of the creek mouth sites is a puzzling result of the PCA, with one site to the left near smallmouth-predominated transects and the other to the right fairly close to high spotted bass abundance sites. Since neither creek mouth transect was found to harbor higher abundances of either species, this suggests that other influential variables may be missing from this analysis.

Distribution patterns of the two bass species observed in the New River-Byllesby system permit some generalizations concerning habitat use. Electrofishing data as well as offshore netting data supported the conclusion that the spotted bass was the primary bass in the reservoir. Overall, smallmouth bass predominated in the river.

Within the river sites, smallmouth bass abundance was considerably greater in the

Table 11. Results of principal components analysis of habitat variables from the 8 Byllesby Reservoir sites, showing the relative amount of variation between sites explained by the first three principal components. The three components accounted for 75% of the variation in the river habitat data. No other component had an eigenvalue greater than 1.0.

| Principal Component | Eigenvalue | Variance explained | |
|---------------------|------------|--------------------|------------|
| | | Proportion | Cumulative |
| PC1 | 2.519 | 31.5% | 31.5% |
| PC2 | 1.972 | 24.7% | 56.1% |
| PC3 | 1.507 | 18.8% | 75.0% |

Table 12. Reservoir habitat variable loadings on the first three principal components, based on data from 8 river sites.

| River Habitat Variable | Eigenvectors | | |
|-----------------------------|--------------|-------|-------|
| | PC1 | PC2 | PC3 |
| water depth | 0.03 | 0.65 | 0.27 |
| substrate* | -0.37 | 0.15 | -0.37 |
| bedrock ledges | -0.52 | 0.25 | 0.16 |
| undercut banks | 0.40 | 0.21 | 0.31 |
| boulders | 0.02 | 0.42 | -0.62 |
| woody debris | 0.47 | 0.44 | -0.10 |
| overhanging bank vegetation | 0.35 | -0.22 | 0.09 |
| aquatic macrophytes | -0.31 | 0.19 | 0.51 |

* substrate scale ascribes low values for small particles and increasingly higher values for larger particles.

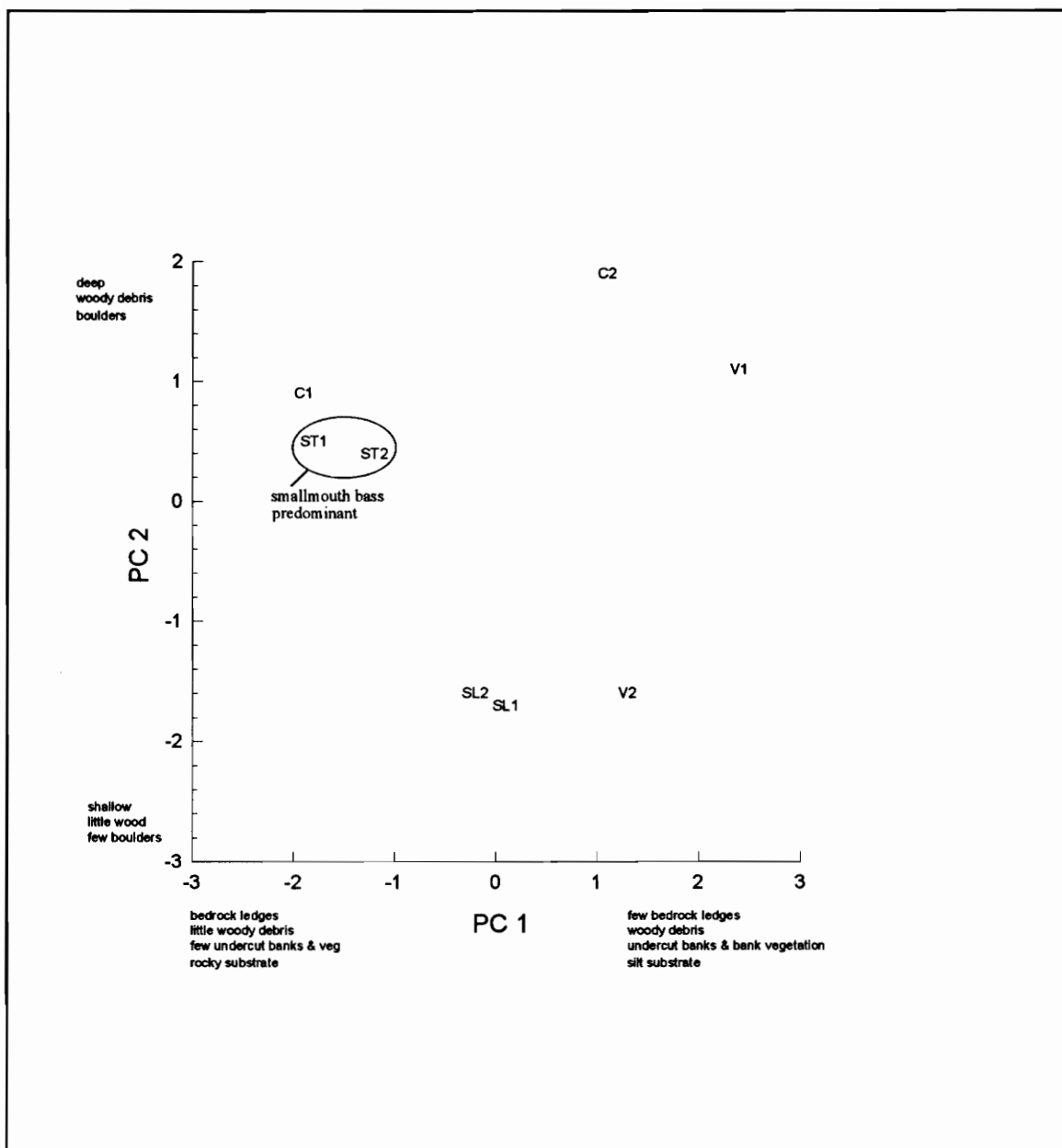


Figure 6. Plot of impoundment transects on the first two principal components of impoundment habitat data. See Table 12 for variable loadings on the components, and Table 13 for a legend of transect codes and their ranking in terms of bass abundance.

