

Habitat and Diet Partitioning between Shoal Bass and Largemouth Bass in the Chipola River, Florida

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Abstract.—We investigated the macrohabitat use, microhabitat use, and food habits of shoal bass *Micropterus cataractae* and largemouth bass *M. salmoides* in the upper Chipola River, Florida. We electrofished two macrohabitats (pools and shoals) during the summer (May–August) and fall (September–December) of 1999 and 2000. The ratio of shoal bass to largemouth bass differed among macrohabitats, being highest in the shoals and lowest in the pools. Age-0 and adult (age-1 and older) shoal bass were collected in areas of higher-than-average percentages of rocky substrate in both shoals and pools. Age-0 and adult largemouth bass were associated with areas of reduced current velocity and those with higher-than-average amounts of woody debris. Though the diets of age-0 and adult shoal bass and largemouth bass were similar, a few differences were apparent. Age-0 largemouth bass diets contained grass shrimp *Palaemonetes* spp., whereas age-0 shoal bass diets contained mostly mayflies (order Ephemeroptera: families Baetidae and Isonychidae). Crayfish and fish were the primary food resources of adult shoal bass and adult largemouth bass, and crayfish became more prevalent than fish in larger individuals of both species. Largemouth bass transitioned to a crayfish-dominated diet at a smaller size than did shoal bass. Considering that we found substantial differences in the habitat associations of these species but relatively few diet differences, habitat partitioning may be important for the coexistence of shoal bass and largemouth bass in rivers and streams. Future shoal bass conservation efforts should focus on maintaining a diversity of habitats where these species coexist and on protecting relatively rare shoals.

Shoal bass *Micropterus cataractae*, the most recently described species of black bass *Micropterus* spp., is believed to be threatened by habitat loss throughout its limited range. Its endemic range is the Apalachicola–Chattahoochee–Flint River drainage of Florida, Alabama, and Georgia, and introductions have been limited to the Ocmulgee River in Georgia (Williams and Burgess 1999). The range of shoal bass is diminishing due to the destruction of natural riverine habitat by impoundments (Williams and Burgess 1999). Although shoal bass can survive and reproduce in ponds (Smitherman and Ramsey 1972), they do not persist in impoundments (Ramsey 1975; Williams and Burgess 1999). Thus, shoal bass have disappeared from much of the Chattahoochee River and its tributaries in Georgia and Alabama (Williams and Burgess 1999). Within Florida, shoal bass are restricted to a segment of the upper Chipola River and an area below Jim Woodruff Dam on the Apalachicola River. These populations are threatened

by pollution and siltation in the Chipola River (Ogilvie 1980; Williams and Burgess 1999) and by dredging and irregular flows in the Apalachicola River (Williams and Burgess 1999). Shoal bass are considered a species of special concern in Alabama (Ramsey 1976) and threatened in Florida (Gilbert 1992).

Unfortunately, a paucity of work has addressed the biology and ecology of shoal bass. Williams and Burgess (1999) concluded that future conservation efforts should include studies to determine the microhabitat requirements of the species. Although shoal bass generally are thought to inhabit shoals in rivers and streams (Ramsey 1975; Gilbert 1992; Williams and Burgess 1999), few previous studies have attempted to verify this association. Wright (1967) collected shoal bass and largemouth bass *M. salmoides* at a 10:1 ratio from shoals and a 3:1 ratio from pools. Hurst (1969) collected shoal bass in both pool and riffle areas but collected largemouth bass mainly from large, deep pools. Shoal bass diets have been examined by few investigators but have been found to consist of fish and crayfish (Wright 1967; Hurst 1969; Ogilvie 1980).

Shoal bass share their range with endemic largemouth bass. Largemouth bass are widely distrib-

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uted, and many previous studies have examined their biology and ecology. However, previous research has focused almost exclusively on lentic populations (Hamilton and Powles 1983), even though largemouth bass are common in a wide range of lotic habitats (Jenkins and Burkhead 1993) and are often abundant in streams (Fajen 1975).

Largemouth bass are generally reported to inhabit pools and backwater areas in rivers and streams (Trautman 1957; Wydoski and Whitney 1979) but may be habitat generalists in lotic systems. For example, Schramm and Maceina (1986) found largemouth bass in a wide range of habitats in the Santa Fe River, Florida. Sowa and Rabeni (1995) found largemouth bass biomass and density were positively correlated to maximum summer temperature, mean depth, pool area, and pool:riffle ratio, whereas canopy cover and gradient were negatively correlated to largemouth bass biomass and abundance in Missouri streams.

Largemouth bass are generally considered piscivores (Heidinger 1975) but may prey on a wide variety of aquatic organisms (Jenkins and Burkhead 1993). Previous studies of largemouth bass diets in lotic environments have determined that fish were their primary prey (Scalet 1977; Davies 1981; Hamilton and Powles 1983). However, Schramm and Maceina (1986) found that crayfish were the primary food resource of largemouth bass in the Santa Fe River, Florida.

Shoal bass and largemouth bass are naturally sympatric throughout the range of shoal bass (Williams and Burgess 1999). These species are potential competitors for prey and space because they have similar morphology and prey. Because these fishes are naturally sympatric, they may exhibit resource partitioning to reduce interspecific interactions and facilitate coexistence. Previous studies of sympatric black bass populations have variously documented differences in spatial resource use (Sowa and Rabeni 1995; Sammons and Bettoli 1999), spatial but not food resource use (Janssen 1992; Scott and Angermeier 1998), food but not spatial resource use (Scalet 1977), neither food nor spatial resource use (Hubert 1977), and both spatial and food resource use (Warden and Hubert 1980; Schramm and Maceina 1986).

