Diets of Juvenile and Sub-Adult Size Classes of Three Micropterus spp. in the Flint River, Georgia: Potential for Trophic Competition

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Diets of Juvenile and Sub-adult Size Classes of Three *Micropterus* spp. in the Flint River, Georgia: Potential for Trophic Competition

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Abstract - Concerns over the recent introduction of *Micropterus punctulatus* (Spotted Bass) on native *M. salmoides* (Largemouth Bass) and *M. cataractae* (Shoal Bass) prompted a one-year investigation into the food habits of these three congeneric species to determine diet overlap and potential for trophic competition in the Flint River, GA. Diet analyses among species were conducted for two size classes of fish: juvenile (<200 mm total length) and subadult (200–300 mm TL). Because Spotted Bass had become established in the Flint River only a few years prior to this study, few fish >300 mm were collected; thus, diet overlap was not compared among species for larger fish. Juvenile and subadult Largemouth Bass diets were dominated by fish in all seasons, mainly sunfishes (e.g., *Lepomis auritus*, *L. macrochirus*). In contrast, Shoal Bass diets were generally dominated by insects and crayfish in the juvenile and subadult size classes, respectively. Juvenile Spotted Bass diets were variable and dominated by fish and insects depending on season. Overall, diets of introduced Spotted Bass appeared to occupy an intermediate position between Shoal Bass and Largemouth Bass. Significant diet overlap between Shoal Bass and Spotted Bass occurred in 50% of the samples, but only in 29% of the samples between Spotted Bass and Largemouth Bass and never between the two native Bass species. Thus, concerns about the trophic effects of Spotted Bass on Shoal Bass appear to be legitimate.

Introduction

Collectively, *Micropterus* spp. (black basses) constitute some of the most popular and economically valuable freshwater sport fisheries in North America. In 2006, an estimated 10 million anglers spent 161 million days fishing for black basses in the USA, representing approximately 40% of all anglers and angling effort in freshwater systems other than the Great Lakes (USFWS and USBOC 2008). Forty-five percent of those freshwater anglers reported fishing in river and streams in 2006, which represents a significant proportion of effort and expenditures. In the southeastern USA, many rivers contain endemic species of black basses, some of which are obligate lotic species. Interest and use of these endemic black bass fisheries by anglers has increased; however, little is known about the biology of these species, which may hinder efforts to manage them.

Micropterus cataractae Williams and Burgess (Shoal Bass) is endemic to the Apalachicola drainage and occurs naturally throughout the Chattahoochee

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and Flint river systems. Not formally described until 1999 (Williams and Burgess 1999), Shoal Bass have been rarely studied and very little information exists on the biology of this species. However, Shoal Bass are thought to be declining in abundance in many localities within its native range (Boschung and Mayden 2004, Wheeler and Allen 2003, Williams and Burgess 1999). Shoal Bass are habitat specialists, generally found in rocky shoals in medium- to large-sized streams and rivers, and are intolerant of reservoir conditions (Boschung and Mayden 2004, Stormer and Maceina 2009, Wheeler and Allen 2003). Throughout their native range, Shoal Bass occur in sympatry with native stocks of *Micropterus salmoides* Lacepède (Largemouth Bass). Yet Largemouth Bass and Shoal Bass rarely occupy the same habitat in streams, with Largemouth Bass typically occurring in pools and slower runs (Hurst 1969, Wheeler and Allen 2003).

Micropterus punctulatus Rafinesque (Spotted Bass) is native to Gulf Coast drainages west of the Apalachicola River to the Guadalupe River drainage in Texas (Boshung and Mayden 2004). However, the species has also been illegally introduced by anglers into lotic systems across the southeastern USA, including the Apalachicola Basin, and may pose a substantial competitive threat to Shoal Bass given their similar habitat use in streams (Horton and Guy 2002, Hurst et al. 1975, Tillma et al. 1998, Vogele 1975). In Alabama, many streams in which Shoal Bass have been collected historically are now dominated by Spotted Bass (Stormer and Maceina 2008). Spotted Bass appear to be a habitat generalist (Vogele 1975), and may be able to outcompete Shoal Bass when both are found sympatrically (Miller 1975, Smitherman 1975). Many river systems in the range of Shoal Bass are being degraded due to changes in land use and increased demand for water supplies (Williams and Burgess 1999), and degradation of habitat in systems where both species are found may favor Spotted Bass, which is more adaptable, over Shoal Bass.

Diets of Largemouth Bass, Spotted Bass, and Shoal Bass in rivers may be relatively similar, consisting of fish, aquatic insects, and crayfish (Scott and Angermeier 1998, Vogele 1975, Wheeler and Allen 2003). Wheeler and Allen (2003) found that diets of Shoal Bass and Largemouth Bass were relatively similar and dominated by crayfish in the Chipola River, FL. Hurst (1969) found little difference between diets of Shoal Bass and Spotted Bass in Halawakee Creek, AL, with both species feeding heavily on fishes and crayfishes. Thus, Spotted Bass may also compete with other Black Basses for food as well as habitat. Due to concerns about the possible trophic interactions among these three congenerics, research was undertaken to 1) determine diet composition and trophic ecology of Largemouth Bass, Shoal Bass, and Spotted Bass, and 2) identify sizes and seasons of diet overlap between native black basses and the introduced Spotted Bass in the Flint River, GA.