Table 13. Bass catch per unit effort in Byllesby impoundment electrofishing transects (CPUE=number of fish/100m; each transect sampled 6 times).

| smallmouth bass | | spotted bass | |
|-----------------|----------------|--------------|----------------|
| Transect | Mean CPUE (SD) | Transect | Mean CPUE (SD) |
| ST1 | 7.33 (7.3) | V1 | 10.67 (6.0) |
| ST2 | 5.17 (3.5) | V2 | 10.33 (6.6) |
| V2 | 3.17 (3.2) | SL1 | 5.67 (5.0) |
| V1 | 1.17 (1.3) | ST2 | 5.00 (2.8) |
| C2 | 0.50 (0.8) | C1 | 4.67 (3.9) |
| SL2 | 0.50 (0.8) | C2 | 3.67 (2.1) |
| C1 | 0.33 (0.5) | SL2 | 3.67 (3.1) |
| SL1 | 0.33 (0.8) | ST1 | 3.50 (1.6) |

ST=steep rocky shoreline
 C=impounded creek mouth
 V=vegetated bank
 SL=silt flat
 1=lower impoundment (near dam)
 2=upper impoundment

river section above the impoundment than below, except for the smallest size class. Spotted bass abundance did not differ significantly between upper and lower river sites, although the small size class was considerably more abundant in the lower site (Figure 3). Both species were more abundant in riverbank transects compared to midriver, but the difference for spotted bass was more drastic, causing a shift in species predominance between the two locations. Riverine smallmouth bass were found in the presence of boulders and other rocky substrates, and in areas of higher current velocities that lacked overhanging vegetation and woody debris. Spotted bass were found in greater numbers in areas with woody debris, bank vegetation, lower current velocities, and silty substrates.

In the reservoir, smallmouth bass were predominant in steep-banked areas, characterized by the presence of bedrock ledges, rocky substrates, and aquatic macrophytes. Spotted bass catch rates nearly doubled in transects with dense, overhanging bank vegetation, undercut banks, silty substrates, and woody debris as cover. Although the habitat variables mentioned are obviously just a subset of potentially influential environmental variables (temperature, light intensity, and turbidity are others), they do depict the differences in habitat utilization by the two bass species observed in the Byllesby area.

Growth and condition comparisons

The New River-Byllesby bass tagging program undertaken in this study marked a total of 187 bass over 200 mm TL. Fifty-six smallmouth bass were tagged, 29 of which were in the river and 27 in the impoundment. No smallmouth bass were recaptured in the

New River-Byllesby system, thus no information on smallmouth bass movement was gained. However, past work has demonstrated the existence of consistent, predictable home ranges for smallmouth bass (Gerking 1953, Funk 1955, Munther 1970, Todd and Rabeni 1989). Therefore, growth and condition data on smallmouth bass will be presented as indicators of fitness in riverine and impounded habitats.

A total of 131 spotted bass were tagged, 31 river bass and 100 impoundment bass. The spotted bass population yielded 23 recaptures out of 131 tagged, a recapture rate of 17.6%. Thirty-one spotted bass were tagged in the river, of which 5 were recaptured (16%). In every river case, the recapture was in the same transect that tagging occurred, indicating a substantial degree of site fidelity in riverine spotted bass. River recaptures occurred between 2 and 10 months after tagging. Eighteen out of 100 spotted bass tagged in the impoundment were recaptured (18%). Recapture occurred within 100 m of the initial tagging site 16 of 18 times, or 89% of recaptures. In one case, a spotted bass moved 0.4 km toward the upper reservoir; in another case, a bass moved approximately 1 km from the middle section of the reservoir to the upper section. Impoundment recaptures ranged from 2 weeks to 11 months after tagging.

Assumptions about habitat fidelity within river or impoundment sites were not supported because: 1) some spotted bass movement was observed; 2) literature on smallmouth bass indicated that home ranges could encompass more than one habitat type as defined in this study (Todd and Rabeni 1989). However, no evidence pointed to movement between river and reservoir. Mark-recapture results indicate that movement

between reservoir and river occurs infrequently at best, at least for spotted bass. The literature on smallmouth bass movement supports the assumption that river and reservoir sampling locations are far apart enough to make intermingling unlikely (Todd and Rabeni 1989). Therefore, statistical comparisons of growth and condition of both species will be made between river and impoundment sites.

Intraspecific comparisons of growth rates between river and reservoir samples showed only one case of differences in length-at-age for either species (Table 14). Age one smallmouth bass from the upper river were significantly smaller than those from the river below the dam (ANOVA; $P=0.029$). Spotted bass from reservoir or river sites showed no differences in growth (Table 15).

Relative weight (W_r) of adult smallmouth bass did not differ significantly between reservoir and pooled river or between upper and lower river sites (Table 16). Smallmouth bass average relative weight ranged from 93 in the reservoir to 90 in the river sites. Spotted bass mean W_r was higher in the below-dam river site (92) compared to the up-river site (86), with an average of 90 in the reservoir.