We investigated the habitat use and food habits of shoal bass and largemouth bass in a lotic system. Our objectives were to test (1) whether the ratio of collected shoal bass to largemouth bass varied between macrohabitats (i.e., pools and shoals), (2) whether shoal bass or largemouth bass were as-

sociated with different microhabitat parameters (i.e., current velocity, substrate, woody debris, and depth) than the average conditions within both pools and shoals, and (3) whether diets were similar between shoal bass and largemouth bass.

Methods

Study site.—The Chipola River is a low-gradient stream (0.17 m/km; Bass and Cox 1985) that flows 201 km south from Alabama to its confluence with the Apalachicola River. Its watershed area is 3,124 km², and average discharge is 42.8 m³/s (Bass and Cox 1985). Although the Chipola River receives some surface runoff, it is primarily spring fed (Parsons and Crittenden 1959; Bass and Cox 1985), resulting in low turbidity (Parsons and Crittenden 1959) and relatively stable year-round water temperatures (range, 10–24°C; Parsons and Crittenden 1959; Bass and Cox 1985). The substrate is primarily sand and cobble, with limestone outcrops (Parsons and Crittenden 1959). The watershed is relatively pristine, containing some agricultural developments and small towns (Winger et al. 1987).

The 48-km section of river between the towns of Marianna and Clarksville, Florida, is inhabited by shoal bass and largemouth bass. This section of river is characterized by two primary macrohabitats, pools and shoals, with pools being the dominant macrohabitat. Pools are characteristically narrow (mean width, 31 m), long (>1 km), deep (mean, >2 m), and slow flowing. Shoals are shorter (<200 m), wider (mean, 66 m), shallower (mean depth, <1 m), and have higher current velocities than the pools. Shoals also contain beds of eelgrass *Vallisneria americana*, whereas pools are devoid of aquatic macrophytes. We selected three pools and three shoals for sampling. The three shoals were locations where previous studies collected shoal bass, and the pools were adjacent to the shoals. All study units were located within a 15-river-kilometer (rkm) section.

Fish collection.—Fish and microhabitat sampling were conducted in summer (May–August) and fall (September–December) of 1999 and 2000. Fish were collected by boat electrofishing with DC. Habitat differences between pools and shoals required different electrofishing techniques for effective fish collection. Shoals were electrofished by moving upstream in such a way that all areas deep enough to navigate were exposed to the electric field. Due to the presence of shallow areas (<0.25 m), the entire area of the shoals could not be navigated; however, many areas too shallow to

navigate were within reach of the cathode probe. Pools were electrofished by drifting longitudinally down the habitat unit while moving laterally between the right bank, left bank, and the center of the channel. Units were sampled as many as three times in each season but always with at least 48 h between samples. Because pools are the primary macrohabitat in the upper Chipola River, we weighted our sampling effort in favor of pools.

Areas where shoal bass or largemouth bass were collected were marked with a weighted buoy for microhabitat measurements. The buoys were color coded to distinguish between age-0 fish and those older than age 0 (hereafter referred to as adults) and between shoal bass versus largemouth bass. Ages of fish that appeared to be age 0 in the field were verified by examining sagittal otoliths in the laboratory. Ad hoc sampling in areas adjacent to the three shoals and three pools was used to supplement fish collections for diet analysis.

Macrohabitat analysis.—Because habitat differences between pools and shoals required different electrofishing techniques, we could not use electrofishing catch per effort to compare the relative abundances of shoal bass and largemouth bass between macrohabitats. We tested whether the proportion of shoal bass to largemouth bass differed among macrohabitats with a weighted-least-squares analysis of proportions (WLSAP; Statistical Analysis System [SAS] Catmod procedure; SAS 1994; Stokes et al. 2000). The WLSAP tested whether the proportion of shoal bass to largemouth bass differed across macrohabitat types, seasons, and years.

Microhabitat characterization and analysis.—We characterized the microhabitat associations of age-0 and adult shoal bass and largemouth bass by measuring or estimating physical habitat at the location where individuals were collected. Microhabitat parameters were measured at an area designated longitudinally (i.e., upstream–downstream axis) as 10 m wide, centered at the point the individual was captured, and latitudinally as the left, right or center third of the stream. The area contained in each interval was variable, dependent on stream width.

We characterized microhabitat conditions in the pools and shoals using four permanent transects in each habitat unit. Permanent transects were perpendicular to the channel and approximately evenly spaced through each unit. A tree on the bank adjacent to the transect was marked with paint, allowing the same fixed transects to be used throughout the study. During each sampling event

(i.e., summer and fall of 1999 and 2000), microhabitat characteristics were recorded from three intervals equally spaced across each transect (e.g., two near the bank and one midchannel). The longitudinal width (i.e., upstream–downstream axis) of the intervals was defined as 10 m on either side of the transect. The area contained in each interval was variable, dependant on stream width. Thus, the intervals of the fixed transects were statistically comparable to the areas where fish were collected.