Field-Site Description

The Flint River is a major tributary of the Apalachicola River and flows 565 km from its headwaters near Atlanta, GA, to its confluence with the Chattahoochee River at Lake Seminole and drains 21,917 km^2. The upper reaches of the Flint River flows through the Piedmont region of Georgia and is characterized by a series of wide, granite shoals with fast current interspersed with narrower run and pool areas with deeper water and less flow. At the Fall Line, the river drops approximately 125 m in elevation over 80 km. Below the Fall Line, the river becomes similar to a typical Coastal Plain stream, characterized by sandy substrate with greater amounts of woody debris present in the channel; however, this portion of the Flint River also has some limestone outcroppings and greater base flows, associated with springs and the addition of ground water from the Florida aquifer (Opsahl et al. 2007). The Flint River flows over 320 km before being impacted by the first of three mainstem impoundments, making it one of only 42 rivers in the USA with >200 km of unimpeded flow (Benke 1990). A significant fishery has developed for Shoal Bass on the Flint River, GA, which represents the largest remaining intact ecosystem for Shoal Bass in their native range. Spotted Bass were first documented from the Flint River, GA, above Lake Blackshear in 2005, and their population has grown substantially since then (J. Evans, Georgia Department of Natural Resources, Ft. Valley, GA, pers. comm.). Major sport fish occurring in the Flint River include Largemouth Bass, Shoal Bass, *Morone saxatilis* Walbaum (Striped Bass), *Ictalurus punctatus* Rafinesque (Channel Catfish), *Lepomis auritus* L. (Redbreast Sunfish), *Pylodictus olivarus* Rafinesque (Flathead Catfish), and now the introduced Spotted Bass.

Methods

Black basses were collected for diet analyses from seven sites along a 207-km stretch of the unimpounded reach of the Flint River in fall 2007 (September–October), winter 2007 (December), spring 2008 (April), and summer 2008 (July). All fish were collected in 1-hour transects that sampled pool, riffle, and run mesohabitats along the shoreline in each site using a boom-mounted electrofishing boat; diets were collected from every black bass sampled. Fish <200 mm TL were placed in a 300-mg/L solution of MS-222 until the fish expired, then placed on ice; stomachs were excised, and diets were examined from these fish in the laboratory. Stomach contents were removed from larger fish using clear acrylic tubes, and the fish were then released (Van Den Avyle and Roussel 1980).

Food items were identified to the lowest practical taxonomic level (order, suborder, or family for invertebrates, and family, genus, or species for fishes). Total lengths and wet weights of consumed fishes were estimated from standard lengths, vertebrae lengths, or otolith radius using regression equations from this study or from literature sources (Carlander 1969, 1977, 1997; Irwin 2001). All invertebrates were measured for total length; wet weights were predicted from total length using regression equations from Smock (1980) and Tiunova (1997). Mean lengths of each diet group were calculated for each black bass length group-sampling date combination and used in cases where accurate lengths of diet items could not be obtained. Diet items were grouped into categories (Table 1), and diet composition was described using these categories in the relative importance (RI) index developed by George and Hadley (1979), which is designed to reduce biases associated with using a single measure of diet (Wallace 1981). This index assigns equal value to a diet item's percent frequency of occurrence, percent of total weight, and percent of total number of all diet items from a specified sample. The index ranges from 0 to 100, with high values meaning the diet item was more important in a diet than those items with lower values.

To quantify diets, black basses were divided into two length groups: juvenile (<200 mm TL) and subadult (200–299 mm TL). Because Spotted Bass had become established in the Flint River only a few years prior to this study, few Spotted Bass >300 mm were collected; thus, diet overlap was not compared among species for larger fish. To assess potential competition among species and size groups, overlap in diet composition was assessed in each season using the percent resource overlap index (PROI) developed by Schoener (1970). Wallace (1981) suggested that PROI is the best possible measure of diet overlap when prey relative abundance is unknown, and as in that study, we considered values > 60 to indicate high overlap. Diet overlap was only calculated between species that had at least five fish that contained food in each season and size-group combination. An analysis of covariance was used to test differences in slopes of the relation between black bass length (independent variable) and fish prey length (independent variable) across all seasons pooled and across the entire length range of black bass collected during this study (SAS Institute 2003).