Overall, growth and condition measures revealed that differences in bass fitness between river and impoundment locations were not great. Smallmouth growth to age one was significantly higher in the lower river, and spotted bass condition was significantly higher there as well. Growth at all ages, as well as condition, of both species tended to be greater in the river below the dam than in the upper river. However, sample sizes were

Table 14. Smallmouth bass mean length-at-age comparisons - river and impoundment sites. Results of an ANOVA test of the hypothesis that mean total lengths (TL) are the same among habitats. Means with continuous bars are not significantly different (Duncan's multiple range test).

| Age | Location | <i>N</i> | Mean TL in mm (SD) | <i>F</i> -value | <i>P</i> |
|-----|-------------|----------|-----------------------|-----------------|----------|
| 1 | lower river | 18 | 123.7 (17.8) | 3.68 | 0.03 |
| | impoundment | 45 | 115.0 (20.9) | | |
| | upper river | 37 | 107.3 (23.6) | | |
| 2 | lower river | 7 | 182.8 (49.5) | 0.78 | 0.47 |
| | impoundment | 21 | 167.6 (33.2) | | |
| | upper river | 11 | 160.4 (36.2) | | |
| 3 | lower river | 4 | 281.7 (25.6) | 0.52 | 0.60 |
| | impoundment | 9 | 268.6 (16.9) | | |
| | upper river | 7 | 267.4 (30.4) | | |
| 4 | river | 4 | 332.8 (9.5) | 2.48 | 0.19 |
| | impoundment | 2 | 300.0 (27.2) | | |

Table 15. Spotted bass mean length-at-age comparisons - river and impoundment sites. Results of an ANOVA test of the hypothesis that mean total lengths (TL) are the same among habitats. Means with continuous bars are not significantly different (Duncan's multiple range test).

| Age | Location | <i>N</i> | Mean TL in mm (SD) | <i>F</i> -value | <i>P</i> |
|-----|-------------|----------|-----------------------|-----------------|----------|
| 1 | lower river | 33 | 109.9 (16.1) | 0.66 | 0.52 |
| | impoundment | 77 | 112.5 (20.1) | | |
| | upper river | 35 | 108.3 (18.7) | | |
| 2 | lower river | 19 | 187.3 (29.2) | 0.15 | 0.87 |
| | impoundment | 46 | 189.2 (30.5) | | |
| | upper river | 17 | 184.4 (36.8) | | |
| 3 | lower river | 12 | 254.6 (24.1) | 0.69 | 0.51 |
| | impoundment | 19 | 255.3 (23.9) | | |
| | upper river | 5 | 240.4 (37.4) | | |
| 4 | lower river | 13 | 299.5 (28.8) | 0.24 | 0.79 |
| | impoundment | 9 | 292.5 (14.1) | | |
| | upper river | 4 | 289.6 (45.2) | | |

Table 16. Bass mean relative weight (Wr) intraspecific comparisons - river versus impoundment. Results of an ANOVA test of the hypothesis that mean Wr is the same among habitats; means with continuous bars are not significantly different (Duncan's multiple range test).

| Location | N | Mean Wr | SD | F -value | P |
|------------------------|-----|-----------|-------|------------|------|
| <u>smallmouth bass</u> | | | | | |
| impoundment | 44 | 92.86 | 8.63 | 0.93 | 0.40 |
| lower river | 14 | 90.61 | 10.45 | | |
| upper river | 29 | 90.12 | 8.51 | | |
| <u>spotted bass</u> | | | | | |
| lower river | 25 | 92.31 | 8.79 | 3.17 | 0.04 |
| impoundment | 121 | 89.80 | 7.17 | | |
| upper river | 16 | 86.42 | 5.92 | | |

not large.

Description of diet and diet overlap

Diet of smallmouth and spotted bass in the New River-Byllesby system was found to be very similar. Young bass (40-80mm TL) preyed heavily on aquatic insects, which averaged 71% and 85% of total stomach contents for young spotted and smallmouth bass, respectively (Fig. 7). Terrestrial insects, crayfish, and fish became increasingly important diet components for both species as they grew larger.

Smallmouth bass adults (>150mm TL) consumed primarily fish, followed by aquatic insects, terrestrial insects, and crayfish. The primary food items for adult spotted bass were crayfish, fish, aquatic insects, and terrestrial insects. Overall interspecific diet overlap, as described by the Schoener overlap index (α), was calculated as 0.71, 0.74, and 0.70, respectively for the small, medium, and large size classes.

Riverine bass exhibited fairly high interspecific diet overlap, ranging from 0.57 for larger bass to 0.68 for the middle size class. No overlap value was calculated for small bass in the river because of a dearth of young smallmouth. The small riverine smallmouth collected were heavy consumers of aquatic insects, averaging 89 percent of total stomach content (Fig. 8). Small riverine spotted bass consumed similar proportions of aquatic insects, and were more piscivorous than smallmouth bass. Mayfly larvae (Ephemeroptera) were a particularly important food for the young of both species, followed by true flies (Diptera).