Microhabitat and cover variables were measured or estimated for each interval of the fixed transects and for the areas where individual shoal bass or largemouth bass were collected. Mean depth was estimated to the nearest 5 cm with a depth rod. Mean current velocity was measured at 60% of depth, at a point representative of the interval (judged visually), with a Marsh-McBirney model 201M portable water current meter. Substrate was recorded as the visually estimated percentage of silt (<0.062 mm), sand (>0.062–2 mm), gravel (>2–16 mm), pebble (>16–64 mm), cobble (>64–256 mm), boulder (>256 mm), and flat bedrock. The total percentage of the substrate classified as cobble and boulder was summed and used to indicate rocky substrate particles. Rocky substrate percentage was used in the analysis because it provided an easily interpretable index of substrate coarseness and because there is a reported association of other black basses with these substrates (Leonard and Orth 1988; Todd and Rabeni 1989; Lobb and Orth 1991). The percent area covered by eelgrass was also visually estimated. Individual pieces of woody debris were visually counted in four categories (I–IV) based on length and diameter, as done by Dolloff et al. (1993). The four categories we used were: (I) 1–5 m in length and 5–10 cm in diameter, (II) 1–5 m in length and over 10 cm in diameter, (III) over 5 m in length and 5–10 cm in diameter, and (IV) over 5 m in length and over 10 cm in diameter. In the case of fallen trees, branches connected to a larger trunk were categorized and enumerated individually. From these counts and categories, a woody debris index (WDI) was calculated as

$$\begin{aligned} \text{WDI} = & (\text{Wood I}) + [2 \times (\text{Wood II})] \\ & + [3 \times (\text{Wood III})] \\ & + [4 \times (\text{Wood IV})], \end{aligned} \quad (1)$$

where Wood I–IV represent numbers of woody debris of each size category in the interval. This index was weighted so that larger size-classes of

debris received an arbitrarily higher value. Larger values of WDI are used to indicate greater amounts of woody debris in the interval. Percent area coverage of eelgrass was estimated visually in each interval. The first author measured or estimated all microhabitat parameters except mean current velocity throughout the study.

We validated the visual estimation of substrate composition. Substrate composition of 15 approximately 25-m², shallow (depth, <1 m) locations in a shoal was visually estimated as previously described. Locations were selected to reflect as much variation in substrate particle composition as possible. After visually estimating the substrate at a location, we randomly tossed a 0.5-m² ring, divided by string into 16 equal sections, into the location 10 times. The dominant substrate particle category was recorded in each of the sections for every toss. For each location, the percentage of the 160 sections (16 sections \times 10 tosses) dominated by rocky substrate was compared to the visual estimation of percent rocky substrate. The areas used to verify the visual estimation of substrate particles contained substrates ranging from sand to boulder. There was a significant linear correlation ($R = 0.94$, $P < 0.001$) between the visual estimation of rocky substrate and the observed proportion of sections dominated by rocky substrate. Thus, the visual estimation appeared to be an adequate index of substrate composition.

We used a multivariate analysis of variance (MANOVA) to test the null hypothesis that microhabitat variables collectively were similar between the permanent transects (average conditions of the macrohabitat) and the areas where individuals were collected. The analysis was repeated for age-0 and adult individuals of both species. The MANOVAs were conducted for individuals in pools and shoals (eight analyses total) based on the microhabitat observations (i.e., intervals) from the fixed transects and the microhabitat data from areas where individuals were collected. Current velocity, depth, percent rocky substrate, and WDI score were used as response variables, and year (1999, 2000), season (summer, fall), species presence (e.g., at least one individual was or was not collected), and the interaction between species presence and season were used as predictor variables. In addition, eelgrass abundance was used as a response variable for the shoals. Data were log₁₀ transformed as necessary to help meet the assumption of a multivariate normal distribution (Zar 1988). We used Wilk's lambda (SAS 1994) to test the null hypothesis that year, season, species

presence, and the species presence \times season interaction had no effect on the mean microhabitat observations. In cases of an overall significant MANOVA for the effect of species presence, one-way analyses of variance (ANOVA) were used to determine microhabitat parameters that contributed to the significant difference between the areas where individuals were collected and the permanent transects.

Diet collection and analysis.—Transparent acrylic tubes (Van Den Avyle and Roussel 1980) were used to remove the stomach contents of all shoal bass and largemouth bass larger than 200 mm total length. A flexible claw retriever (Dimond 1985) assisted in the removal of large items and crayfish. The removed stomach contents were placed on ice and returned to the laboratory, where the items were enumerated, identified, and weighed. Shoal bass and largemouth bass 200 mm or smaller were placed on ice and returned to the laboratory, where they were dissected and their stomach contents removed, enumerated, identified, and weighed to the nearest 0.001 g. When possible, fish remains were identified to genus (based on Oates et al. 1993) and insects to order.

Diet was quantified for each species in terms of percent by weight. Pianka's (1973) index of diet overlap (O) was used to index the similarity of the diets of the two species. Pianka's Index is defined as:

$$O = \sum p_{2i}p_{1i} / \left(\sum p_{2i} \times \sum p_{1i} \right)^{0.5}, \quad (2)$$

where O is the overlap in resources between species 1 and 2, p_{1i} is the weight of resource category i found in species 1, and p_{2i} is the weight of resource category i found in species 2. The resource categories were fish, crayfish, insects, other invertebrates, and other prey items. Overlap (i.e., similarity) values range from 0 (none) to 1 (complete). EcoSim software (Gotelli and Entsminger 1997) was used to generate null models and to calculate the probability of observed diet overlap occurring by chance. Driscoll and Miranda (1999) used EcoSim software to evaluate diet overlap among age-classes of yellow bass *Morone mississippiensis* in Mississippi River oxbow lakes. A randomization algorithm (RA2, Gotelli and Entsminger 1997) was selected that generated null models for each species based on only those prey items observed in the diets.