Ontogenetic diet shifts were evaluated among the black bass species using logistic regression (SAS Institute 2003) over the entire length range of fish collected for diet analyses. The entire length range of fish was used for these analyses to more accurately describe broad changes in diets as the fish grew (Wheeler and Allen 2003). In this application, the binary response variable was presence or absence of fish prey in the diet of a black bass and was modeled as the log-odds ratio using the logit link function. The linear model used was:

$$\text{logit(p)} = \text{a} + \text{B}_1(\text{TL}) + \text{B}_2(\text{species}) + \text{B}_3(\text{species x TL}),$$

where logit(p) is the log-odds ratio of fish prey presence to absence in the diet, a is the intercept value, TL is the total length (mm) of each fish, species is the main effect of the categorical variable species type (Largemouth Bass, Shoal Bass, or Spotted Bass), species x TL is the interaction between species and TL, and B_1–B_3 are the logistic regression coefficients. Due to the low numbers of large Spotted Bass collected, this analysis was only conducted for Spotted Bass ≤300 mm TL. Predicted probability of piscivory (p) was estimated from logit(p) using:

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

Wald's chi-square statistic was used to test the significance of the individual model terms (SAS Institute 2003). A similar analysis was conducted to assess the probability of fish or crayfish dominating the diet (by weight) of each species. Significance for all statistical tests was judged at $P \leq 0.05$.

Results

A total of 316 Largemouth Bass, 341 Shoal Bass, and 321 Spotted Bass were collected for diet analyses over the four seasons. Of these fish, diet information was obtained for 177 Largemouth Bass, 195 Shoal Bass, and 176 Spotted Bass (i.e., the other fish had empty stomachs). Insects from 7 orders and 9 families, and fish from 8 families and at least 9 genera, were identified in black bass diets (Table 1). Because most fish groups other than cyprinids were easily identified by either the presence of hard bony structures (sunfishes, darters, black basses), or soft anatomical features (shad), most unidentified fish (grouped under "other fish" category) were likely cyprinids. However, for the sake of analysis, they were considered as unidentified fish and grouped accordingly.

Table 1. Classification of diet items used for relative importance index and percent resource overlap index analyses. Diet items were grouped to reflect their approximate taxonomic relationship whenever possible. However, items that could be easily mistaken for each other were grouped based on morphology and maximum adult size. The "Other Fish" category consisted of unidentified fish and rarely eaten species that did not fit into other categories.

Items (order, family, genus, species)	Category
Decapoda	Decapoda
Anisoptera (Gomphidae, Macromiidae) (larvae only)	Odonata
Ephemeroptera (Ephemeridae, Baetidae) (larvae only)	Ephemeroptera
Megaloptera (Corydalidae-Corydalus spp.) (larvae only)	Megaloptera
Odonata (adult), Ephemeroptera (adult), Orthoptera, Hymenoptera, unidentified winged insects	Terrestrial insects
Plecoptera (Perlidae) (larvae only), Hemiptera (Corixidae, Gerridae, Veliidae), unidentified insects	Other insects
Micropterus salmoides, *M. cataractae*, *M. punctulatus*	Bass
Cyprinella callitaenia (R.M. Bailey & Gibbs) (Bluestripe Shiner), *C. venusta* Girard (Blacktail Shiner), unidentified cyprinids, *Gambusia holbrooki* Girard (Eastern Mosquitofish), *Labidesthes sicculus* (Cope) (Brook Silverside)	Cyprinidae
Percina nigrofasciata (Agassiz) (Blackbanded Darter), unidentified darters	Percidae
Lepomis auritus, *L. macrochirus* Rafinesque (Blugill), *L. microlophus* (Günther) (Redear Sunfish), *L. punctatus* (Valenciennes) (Spotted Sunfish), *L. gulosus* (Cuvier) (Warmouth), unidentified sunfish	Sunfish
Dorsosoma cepedianum (Lesueur) (Gizzard Shad), *D. petenense* (Günther) (Threadfin Shad)	Shad
Ictalurus punctatus, *Minytrema melanops* (Rafinesque) (Spotted Sucker), unidentified fish	Other fish

Diet composition and overlap among species

Juvenile fish. Diets of juvenile Largemouth Bass were dominated by fish in all seasons (Table 2). Sunfishes were important components of juvenile Largemouth Bass in all seasons except for summer, when virtually every fish category was found in their diets except shad. Juvenile Largemouth Bass rarely consumed insects except in spring, when juveniles of all three species consumed large numbers of mayflies, particularly those in the family Baetidae. In contrast, diets of juvenile Shoal Bass and Spotted Bass were much less piscivorus. Juvenile Shoal Bass diets were dominated by insects in all seasons but winter, when diets of all 3 species were composed primarily of fish (Table 2). The primary insect group eaten by juvenile Shoal Bass were mayflies, followed by odonates. Hellgrammites (Megaloptera) were found in the diets of juvenile Shoal Bass in winter, spring, and summer, but composed an important part of their diets only in winter. These insects were not found in the diets of juveniles of the other black basses. Primary fish consumed by juvenile Shoal Bass were cyprinids and darters; high numbers of unidentified fish in winter and summer were also likely cyprinids, as discussed above. Diets of juvenile Spotted Bass were varied, highly piscivorus in fall and winter and highly insectivorous in spring and summer (Table 2). Similar to Shoal Bass, cyprinids and mayflies frequently appeared to be important components of juvenile Spotted Bass diets. Terrestrial insects were eaten more by Spotted Bass than juveniles of either of the other species. Unlike Shoal Bass, odonates were generally a minor component of juvenile Spotted Bass diet. Overall, diet overlap among the species was moderate in most seasons; however, all 3 instances of significant overlap involved Spotted Bass (Table 2). Highest overlap between juvenile black bass diets was observed between Shoal Bass and Spotted Bass in summer.