The mid-sized class of riverine bass primarily consumed aquatic insects. As with

Mean % by weight

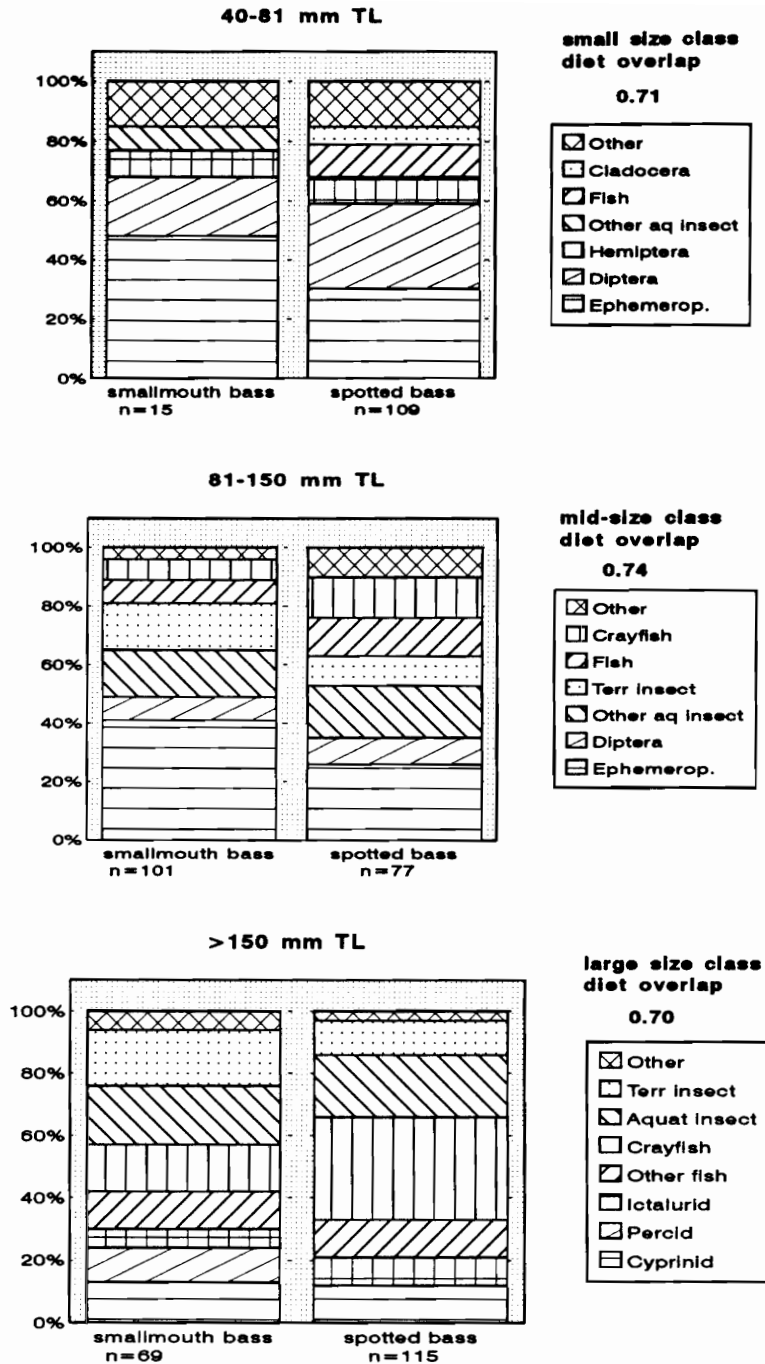


Figure 7. Comparison of the average diet of all smallmouth and spotted bass collected in the New River and Byllesby impoundment, broken down by size class.

Mean % by weight

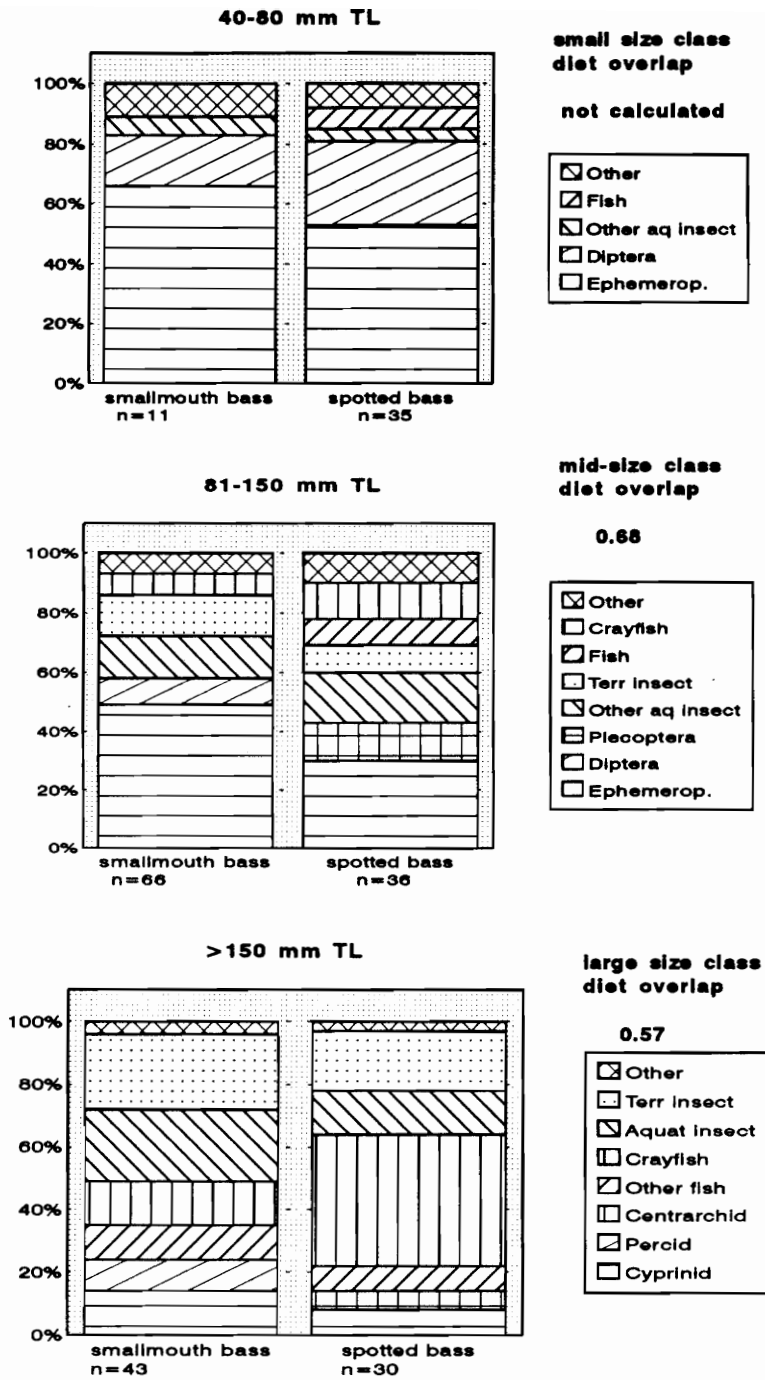


Figure 8. Comparison of the average diet of smallmouth and spotted bass collected in the New River, broken down by size class.