Ontogenetic diet shifts were evaluated with logistic regression. Logistic regression models the probability of a binary response based on contin-

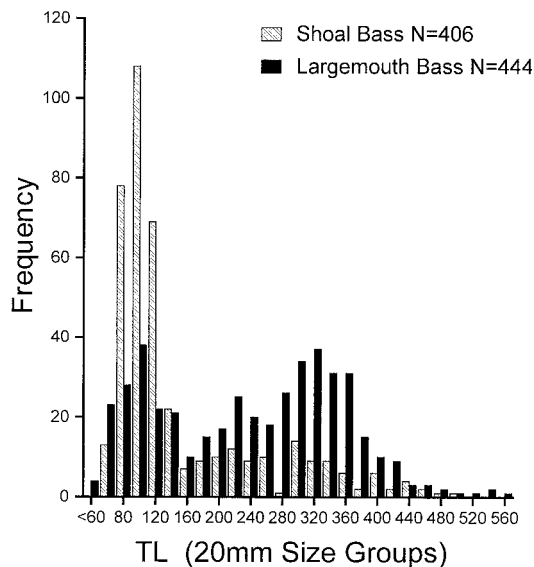


FIGURE 1.—Length-frequency histogram showing size (TL; 20-mm groups) and number of shoal and largemouth bass collected during 1999 and 2000 combined.

uous and/or categorical predictor variables (SAS procedure Logistic; SAS 1994; Stokes et al. 2000). In this application, the binary response variable was fish or crayfish remains dominating (by weight) the diet of shoal bass or largemouth bass. The linear model used was

$$\text{logit}(p) = \alpha + \beta_1 \times \text{TL} + \beta_2 \times \text{species} + \beta_3 \times (\text{species} \times \text{TL}), \quad (3)$$

where $\text{logit}(p)$ is the logistic probability of crayfish (versus fish) dominating the diet of either shoal bass or largemouth bass, α is the intercept value, TL is the total length (mm) of each species, species is the main effect of the categorical variable species type (shoal bass or largemouth bass), species \times TL is the interaction between species and TL,

and β_1 – β_3 are the logistic regression coefficients. The estimate of the $\text{logit}(p)$ was used to obtain the predicted probability of a diet being crayfish dominated, that is,

$$p = e^{\text{logit}(p)} / (1 + e^{\text{logit}(p)}). \quad (4)$$

Wald's chi-square statistic (SAS 1994) was used to test the significance of the individual model terms.

Results

The total amount of electrofishing time was 88.6 h, accumulated from pool (51.5 h), shoal (26.1 h), and ad hoc (10.9 h) collections. A total of 105 adult shoal bass, 316 adult largemouth bass, 288 age-0 shoal bass, and 125 age-0 largemouth bass were collected during this study. Shoal bass ranged from 70 to 480 mm TL, whereas largemouth bass ranged from 60 to 560 mm TL (Figure 1).

The study area generally exhibited slightly lower-than-average monthly discharges for both study years, and average monthly flows were higher in 1999 than 2000. Mean depth and current velocity were greater in 1999 than 2000 in both pools and shoals (Table 1) due to higher rainfall in 1999. The percent rocky substrate was relatively consistent throughout the study. Eelgrass was more abundant in 2000 (Table 1).

Macrohabitat Results

Age-0 shoal bass and largemouth bass were collected from both pools and shoals (Table 2). However, the WLSAP detected differences in the ratio of age-0 shoal bass to age-0 largemouth bass in pools and shoals. We collected too few age-0 individuals in 1999 to test for differences between the two sample years (Table 2). Therefore, the years were pooled for this analysis. Macrohabitat type was the sole significant predictor of the ratio of age-0 shoal bass to age-0 largemouth bass

TABLE 1.—Mean \pm 2 SEs observations for depth, current velocity, percentage rocky substrate, woody debris index (WDI), and eelgrass (% coverage) in the fixed transects of the pools ($N = 36$) and shoals ($N = 36$) during summer (May–August) and fall (September–December), 1999 and 2000, in the Chipola River.

Habitat	Year	Season	Depth (cm)	Velocity (cm/s)	Rocky substrate	WDI	Eelgrass
Pool	1999	Summer	195 \pm 11.6	39 \pm 2.1	23 \pm 4.2	3 \pm 1.3	<1 \pm 0.3
		Fall	173 \pm 9.6	26 \pm 2.0	28 \pm 3.8	2 \pm 0.8	<1 \pm 0.1
	2000	Summer	158 \pm 9.5	15 \pm 1.6	29 \pm 3.7	2 \pm 0.5	<1 \pm 0.1
		Fall	154 \pm 9.8	13 \pm 1.4	33 \pm 4.7	<1 \pm 0.3	10 \pm 4.1
Shoal	1999	Summer	105 \pm 9.5	51 \pm 5.3	29 \pm 3.3	2 \pm 0.6	9 \pm 3.1
		Fall	69 \pm 6.1	31 \pm 2.6	43 \pm 2.6	2 \pm 0.7	26 \pm 4.8
	2000	Summer	63 \pm 5.7	27 \pm 3.2	42 \pm 3.0	2 \pm 0.6	1 \pm 0.8
		Fall	67 \pm 6.3	19 \pm 2.1	42 \pm 3.2	1 \pm 0.3	22 \pm 5.2

TABLE 2.—Number of fish collected from pool and shoal sample sites in the Chipola River as well as from ad hoc sampling of nearby areas that was used to supplement fish collections for diet contents.