Subadult fish. Diets of subadult Largemouth Bass were similar to those of juveniles, and were heavily dominated by fish, particularly sunfishes (Table 3). Crayfish were periodically important in diets of subadult Largemouth Bass; however, insects were rarely eaten. Shad were only important in their diets in winter. Cyprinids were important components of subadult Largemouth Bass diets in spring and summer. Similar to juveniles, diets of subadult Shoal Bass were much less piscivorous than Largemouth Bass. Crayfish were important components of subadult Shoal Bass diets in all seasons but summer (Table 3). Insects were important components of Shoal Bass diets in fall and summer, primarily terrestrial insects. Hellgrammites were found in the diets of subadult Shoal Bass diets in fall, winter, and spring, but were not consumed by subadults of the other two black bass species. Primary fish consumed by subadult Shoal Bass varied with season among cyprinids, sunfishes, and darters; shad were rarely eaten. Once again, diets of subadult Spotted Bass were generally more piscivorous than subadult Shoal Bass, but less than subadult Largemouth Bass (Table 3). Crayfish were also important components of subadult Spotted Bass diets in all seasons but spring. Importance of insects varied in Spotted Bass diets, from 7% in fall to 39% in winter. Mayflies dominated the diets of subadult Spotted Bass in winter

Table 2. Relative importance index and percent resource overlap index (PROI) values for diet items found in juvenile Largemouth Bass (LMB), Shoal Bass (SHB), and Spotted Bass (SPB) collected from the Flint River, GA, over four seasons. Numbers in parentheses denote number of fish collected in each length group with food. PROI comparisons were only made if at least five fish of each species were collected with food; values ≥60 were considered significant overlap. Values represented by a '-' denote this diet item was not found in any species within this season.

	Fall 2007			Winter 2007			Spring 2008			Summer 2008		
Diet	LMB (11)	SHB (11)	SPB (32)	LMB (4)	SHB (6)	SPB (18)	LMB (15)	SHB (24)	SPB (35)	LMB (13)	SHB (19)	SPB (42)
Decapoda	0.00	24.93	3.72	0.00	0.00	8.47	0.00	18.33	10.66	9.35	11.09	1.61
Ephemeroptera	0.00	37.73	33.85	0.00	0.00	22.19	22.41	28.55	20.27	2.83	34.12	36.68
Odonata	0.00	30.75	3.48	0.00	0.00	7.56	3.32	14.08	9.96	0.00	2.90	3.99
Megaloptera	-	-	-	0.00	19.58	0.00	0.00	3.00	0.00	0.00	2.31	0.00
Terrestrial insects	5.32	0.00	1.68	-	-	-	0.00	0.00	16.55	0.00	5.93	25.31
Other insects	0.00	0.00	1.31	0.00	10.41	0.00	5.79	0.00	5.46	20.30	5.30	1.41
Bass (*Micropterus* spp.)	-	-	-	-	-	-	-	-	-	8.62	0.00	1.23
Cyprinidae	34.58	0.00	33.71	20.70	13.29	22.28	11.79	0.00	14.84	14.77	19.46	5.66
Percidae (*Percina* spp.)	8.47	0.00	4.91	-	-	-	3.39	10.07	3.59	9.88	0.00	6.89
Sunfish (*Lepomis* spp.)	33.85	0.00	0.00	44.80	12.94	3.34	39.84	8.82	4.51	10.74	1.76	2.40
Shad (*Dorosoma* spp.)	-	-	-	0.00	0.00	8.29	0.00	5.15	0.00	-	-	-
Other fish	17.77	6.59	17.35	34.50	43.78	27.87	13.45	12.01	14.15	23.51	17.13	14.81
PROI: LMB-SHB		7			n/a			50			51	
PROI: LMB-SPB		58			n/a			62			37	
PROI: SHB-SPB		48			45			61			68	

Table 3. Relative importance index and percent resource overlap index (PROI) values for diet items found in subadult Largemouth Bass (LMB), Shoal Bass (SHB), and Spotted Bass (SPB) collected from the Flint River, GA, over four seasons. Numbers in parentheses denote number of fish collected in each length group with food. PROI comparisons were only made if at least five fish of each species were collected with food; values ≥60 were considered significant overlap. Values represented by a '-' denote this diet item was not found in any species within this season.