Mean % by weight

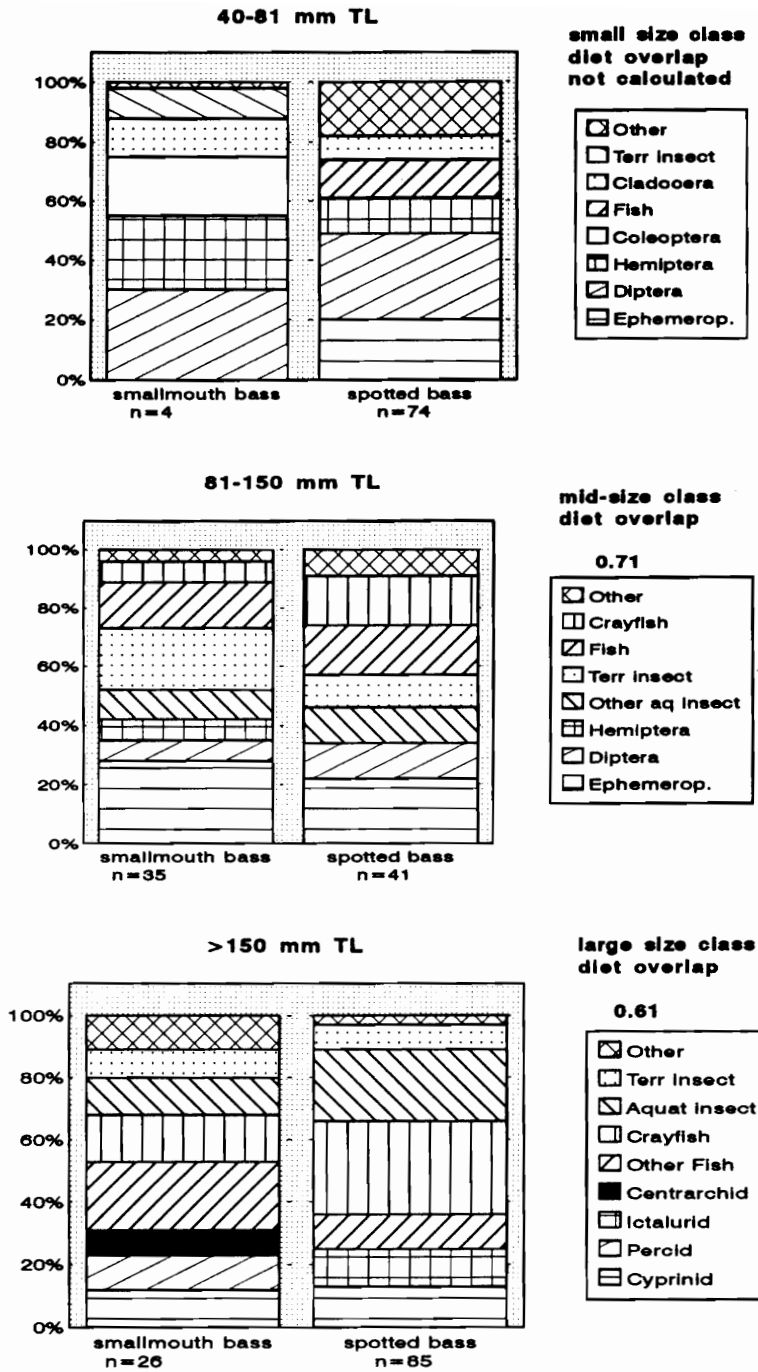


Figure 9. Comparison of the average diet of smallmouth and spotted bass collected in Byllesby impoundment, broken down by size class.

the small size-class, mayfly larvae was the principal food item for both species in the river, with terrestrial insects and crayfish gaining in importance for both species. Fish continued to be more important as prey to spotted bass between 80 and 150 mm compared to smallmouth of this size.

Diet data from larger riverine bass reversed this trend, however, as fish became the main food source of smallmouth bass. The primary food item for adult spotted bass in the river sites shifted to crayfish, followed in importance by fish. Terrestrial and aquatic insects remained major components of the adult diet for both species.

In Byllesby reservoir, overlap in diet was again high. Overlap index values for the middle and large size classes were 0.71 and 0.61, respectively. Due to an inadequate sample of smallmouth bass, overlap was not calculated for the small size class of bass. Although many of the same foods eaten by riverine bass were also consumed by bass in the reservoir, some interesting shifts were noted.

Insects remained the main prey for the young bass, accounting for over 65% of the average stomach contents of both species (Fig. 9). Mayflies decreased in importance for the small bass in the reservoir. Other aquatic insects (i.e., Hemiptera) and micro-crustaceans (Cladocera) were more common prey in the reservoir than river. As in the river, fish constituted a greater portion of the diet of young spotted bass compared to smallmouth.