Species and age-class	Sample		
	Pool	Shoal	Ad hoc
Age-0 shoal bass	118	137	33
Adult shoal bass	83	26	9
Age-0 largemouth bass	82	20	23
Adult largemouth bass	252	34	33

($\chi^2 = 41.77$, $df = 1$, $P < 0.0001$). The ratio of age-0 shoal bass to age-0 largemouth bass was significantly higher in shoals (6.9:1) than in pools (1.4:1).

Adult shoal bass and largemouth bass were collected from both pools and shoals (Table 2). However, the WLSAP also detected differences in the ratio of adult shoal bass to adult largemouth bass in these macrohabitats. The ratio of adult shoal bass to adult largemouth bass was predicted by year ($\chi^2 = 10.88$, $df = 1$, $P = 0.0010$), macrohabitat ($\chi^2 = 8.08$, $df = 1$, $P = 0.0945$), and season ($\chi^2 = 21.41$, $df = 1$, $P < 0.0001$). The main effect of year was significant because the ratio of adult shoal bass to adult largemouth bass was lower in 2000 (1:4.1) than in 1999 (1:3.51). The significant main effect of season resulted from the collection of a higher ratio of adult shoal bass to adult largemouth bass in the summer sampling (1:2.0) than in fall sampling (1:4.3). The ratio of adult shoal bass to adult largemouth bass was greater in the shoals (1:1.3) than in the pools (1:3.1).

Microhabitat Results

All MANOVA analyses detected significant differences between the microhabitats where age-0 and adult shoal bass and largemouth bass were collected and the average conditions of both pools and shoals (Table 3). The presence \times season interaction was never significant (all $P > 0.06$), indicating that generally these species did not change microhabitat associations seasonally. The main effect of presence was always significant (all $P < 0.008$), indicating that both species were associated with microhabitat parameters that differed from the mean microhabitat parameters in pools and shoals (Table 3).

Age-0 and adult shoal bass showed similar trends in microhabitat associations. Age-0 and adult shoal bass were associated with deeper-than-average areas in shoals (one-way ANOVA: $F_{1,149} = 18.1$, $P < 0.001$; $F_{1,155} = 6.1$, $P = 0.015$) and

TABLE 3.—Results of MANOVA analyses testing for differences between the mean habitat observations in intervals where fish were collected (presence) versus the fixed intervals. In addition, effects of season (summer or fall), year (1999 or 2000), and the interaction between presence and season were included in the MANOVA. Because age-0 fish of both species did not fully recruit to the gear until fall sampling, fall habitat observations were used in the MANOVA analyses for age-0 shoal and largemouth bass.

Effect	Wilk's lambda	F	df	P-value
Age-0 shoal bass in pools				
Presence	0.8531	6.6	4, 154	<0.001
Year	0.8270	8.1	4, 154	<0.001
Age-0 shoal bass in shoals				
Presence	0.8608	4.7	5, 145	<0.001
Year	0.8785	4.0	5, 145	0.002
Age-0 largemouth bass in pools				
Presence	0.8005	7.1	4, 114	<0.001
Year	0.6588	14.8	4, 114	<0.001
Age-0 largemouth bass in shoals				
Presence	0.8203	3.4	5, 77	0.008
Year	0.8725	2.3	5, 77	0.058
Adult shoal bass in pools				
Presence	0.9397	3.3	4, 175	0.012
Season	0.9340	3.1	4, 175	0.017
Presence \times season	0.9850	0.7	4, 175	0.617
Year	0.6229	26.5	4, 175	<0.001
Adult shoal bass in shoals				
Presence	0.8968	3.5	5, 151	0.005
Season	0.9400	1.9	5, 151	0.093
Presence \times season	0.9703	0.9	5, 151	0.468
Year	0.7625	9.4	5, 151	<0.001
Adult largemouth bass in pools				
Presence	0.7416	20.0	4, 229	<0.001
Season	0.9299	4.3	4, 229	0.002
Presence \times season	0.9773	1.3	4, 229	0.260
Year	0.7030	24.2	4, 229	<0.001
Adult largemouth bass in shoals				
Presence	0.7068	13.7	5, 165	<0.001
Season	0.9553	1.5	5, 165	0.179
Presence \times season	0.9403	2.1	5, 165	0.069
Year	0.7867	9.0	5, 165	<0.001

shallower-than-average areas in pools ($F_{1,157} = 12.4$, $P < 0.001$; $F_{1,178} = 5.5$, $P = 0.020$). Age-0 and adult shoal bass were collected in areas of higher-than-average rocky substrate in shoals ($F_{1,149} = 4.9$, $P = 0.029$; $F_{1,155} = 9.9$, $P = 0.002$) and pools ($F_{1,149} = 16.3$, $P < 0.001$; $F_{1,178} = 10.3$, $P = 0.002$). Adult shoal bass were found at lower-than-average eelgrass coverage in the shoals ($F_{1,155} = 5.2$, $P = 0.024$).

Age-0 and adult largemouth bass also showed similar trends in microhabitat associations. Age-0 and adult largemouth bass were associated with

deeper-than-average areas in the shoals (one-way ANOVA: $F_{1,81} = 8.5$, $P = 0.005$; $F_{1,169} = 24.9$, $P < 0.001$) and shallower-than-average areas in the pools ($F_{1,117} = 8.8$, $P = 0.004$; $F_{1,232} = 5.8$, $P = 0.017$). Age-0 and adult largemouth bass were collected from lower-than-average current velocities in pools ($F_{1,117} = 3.8$, $P = 0.054$; $F_{1,232} = 5.3$, $P = 0.022$). In both pools and shoals, adult largemouth bass were associated with areas of higher-than-average WDI scores ($F_{1,232} = 67.5$, $P < 0.001$; $F_{1,169} = 22.0$, $P = 0.001$). Adult largemouth bass were found at lower-than-average coverage of eelgrass in the shoals ($F_{1,169} = 16.1$, $P < 0.001$).