	Fall 2007			Winter 2007			Spring 2008			Summer 2008		
Diet	LMB (22)	SHB (25)	SPB (6)	LMB (13)	SHB (26)	SPB (12)	LMB (22)	SHB (20)	SPB (9)	LMB (23)	SHB (12)	SPB (13)
Decapoda	36.51	24.79	28.31	7.62	32.98	18.67	20.30	29.08	17.75	6.01	15.48	33.23
Ephemeroptera	11.11	1.66	0.00	0.00	11.42	35.87	0.00	3.82	9.43	2.13	0.00	15.68
Odonata	3.72	8.06	7.44	0.00	0.00	3.00	0.00	5.81	6.65	0.00	3.74	0.00
Megaloptera	0.00	10.72	0.00	0.00	4.77	0.00	0.00	6.40	0.00	-	-	-
Terrestrial insects	0.00	15.38	0.00	-	-	-	0.00	0.00	7.03	4.84	33.00	0.00
Other insects	0.00	6.65	0.00	4.33	1.90	0.00	0.00	2.63	0.00	2.15	0.00	0.00
Bass (*Micropterus* spp.)	-	-	-	-	-	-	-	-	-	2.72	0.00	0.00
Cyprinidae	10.33	11.80	14.95	4.50	0.00	8.37	19.26	14.70	33.22	28.37	11.96	10.77
Percidae (*Percina* spp.)	5.64	0.00	0.00	5.39	2.16	3.99	0.00	14.15	8.36	0.00	0.00	5.97
Sunfish (*Lepomis* spp.)	30.08	5.35	15.01	24.56	28.18	11.68	36.25	7.01	7.04	26.04	27.09	3.49
Shad (*Dorosoma* spp.)	0.00	4.61	21.33	19.95	0.00	9.99	8.00	0.00	0.00	-	-	-
Other fish	2.61	10.97	12.95	33.64	18.59	8.43	16.19	16.41	10.52	27.75	8.72	30.86
PROI: LMB-SHB		49			55			58			58	
PROI: LMB-SPB		61			46			55			50	
PROI: SHB-SPB		65			52			68			39	

and were again important in summer. Fish were periodically important in diets of subadult Spotted Bass, particularly in fall and spring. Primary fish consumed were cyprinids and sunfishes; however, shad was the dominant fish consumed in fall. Similar to juveniles, diet overlap among subadult black basses was moderate; however, all 3 instances of significant overlap were between native basses and Spotted Bass (Table 3).

Ontogenetic changes in diet

Significant diet overlap was rare among size groups and species combinations in most seasons (Table 4). However, PROI values were ≥60 in 5 of 9 comparisons among species and size groups in spring (Table 4). Fish of all three species consumed numerous mayfly naiads during the spring, which likely increased overlap among species and size groups during this season.

Largemouth Bass in both size groups were highly piscivorous (Tables 2, 3), leading to high diet overlap between these groups in most seasons (Table 4). In general, subadult Shoal Bass were much more piscivorus than juvenile Shoal Bass, resulting in low to moderate diet overlap between these groups except in spring, as noted above. Overlap between juvenile and subadult Spotted Bass was low to moderate in fall and summer and high in winter and spring (Table 4). In general, juvenile Spotted Bass consumed more insects than subadult fish, and crayfish were more important in the diet of subadult fish than juveniles (Tables 2, 3). High overlap between these length groups in winter likely resulted from heavy predation on mayflies by both groups, as well as similar consumption of

Table 4. Percent resource overlap index (PROI) values for diet comparisons among size groups for black bass species collected over four seasons in the Flint River, GA. PROI comparisons were only made if at least five fish of each species were collected with food. Values ≥ 60 were considered significant overlap.

		Subadult		
Season	Juvenile	Largemouth Bass	Shoal Bass	Spotted Bass
Fall 2007				
	Largemouth Bass	49	34	43
	Shoal Bass	42	41	39
	Spotted Bass	36	35	35
Winter 2007				
	Largemouth Bass	63	47	29
	Shoal Bass	55	38	29
	Spotted Bass	52	42	62
Spring 2008				
	Largemouth Bass	62	45	46
	Shoal Bass	44	60	60
	Spotted Bass	44	60	67
Summer 2008				
	Largemouth Bass	62	41	56
	Shoal Bass	54	42	56
	Spotted Bass	34	48	46

darters and shad. In spring, predation on crayfish, odonates, sunfishes, and unidentified fish was similar between juvenile and subadult fish, leading to high diet overlap (Tables 2, 3).

Logistic regression analyses revealed the occurrence of an ontogenetic shift in the diets of all three species. The onset of piscivory occurred at smaller sizes in Largemouth Bass than in the other 2 species, as the likelihood of piscivory was near 90% in the smallest fish collected, compared to 53% for Spotted Bass and 41% for Shoal Bass (Fig. 1). At 100 mm, Largemouth Bass were 7.9 and 3.4 times as likely to have fish in their diet than Shoal Bass or Spotted Bass, respectively (Wald chi-square ≥ 18.4, df = 1, $P < 0.001$). However, the probability of a fish occurring in the diets of Largemouth Bass decreased as fish