Mid-sized reservoir bass also reduced dietary reliance on mayfly larvae compared to in the river, although mayflies remained the most common insect prey. Piscivory

appeared considerably more frequently in reservoir bass of this size compared to riverine bass.

Adult bass in the reservoir followed similar ontogenetic trends as those found in the river, with fish becoming the main prey for smallmouth bass (over 50% of average stomach content), and large spotted bass preying more heavily on fish and crayfish than smaller sized conspecifics. Compared to each other, the two species showed similar diets in the reservoir with slight divergence. Both species relied on minnows (Cyprinidae) at about the same level (12-13%), but Ohio logperch *Percina caprodes* were consumed by smallmouth bass almost as much. This species did not appear as prey in the stomachs of spotted bass. Conversely, catfishes (*Ictalurus punctatus* and *Pylodictis olivaris*) were an important prey for spotted bass but not so for smallmouth bass. As in the river, reservoir spotted bass were greater predators of crayfish than similar sized smallmouth.

In sum, diets of both bass species were quite similar, with overlap values bordering or exceeding 0.60. Several differences between the species were noteworthy, however. Fish appeared to be a stronger component in the diet of smaller spotted bass relative to smallmouth of this size. Certain fish taxa, most notably logperch and catfishes, appeared as a prominent item in the diet of one species but not in the other. Crayfish were consistently more utilized as prey by spotted bass than smallmouth. Otherwise, major prey were similar in kind between the bass, differing only in degree of predation. Intraspecific shifts in diet were observed between river and impoundment, which were presumably due to differences in prey availability.

DISCUSSION

Fitness

Overall differences in relative fitness, as measured by growth and condition, were not distinguishable between river and reservoir in my data. Weak evidence did indicate that fitness for bass was higher in the river below Byllesby dam compared to the river upstream of the reservoir. Growth for age 1 smallmouth was significantly higher and relative weight for spotted bass was significantly greater there as well. Other comparisons showed that mean growth and condition were consistently higher in the lower river compared to upper river. Although food availability may have been greater in the lower river, I did not measure prey availability. However, other work has indicated that productivity in the New River may be enhanced below an impoundment relative to other areas in the river (Virginia Polytechnic Institute & State University 1985; Easton and Orth 1992) due to the release of organic seston from the impoundment to the tailwaters. The seston carries algae and bacteria-rich detritus which promotes production of aquatic insects, a primary food of both species of bass through ontogeny.

No differences in annual growth rate were discovered between the pooled reservoir and river sites in the Byllesby vicinity of the New River, but a comparison of bass growth rates in this system with growth rates for other Virginia bass (Banach 1989; Table 17) indicated that growth of both species was near average or better in the vicinity of Byllesby. Data for the smallmouth bass Virginia average came from 16 water bodies,

Table 17. Mean back-calculated lengths of bass at ages 1-3 from the New River and Byllesby Reservoir, compared to those reported by Banach (1989) representing the statewide average for Virginia.

| Species | Habitat/ Location | Total Length at Age (mm) | | | Source |
|--------------------|------------------------|--------------------------|-----|-----|---------------|
| | | 1 | 2 | 3 | |
| Smallmouth bass | River | 113 | 169 | 273 | Present Study |
| | Reservoir | 115 | 168 | 269 | |
| | Virginia State Avg. | 97 | 174 | 291 | Banach 1989 |
| Spotted bass | River | 109 | 185 | 250 | Present Study |
| | Reservoir | 113 | 189 | 255 | |
| | Virginia State Avg. | 92 | 169 | 232 | Banach 1989 |

both lotic and lentic. Spotted bass figures were from Claytor Lake only (Rosebery 1950). Moderately good growth in Byllesby suggests that resource availability is not having an adverse impact on growth.

Relative weight (W_r) also showed no differences in pooled data from river vs. reservoir. Given that the "ideal" W_r value (100) is based on 75th percentile length-weight relationships from the entire range of the species (Murphy 1991), the values generated in this study suggest that Byllesby area bass were in relatively good condition. Records of "citation" smallmouth bass (weight greater than 1.8 kg; $n=218$) from Virginia showed that the mean W_r was 91 (Austen and Orth 1985), providing further evidence of good condition in Byllesby area bass. Sound fish condition combined with fairly good growth rates imply that resource availability was not reducing the fitness of bass populations in the New River-Byllesby system during the study, and thus competitive pressures were not acute.

Diet

Several researchers have reported on foods utilized by sympatric populations of smallmouth and spotted bass, but few attempts have been made to relate findings to possible competitive interactions. Applegate et al. (1967) noted that slow-growing centrarchids, including bass, as juveniles relied on littoral benthos as primary food, and implied that they may be competing for this resource in Bull Shoals Reservoir, Arkansas-Missouri. From the same reservoir, Aggus (1974) inferred from differences in stomach contents that adult smallmouth bass may forage more in shallower littoral areas than spot-

ted bass. Bohn (1975) described the similarity of smallmouth and spotted bass diets in a recently-created West Virginia impoundment at the same time he reported decline in the stocked smallmouth population, but made no mention of species interactions.

Rosebery (1950) conducted research on Claytor Lake on the New River in Virginia which included food habit determinations of smallmouth and numerically dominant spotted bass. He noted that the diet of Claytor Lake smallmouth was "about the same" as that for the spotted bass and further remarked on the slow growth of Claytor lake basses. Rosebery concluded that forage availability must limit the growth rate but he did not mention the possibility of competitive interactions.