Diet Analyses

Stomach contents were examined for 288 (77 empty) age-0 shoal bass and 125 (25 empty) age-0 largemouth bass. All diets collected in 1999 were weighed, but because higher numbers of age-0 shoal bass and age-0 largemouth bass were collected in 2000, the age-0 diets were subsampled. Individuals collected during 2000 were randomly subsampled until 10 (nonempty) individuals per length group were examined. There was a higher overlap in the diets of age-0 shoal bass and age-0 largemouth bass than would be expected to occur by chance alone ($O = 0.88$, $P = 0.054$), indicating that their diets were generally similar. The diets of most age-0 shoal bass and age-0 largemouth bass were dominated by unidentifiable fish, and both species exhibited increasing prevalence of fish in the diets with increasing TL (Figure 2).

However, the high diet overlap values may exaggerate diet similarity due to the prevalence of relatively heavy fish remains. Differences in diets were apparent when prey items were compared by size-classes, especially for individuals less than 150 mm TL (Figure 2). Age-0 shoal bass diets were dominated by mayflies (order Ephemeroptera: families Baetidae and Isonychidae), whereas age-0 largemouth bass showed a higher prevalence of grass shrimp *Palaemonetes* spp. in their diets (Figure 2). Diets consisting of over 200 individual mayflies were common in age-0 shoal bass, but this phenomenon was not observed in age-0 largemouth bass.

Stomach contents of 118 (35 empty) adult shoal bass and 319 (124 empty) adult largemouth bass were examined. There was a higher overlap in the diets of adults of both species than would be expected to occur by chance alone ($O = 0.86$, $P = 0.073$). Crayfish and fish dominated the adult diets of both species (Figure 2). Although the majority

of fish remains were unidentifiable, darters *Percina* spp. and madtoms *Noturus* spp. were most common in the diets of adult shoal bass, whereas darters and sunfishes *Lepomis* spp. were most prevalent in the diets of adult largemouth bass.

The logistic regression analysis revealed the occurrence of an ontogenetic shift in the diets of adult shoal bass and adult largemouth bass. Crayfish became increasingly more dominant than fish in the diets of large individuals of both species (main effect of TL $\chi^2 = 46.9$, $P < 0.001$, Figure 3). The diet shift is modeled by:

$$\begin{aligned} \text{logit}(p) = & -3.2108 + 0.0113 \times \text{TL} \\ & - 0.7767 \times (\text{species}) \\ & + 0.00541 \times (\text{species} \times \text{TL}) \end{aligned}$$

where species is equal to -1 for shoal bass and $+1$ for largemouth bass. Largemouth bass made the transition to a crayfish-dominated diet faster and at a smaller TL than did shoal bass (species \times TL interaction $\chi^2 = 10.8$, $P = 0.001$, Figure 3). For example, the logistic regression predicted that a 239-mm TL largemouth bass would have an equal probability of displaying a crayfish-dominated or fish-dominated diet, whereas for shoal bass, such diets did not reach equal probability until 413 mm TL.

Discussion

Age-0 and adult shoal bass and largemouth bass were collected from both pools and shoals, indicating that both species were somewhat generalistic in their macrohabitat associations. The upper Chipola River contains primarily pool habitat, and shoal habitat makes up a relatively minor proportion of the area. Thus, we invested greater effort in sampling pools, and we collected more shoal bass (except age-0 fish) and largemouth bass from the pools. Physical differences in pools and shoals prevented us from using electrofishing catch per effort to assess differences in the abundance of these species across macrohabitats. However, we detected differences in the ratio of one species to another in the different macrohabitats, which indicated habitat differences between these two species. The ratio of shoal bass to largemouth bass was highest in the shoals and lowest in the pools, indicating that shoal bass represented a significantly greater percentage of the black bass assemblage in shoals. This trend was consistent for both age-0 and adult fish and consistent with previous studies (Wright 1967; Hurst 1969).