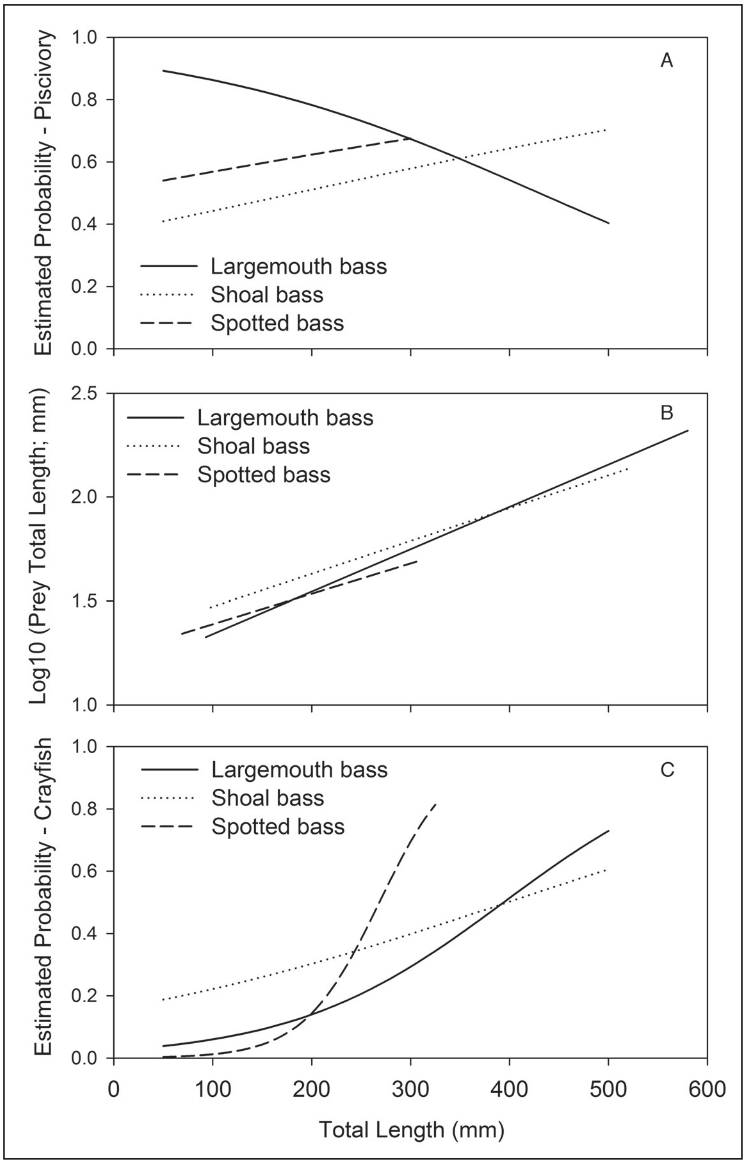

Figure 1. Estimated probability of piscivory versus total length (A), fish prey total length to black bass total length relations for fish found in stomachs (B), and estimated probability of an individual fish exhibiting a crayfish-dominated diet (by weight) (C), for three black bass species in the Flint River, GA. Spotted Bass probabilities were only calculated for fish <300 mm due to small numbers of fish present in the river over that size.

length increased; whereas, this probability increased with fish length for both Spotted Bass and Shoal Bass (Fig. 1). At 200 mm, Largemouth Bass were still 3.5 and 1.9 times as likely to have fish in their diet than Shoal Bass and Spotted Bass, respectively (Wald chi-square ≥ 15.7, df = 1, $P < 0.001$), whereas, the probability of piscivory was similar among species at 300 mm (Wald chi-square ≤ 2.7, df = 1, $P > 0.10$). Shoal Bass and Largemouth Bass were equally likely to have fish in their diets at approximately 350 mm TL, but above that length, Shoal Bass were more likely to contain fish in their diets than Largemouth Bass (Fig. 1). All three black bass species consumed larger fish prey as TL increased (Fig. 1). Based on analysis of covariance, slopes of the prey length-bass length relations were different between Largemouth Bass and the other two species ($F = 4.94$; df = 2, 423; $P < 0.05$), meaning that as bass length increased, the length of fish prey consumed by Largemouth Bass increased at a greater rate than Spotted Bass or Shoal Bass (Fig. 1). In contrast, Shoal Bass and Spotted Bass increased their size of fish prey consumed at similar rates as bass size increased; however, Shoal Bass consumed larger prey than Spotted Bass across all fish lengths ($F = 4.93$; df = 2, 425; $P < 0.05$).

In general, crayfish became increasingly more dominant than fish in the diets of all three species as fish size increased (Fig. 1). At 100 mm, Shoal Bass were 4.5 and 4.7 times more likely to have diets dominated by crayfish than Largemouth Bass and Spotted Bass, respectively (Wald chi-square ≥ 5.9, df = 1, $P \leq 0.015$). Similarly, at 200 mm, Shoal Bass were 2.7 and 1.9 times more likely to have diets dominated by crayfish than Largemouth Bass and Spotted Bass, respectively (Wald chi-square ≥ 7.5, df = 1, $P \leq 0.006$). However, the rate of increase of crayfish-dominant diets increased with TL at a faster rate in Spotted Bass than Shoal Bass and Largemouth Bass (Fig. 1). At 300 mm TL, Spotted Bass were more than twice as likely to have crayfish-dominant diets than Largemouth Bass (Wald chi-square = 11.3, df = 1, $P = 0.001$). Similarly, the estimated probability of Spotted Bass having crayfish-dominant diets was almost double that of Shoal Bass at 300 mm TL; however, the comparison was not significant (Wald chi-square = 1.5, df = 1, $P = 0.225$), likely due to low sample size of Spotted Bass of that length. The logistic regression model predicted that both Largemouth Bass and Shoal Bass would have equal probabilities of having crayfish-dominant or fish-dominant diets at approximately 400 mm TL; at larger lengths, Largemouth Bass were more likely to have crayfish-dominant diets than Shoal Bass (Fig. 1). In contrast, Spotted Bass were equally likely to have crayfish- or fish-dominant diets at approximately 250 mm TL.