In one of the few studies that compared resource use of the two fishes directly, Kelso (1983) examined food habits and foraging habitat of juvenile littoral fishes in Claytor Lake, Virginia, to assess trophic overlap and competition. Postlarval young-of-year smallmouth and spotted bass were included in the investigation. He reported that smallmouth postlarvae remained in the littoral zone for a shorter time than spotted bass. Overlap in diet composition was relatively low for the period that they shared littoral foraging habitat. While both species fed primarily on zooplankton, smallmouth juveniles consumed predominantly pelagic zooplankton, while spotted bass juveniles relied more heavily on vegetation-associated zooplankton. Kelso concluded that juvenile bass segregated both by diet and by a temporal shift in habitat use.

Results of my diet study agree with existing information on foods of the smallmouth bass (Surber 1941; Applegate et al. 1967; Austen and Orth 1985; Roell and

Orth 1993) and spotted bass (Rosebery 1950; Applegate et al. 1967; Smith and Page 1969). Diet patterns in evidence from my New River and Byllesby bass data suggest that foraging there by juvenile and older fish was based primarily on availability . Although no prey availability assessments were done, certainly shifts in diet between river and impoundment (e.g., heavy use of mayflies by both species in the river versus light use in the reservoir) indicate the adaptability of both species to prevailing food resource conditions. Additional anecdotal evidence supports this further. Stomach contents from both species and all size classes collected over a period of a few days in the spring contained large quantities of winged hymenopterans, indicating the bass were taking advantage of a swarming event that had just occurred. This plasticity in food habits is well known in the smallmouth bass literature (Coble 1975; Probst et al. 1984; Austen and Orth 1985), and available evidence suggests that spotted bass are similarly non-selective.

At least in reservoirs, species of young-of-year bass may partition available food resources (Kelso 1983), but juvenile and adult bass have not been shown to do so. Available evidence to date demonstrates the similarity of the two species' diets, and their plasticity in food resource use, providing no basis for trophic segregation as a means of resource partitioning between them. This statement must be qualified, however, because of the my study's lack of food availability data and an inability to evaluate resource conditions different from those present during the study.

For example, if food availability decreased, would the bass continue to prey on the broad range of diet items, competing for the dwindling supplies? Or, as the competitive

pressures intensify, would the species concentrate foraging efforts on prey that they are more successful at obtaining? Subtle differences in diet evident from the literature and from the Byllesby area bass (e.g., the degree of reliance of young smallmouth bass on mayflies versus young spotted bass piscivory, the differences in species of fish consumed, and more extensive use of crayfish by spotted bass) show some signs of potential specialization during times of "competitive crunch" (Wiens 1977). In order to address these questions, manipulative experiments would be required to control food availability and fish densities in sympatry and allopatry.

Habitat use: bass abundance and distribution

Other research has indicated that habitat is more important than food as a mechanism of ecological segregation in sympatric centrarchids (Werner and Hall 1977; George and Hadley 1979) and salmonids (Nilsson 1967). The results of the present investigation show significant differences in use of riverine and impoundment habitats by smallmouth and spotted bass, while overlap in diet was generally high. Overall, smallmouth bass was the dominant species in the river, while spotted bass were more abundant in the reservoir. Site characteristics associated with high smallmouth bass abundance were boulders, steep, rocky substrates, and areas of higher current velocities. Other researchers have noted smallmouth bass associations with rocky substrates in streams (Munther 1970; Rankin 1986; Todd and Rabeni) and, in reservoirs, with areas featuring pronounced relief (Hubert and Lackey 1980). I found spotted bass to occur in greatest abundances at sites with overhanging bank vegetation and woody debris as cover,

silty substrates, and lower current velocities. Others have reported the tendency of spotted bass to occupy waters that are warmer, more sluggish, and more turbid compared to typical smallmouth bass habitats. This would seem consistent with the characteristics of the more southerly, central Mississippi basin native range of the spotted bass.

A study investigating habitat use by the fish assemblage in the New River in West Virginia (Lobb and Orth 1991) gives a description of riverine habitat use by sympatric smallmouth and spotted bass. Considerably more smallmouth bass (855) than spotted bass (64) were collected from various habitats of this section of the New River. Spotted bass are characterized as utilizing edge-of-pool habitats while smallmouth are characterized as "generalist" since they were relatively abundant in all the dominant habitats. Greatest abundance of both species were found in habitats with abundant snags as cover.

The predominance of smallmouth bass and their habitat use overlap with spotted bass in the New River in West Virginia makes an interesting comparison with the data from the Byllesby area. In the river-run type habitat sampled in this study, smallmouth were found in both margin and midriver transects, supporting the "generalist" label, whereas spotted bass were more limited in distribution and closely associated with the river banks.

The river section above the impoundment supported a greater abundance of smallmouth bass, while spotted bass were more abundant in the tailwaters of Byllesby dam. This may be due to the fact that the lower section is contained between two hydropower reservoirs (Figure 1), where the spotted bass clearly is predominant. Recruitment from the

reservoir to this river section may keep spotted bass abundance high.

However, a note of caution must be expressed here regarding interpretation of my river data. River sites had to be selected due to accessibility requirements; therefore, conclusions based on this data set cannot be said unequivocally to represent river populations. Only pool-run habitat types were sampled, with no riffles or extensive backwater areas included. Therefore, the conclusions concerning river bass habitat use must be applied only to the local area of sampling, not river distributions in general. Nevertheless, my river data do show interspecific distributional differences, and support the conclusion that the two species exhibit spatial segregation.