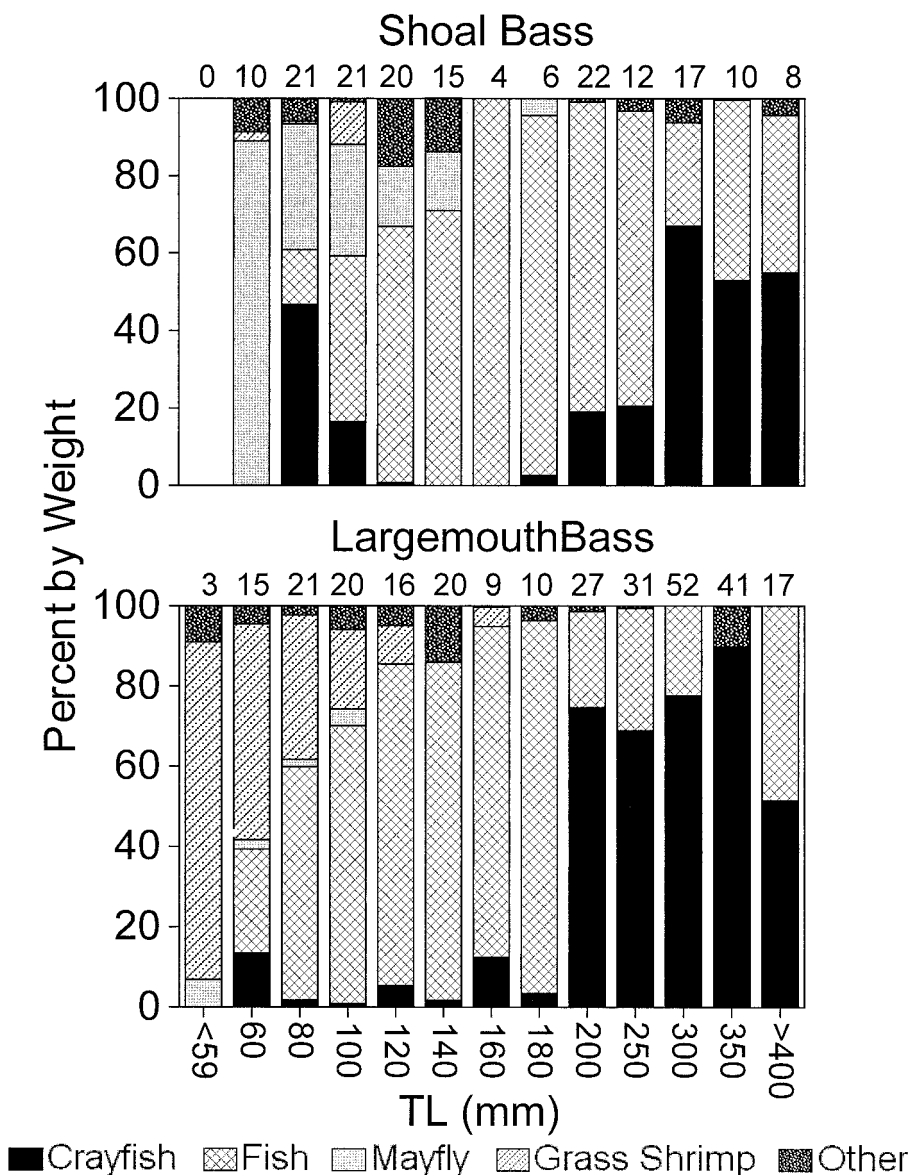


FIGURE 2.—Percent by weight of prey items in the diets of shoal and largemouth bass collected during 1999 and 2000 combined. The number of stomachs containing prey items is listed over the respective length category column. Diets of individuals smaller than 200 mm TL were subsampled in 2000.

Macrohabitat associations of age-0 individuals may have been influenced by differing nesting preferences of shoal bass and largemouth bass. Previous studies have observed shoal bass nests in a shoal (Wright 1967) and just upstream of a riffle (Hurst 1969), whereas largemouth bass in lotic systems are believed to nest in pools (Jenkins and Burkhead 1993). Given the reported nesting preferences of shoal bass and the high proportion

of age-0 shoal bass in shoals, these areas may represent spawning habitat for adults, nursery habitat for shoal bass, or both. However, we did not document spawning habitat or movement of either species, which warrants further investigation.

Age-0 and adult individuals of both species showed differences in habitat use from the mean microhabitat observations in the pools and shoals. Age-0 and adult individuals of both species were

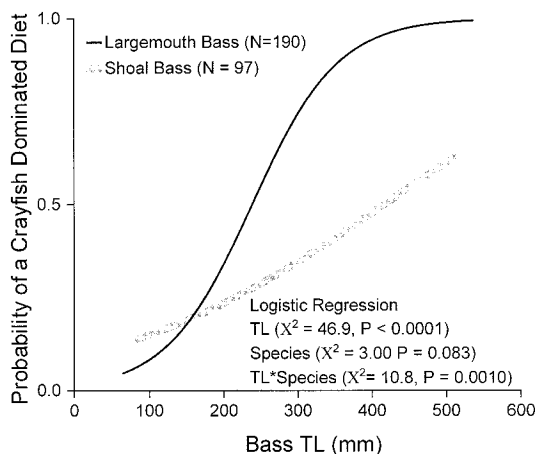


FIGURE 3.—The relationship between TL (mm) and the probability of an individual largemouth bass or shoal bass exhibiting a crayfish-dominated diet (by weight). Results of the logistic regression analysis are shown (see text).

associated with deeper-than-average areas in the shoals and shallower-than-average areas in the pools. These observations likely result from a gear bias, because our electrofishing equipment was not able to reach all the shallow areas in the shoals and was likely ineffective in sampling the deepest areas in the pools (>2 m). Therefore, the habitat associations we identified probably exclude shallow areas in shoals and deep sections of the pools.

Shoal bass were associated with areas of higher-than-average percentages of rocky substrate, whereas largemouth bass were not. Age-0 shoal bass were associated with higher-than-average percentages of rocky substrate in pools, and adult shoal bass were associated with higher-than-average percentages of rocky substrate in both pools and shoals. Cobble and boulder substrate is commonly considered an important habitat type for smallmouth bass *M. dolomieu*. Age-0 smallmouth bass commonly associate with cobble substrate (Leonard and Orth 1988; Livingstone and Rabeni 1991), and adults are known to use boulders as cover in areas that are surrounded with other substrates, such as cobble (Leonard and Orth 1988; Todd and Rabeni 1989; Lobb and Orth 1991). Our results suggest similar habitat associations for shoal bass.