Discussion

Diets of native Largemouth Bass and Shoal Bass exhibited clear evidence of resource partitioning, as would be expected by two sympatric species that coevolved. Largemouth Bass were highly piscivorus in all seasons, which is typical for this species (Long and Fisher 2000, Scalet 1977, Timmons and Pawaputanon

1982). In contrast, Shoal Bass diets were diverse and often dominated by insects. Food habits of Shoal Bass are not well known; however, Wheeler and Allen (2003) also observed high predation on insects, particularly mayflies, by Shoal Bass in the Chipola River, FL. Occurrence of >200 mayfly naiads was commonly observed in individual stomachs of small Shoal Bass in the Chipola River; such mayfly abundance was never observed in stomachs of similar-sized Largemouth Bass (Wheeler and Allen 2003). Similarly, mayfly naiads were the most important item in the spring and summer diets of juvenile Shoal Bass in the Flint River, with 200–300 naiads found in the stomachs of individual fish. However, unlike the Chipola River study, Largemouth Bass juveniles also preyed upon mayflies to a high degree in spring, but not in summer. Apparently, both species of black bass used this food resource during periods of high mayfly naiad abundance, but Shoal Bass appeared to be more adapted to an insect diet than Largemouth Bass in the Flint River.

As fish size increased in the Flint River, Largemouth Bass diet shifted from fish to crayfish, until crayfish became the dominant food item of fish >400 mm. Crayfish was generally more important in diets of juvenile and subadult Shoal Bass than Largemouth Bass, but the likelihood of Shoal Bass piscivory increased with fish size. However, the probability of Shoal Bass having a crayfish-dominant diet also increased with fish size. The difference in the patterns between the congeneric species indicated that while Largemouth Bass shifted their diets from fish to crayfish as they grew, fish remained an important component of large Shoal Bass diets, even though the chances of crayfish dominating the diets of individual fish were higher for big fish than smaller fish. Similar diet shifts have been observed in black basses by researchers working on rivers in the southeastern USA (Schramm and Maceina 1986, Wheeler and Allen 2003). In the Chipola River, FL, diets of both Shoal Bass and Largemouth Bass became dominated by crayfish as fish size increased; however, Largemouth Bass made the transition faster and at smaller sizes than Shoal Bass (Wheeler and Allen 2003). Largemouth Bass in the Chipola River had an equal probability of having a crayfish- or fish-dominated diet at 239 mm, while this did not occur for Shoal Bass until 413 mm. In contrast, both Largemouth Bass and Shoal Bass reached equal probability at approximately 400 mm in the Flint River. Because the Flint River is a much larger river than the Chipola River, it is conceivable that a higher abundance of prey fishes existed in the Flint River, allowing Largemouth Bass to delay switching to crayfish until later. However, the Chipola River is known to have dense populations of crayfish (D. Krause, Florida Fish and Wildlife Conservation Commission, Holt, FL, pers. comm.), which may have influenced diet selection of *Micropterus* species inhabiting that river.

Reasons for these diet shifts are unknown, especially because crayfish are lower in caloric density than fishes (Pope et al. 2001), and would therefore appear to be a less-preferred food (Diana 1995). One potential explanation for this switch is that there may be a relative lack of large-bodied fishes available in the Flint River for Black Bass predation, making crayfishes a more preferred prey than would have been expected based on caloric value alone. Crayfishes are commonly abundant in lotic environments (Charlebois and Lamberti 1996), and the Flint River is no exception. Habitat use of black basses may also play a part in diet choice. Radio-tagged Largemouth Bass in the Flint River were frequently found in slower habitats characterized by sandy substrate and woody debris; whereas, radio-tagged Shoal Bass were commonly found in fast-flowing, rocky habitats (Goclowski 2010). During collection of black basses for diet analysis in the Flint River, rocky shoal areas with current had noticeably higher overall fish abundance than slower, sandy areas. Thus, Shoal Bass may be more able to maintain higher rates of piscivory at large sizes than Largemouth Bass due to variable prey abundance and availability across the preferred habitats of black basses.

Regardless of the diet shifts observed for both species, overlap in food habits was relatively low to moderate between the two native congenerics in the Flint River. In contrast, diet overlap of adult Largemouth Bass and Shoal Bass was found to be high in the Chipola River, FL, due to high predation on crayfish by both species (Wheeler and Allen 2003). Although a shift to crayfish was observed for both species in the Flint River, Shoal Bass diets continued to also include insects and fish, which lessened the potential for competition between the two species.