In reservoirs, no research has explicitly studied juvenile and adult smallmouth and spotted bass habitat partitioning. However, data from Claytor Lake, an impoundment on the New River approximately 20 km downstream of Byllesby, permits an examination over time of the relative performance of populations of the two species in that impoundment. Rosebery (1950) assessed standing crop of Claytor Lake fishes by cove rotenone sampling; standing crop was reassessed using the same method 30 years later by the Virginia Department of Game & Inland Fisheries (VDGIF 1981). In both 1950 and 1981, mean biomass of spotted bass was roughly twice that of smallmouth in the coves sampled. The 1981 report cites Rosebery's explanation that the spotted bass utilizes littoral zones while other black basses favor deeper water, thus biasing cove rotenone population estimates in favor of spotted bass. This contradicts reports by other investigators (Dendy 1946; Vogele 1975a) of spotted bass preference for deep waters. Rosebery set gillnets

and hoopnets in deeper waters and caught significantly more spotted bass than other black bass in both types of nets, suggesting that spotted bass were utilizing deeper waters as well. Net catch during the present study indicated that the relative proportions of the two species is similar in both littoral and offshore habitats, further suggesting that, at least in the shallower reservoirs on the New River, spotted bass are not more littoral in habits than smallmouth. Given this, it appears that spotted bass have maintained a dominant position in terms of abundance in the fish assemblage of Claytor Lake over time. These data agree with the results from the Byllesby reservoir demonstrating the predominance of spotted bass in lentic waters.

One potential explanation for the observed differences in abundance and distribution is that habitat segregation could arise from differences in spawning habitat that persist through time. However, work done by Vogele in Bull Shoals Reservoir, Arkansas (1975a and 1981) gave no evidence of spawning habitat segregation, although he does not make any direct comparisons in the cited works. Smallmouth bass nests were at depths ranging from 1.1-5.2 m (\bar{x} = 2.8 m) on substrates of broken rock accumulations, gravel, or occasionally on solid rock ledges. Spotted bass nests were located at 0.9-6.7 m depth (\bar{x} = 3 m) on more variable substrates: broken rock, large flat rocks, rock ledges, patches of gravel and sand, compacted soil, and rootwads. Cover of various sorts was reported near many of the nests of both species (with no interspecific differences in preference apparent), but many nests were without nearby cover. Nest surveys were conducted in the same areas, and timing of spawning overlapped almost completely, so nests of the two

species must have been intermingled. Densities of spotted bass nests were considerably higher than smallmouth bass nests in the same areas. Pflieger (1975) noted that spotted bass nests in streams were located in pool margins, similar to sites used by smallmouth bass.

The spawning resource axis was not addressed in my investigation, and I have no direct evidence of differences in spawning. A single pair of spotted bass was observed spawning in mid May 1992 on a nest in one of the impounded creek mouths (near site C2) at approximately 1 m depth on soft substrate. No observation of smallmouth bass spawning was made during the study. My data show that small size class spotted bass were more abundant in the reservoir, indicating the greater spawning success for that species there. In contrast, smallmouth bass young were infrequently collected during the study in any of the transects, possibly indicating recent poor reproduction in the area.

Differences in species abundance between locations such as rocky relief areas and silty, vegetated areas are apparent; however, reasons for those differences still are not clear. A more extensive database including preference studies in sympatry and allopatry are needed to address those questions.

Conclusions

My results supported the following main points concerning the use of resources by smallmouth and spotted bass:

- interspecific differences were found in habitat use along a lotic-lentic gradient, with

spotted bass generally more abundant in lentic waters and smallmouth generally found in greater abundance in more lotic areas.

- Diets of the fishes were found to be very similar within lentic and lotic habitats, although experimental manipulations of food availability are needed to explore the possibility of diet shifts.
- Physiological performance indicators (growth and body condition) from both lotic and lentic environments suggest that competition was not constraining growth and survival, at least during the time of the study.

It is interesting to note that the data do not support the prediction that resource partitioning is more pronounced in the presumably more physically stable impounded pool than in the more variable river. The evidence for spatial segregation in the river was no weaker than that found in the impoundment, and interspecific diet overlap index values were actually slightly higher in the impoundment for both middle and large size classes. While this by no means suggests that biotic interactions were more intense in the river, support for the biotic/abiotic gradient in lotic systems outlined by Schlosser (1987) was not found in these results. On the other hand, the effects of power peaking on the hydrologic regime may have had a major impact on spawning success and recruitment. The hydrologic differences between the New River and Byllesby pool may not have been pronounced enough to detect changes in biotic interactions between the two.

In terms of Table 1, both species exhibited high fitness in the study area, with high overlap in diet indicating that food resources were in good supply. Habitat use overlap

was not high, indicating that the species' were segregating in terms of this resource.

Schoener (1982) submitted that strong selection resulting from interspecific competition during periods of low resource availability produces in each species those adaptations most suitable for resources used relatively exclusively by the species.

Alternately, during periods of greater availability, resource use may also expand, with concurrent increase in overlap. To better assess the potential for competition, experiments that control fish density in sympatry and allopatry, as well as food availability under differing environmental conditions such as hydrologic regime and the habitat features measured in this study, are recommended.

In the interim, managers would be well advised to recognize the similarity of these fishes. Evidence to date indicates substantial trophic overlap, and a period of scarce food could cause competitive pressure resulting in poor recruitment, growth, or survival. Any proposed plans for manipulation of fish populations, or habitats where these species are present, should be examined carefully to incorporate the differences in resource use they have thus far demonstrated.

Introductions of spotted bass to streams or impoundments characterized by lower gradients and soft substrates, lacking rocky bottoms and cover types, and largely unable to support healthy smallmouth populations have been proposed (Fajen 1968) and would seem a reasonable way to add to the sport fishery. Any proposed stocking program should, however, be accompanied by a rigorous analysis of the ecological conditions present in the receiving waters, in particular the availability of habitats shown to be utilized

by the two species. A review of the potential trophic impacts (predator-prey, competitive interactions) should be included in the analysis, particularly if stocking into waters that are not part of the species native range.

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VITA

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