Largemouth bass are believed to inhabit pools and backwater areas in lotic situations (Trautman 1957; Wydoski and Whitney 1979). We found evidence to support this presumption. The ratio of shoal bass to largemouth bass was lowest in the

pools, and age-0 and adult largemouth bass were collected in lower-than-average current velocities in pools. Shoal bass were not associated with areas of lower-than-average current velocity in either pools or shoals. Miller (1975) reported that largemouth bass inhabited pools and backwater areas when they occurred in streams with smallmouth bass, spotted bass *M. punctulatus*, and Suwannee bass *M. notius*. Sowa and Rabeni (1995) found largemouth bass were most abundant in streams with high pool:riffle ratios. In addition, Schramm and Maceina (1986) found intermediate-sized (149–299 mm TL) largemouth bass were most abundant in areas of relatively low current velocity (3–25 cm/s) in the Santa Fe River, Florida. Thus, pools may be the preferred habitat of largemouth bass in lotic systems. However, Schramm and Maceina (1986) collected large (>300 mm TL) largemouth bass primarily from a turbulent area with high current velocity (30–92 cm/s) and bedrock substrates. Similarly, we collected some largemouth bass in shoals, suggesting that largemouth bass may be more general in their stream habitat associations than previously believed.

Adult largemouth bass were associated with higher-than-average WDI scores in both the pools and shoals. Age-0 largemouth bass were also associated with higher-than-average WDI scores in the pools. The importance of woody debris in warmwater streams is well documented. Woody debris provides increased invertebrate production (Benke et al. 1985), protection from strong current velocity (Todd and Rabeni 1989), and camouflage from predators or prey (Angermeier and Karr 1984). However, Lehtinen et al. (1997) found no relationship between largemouth bass habitat associations and woody debris in the upper Mississippi River, and Sowa and Rabeni (1995) found no relationships between woody debris and largemouth bass density or abundance in Missouri streams. We found the mean WDI for areas where largemouth bass were collected was higher than the average values in both pools and shoals. Largemouth bass may use woody debris as structure from which to ambush crayfish, as shelter from current, or they may simply be responding to an innate association with this type of structure. Woody debris index scores for microhabitats where shoal bass were collected did not differ from average WDI scores in the pools or shoals.

Generally, we found similar food habits between shoal bass and largemouth bass, with high ($O > 0.8$) diet overlap. The estimate of diet overlap may be inflated since only five prey categories (fish,

crayfish, insects, other invertebrates, and other) were used in the analysis. Some differences in food habits were apparent when food taxa were separated into smaller categories. For example, fish were the primary prey (by weight) of age-0 largemouth bass over 80 mm TL and age-0 shoal bass over 120 mm TL. Prior to the onset of piscivory, age-0 shoal bass primarily consumed baetid mayfly larvae. Age-0 largemouth bass rarely consumed mayflies but frequently consumed grass shrimp, which were almost absent in the diets of age-0 shoal bass. The consumption of grass shrimp and the overall diet of age-0 largemouth bass were similar to the previous observations of Davies (1981) and Schramm and Maceina (1986). Minor differences in the diets of age-0 shoal bass and age-0 largemouth bass may have resulted from differences in prey availabilities in the microhabitats and macrohabitats occupied by the two species. Because of low sample size (Figure 2) for some size categories of shoal bass and largemouth bass, we were unable to analyze diet differences between the pools and shoals. Nevertheless, the prey consumed by both species were generally similar in this study.

Fish and crayfish were the primary prey of adult shoal bass and adult largemouth bass, and the prevalence of crayfish in their diets increased with fish size. However, this transition to a crayfish-dominated diet occurred at a smaller size for largemouth bass than for shoal bass. Adult largemouth bass larger than 239 mm TL preyed almost entirely on crayfish, whereas shoal bass diets were not as exclusive. Roell and Orth (1993) observed a similar trend in the diets of smallmouth bass, and Schramm and Maceina (1986) documented this phenomenon in the diets of largemouth bass and Suwannee bass in a Florida River. This study agrees with previous studies, showing that fish (Wright 1967; Ogilvie 1980) and crayfish (Hurst 1969) are the primary food resources of shoal bass.

Similar species in sympatric situations frequently exhibit resource partitioning, presumably to facilitate coexistence (Hardin 1960). We found substantial differences in the habitat associations of shoal bass and largemouth bass in this study, but comparatively few differences in food habits. Previous studies have shown spatial resource partitioning is more common than food resource partitioning among similar species (Schoener 1974), congeners (reviewed in Ross 1986), and centrarchids (Werner and Hall 1977; George and Hadley 1979; Janssen 1992; Scott and Angermeier 1998). Our study also suggests that habitat parti-

tioning may be more important than diet differences for the coexistence of shoal bass and largemouth bass in the Chipola River, Florida.

Maintaining shoal and pool habitats, as well as a diversity of microhabitats such as rocky substratum and woody debris, may be important for facilitating the coexistence of shoal bass and largemouth bass in streams and rivers. Shoal bass are consistently extirpated from impounded sections of rivers (Ramsey 1975; Williams and Burgess 1999), whereas largemouth bass persist. Given that shoal bass can reproduce in ponds, Ramsey (1975) suggested that competition with lake-dwelling fishes eliminates shoal bass from impoundments. Our results suggest that shoal bass and largemouth bass partitioned resources spatially in the Chipola River. Thus, future shoal bass conservation efforts should focus on maintaining or enhancing stream habitat diversity and on protecting the relatively uncommon shoals.

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