Diets of the introduced Spotted Bass appeared to occupy an intermediate position between the two native black bass species in the Flint River, but were generally more similar to Shoal Bass. Like Shoal Bass, diets of juvenile Spotted Bass were dominated by insects, except in winter when fish became more important. Spotted Bass are typically insectivores in lotic environments (Ryan et al. 1970, Scott and Angermeier 1998, Smith and Page 1969) and occupy shallow rocky shoals (Horton and Guy 2002, Tillma et al. 1998, Vogele 1975), likely filling a similar niche in their native range that Shoal Bass do in the Flint River. Also like Shoal Bass, Spotted Bass diet in the Flint River was extremely diverse. High diversity in Spotted Bass diet has been reported by other researchers working in lotic environments (Ryan et al. 1970, Scalet 1977, Scott and Angermeier 1998, Smith and Page 1969) and appears to be characteristic of this species. Like juveniles, subadult Spotted Bass in the Flint River had a diverse diet; however, crayfish and fish became more important components of their diet at this size. Despite the high diversity observed in Spotted Bass and Shoal Bass diets, significant overlap between these two species was common, occurring in 4 of 8 comparisons across size groups and seasons. In contrast, diet overlap between Spotted Bass and Largemouth Bass was only observed in 2 of 7 comparisons.

Occurrence of fish in Spotted Bass diets increased with fish size in a similar manner to Shoal Bass, although the probability of having a fish in their diet was consistently higher for Spotted Bass than Shoal Bass across all lengths examined. In contrast, while all black basses consistently consumed larger fish as they grew, Shoal Bass consistently consumed larger fish than Spotted Bass at the same lengths. Thus, a typical Spotted Bass in the Flint River was more likely to be piscivorous, but consumed smaller fish, than a typical Shoal Bass, which was corroborated by higher predation on cyprinids and darters by Spotted Bass compared to Shoal Bass. However, the diets of larger Spotted Bass were dominated by crayfish: by 300 mm, they were 80% likely to have a crayfish-dominant diet. Like Shoal Bass, radio-tagged Spotted Bass were often found associated with shoal habitat in the Flint River (Goclowski 2010), areas in which relative abundance of prey fish was high. Despite this, Spotted Bass continued to consume crayfish at a high rate, especially at larger sizes, which may indicate that this species is especially adapted to consume crayfish. Crayfish are well known to be a primary food item of adult Spotted Bass in lentic and lotic environments (Long and Fisher 2000, Ryan et al. 1970, Scalet 1977, Scott and Angermeier 1998), and thus Spotted Bass have the potential to become a significant competitor for this resource with either native species if resources become limiting.

Competition is known to be a major driving force structuring fish communities (Fausch and White 1981, Morita et al 2004, Stein et al. 1995). While most native fish assemblages have evolved mechanisms to reduce competition for food and space (Harmelin-Vivien et al. 1989, Werner and Hall 1979, Werner et al. 1977), the introduction of a new species that has not evolved with the native fishes creates an opportunity for conflict, which may result in negative effects on native species (Huckins et al. 2000, Morita et al. 2004, Moyle et al. 2003). Transfers of black basses from their native range into new areas have been occurring for a long time, but we are only now beginning to realize the ecological consequences of these actions (Jang et al. 2006, Littrell et al. 2007, Moyle et al. 2003). Over the last ten years, the illegal introduction of Spotted Bass outside their native range has reached epidemic proportions. Originally restricted to Gulf coast drainages, Spotted Bass are now found in almost every river system in Georgia, as well as most Atlantic slope drainages in South Carolina and North Carolina (Barwick et al. 2006; J. Rice, North Carolina State University, Raliegh, NC, pers. comm.). The effects of these introductions have not been fully documented; however, evidence exists to suggest that they may be able to hybridize with or outcompete some of the endemic black bass species found in the southeastern USA, especially those that are obligate lotic species, such as Shoal Bass (Barwick et al. 2006, Stormer and Maceina 2008).

In the Flint River, food habits of introduced Spotted Bass were clearly similar to that of native Shoal Bass. However, because little is known about the relative predation efficiency of either species, nor are data available on prey abundance in the Flint River, the ultimate long-term effects of this introduction on native Shoal Bass are impossible to predict. Also, the fact that few adult Spotted Bass were available for diet analyses means that the potential of diet overlap and potential for trophic competion among larger individuals of these species remains unknown. Largemouth Bass, Spotted Bass, and Shoal Bass have apparently been able to coexist in the Ocmulgee River, GA, since the introduction of Spotted

Bass approximately ten years prior to the Flint River introduction (J. Evans, pers. comm.). Given that these two rivers are similar in size and physiography, coexistence of these species is likely in the Flint River. However, negative interactions among native and introduced species may be more likely in smaller systems where habitat and food may be more limiting, such as in tributary streams of the Chattahoochee River in Alabama where Shoal Bass have been replaced by Spotted Bass over the last 30 years (Stormer and Maceina 2008). The results of this study were based on only one year of data, thus these findings should be interpreted with caution. However, this study has indicated that concerns about the trophic impacts of non-native Spotted Bass on Shoal Bass may be warranted, particularly during seasonal periods of limited prey availability.

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