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James M. Long & William L. Fisher

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James M. Long[a]
Oklahoma Cooperative Fish and Wildlife Research Unit
Department of Zoology
Oklahoma State University
Stillwater, OK 74078 USA
and
William L. Fisher
U.S. Geological Survey, Biological Resources Division
Oklahoma Cooperative Fish and Wildlife Research Unit
Department of Zoology, Oklahoma State University
Stillwater, OK 74078 USA

ABSTRACT

We quantified the diets of juvenile and adult largemouth bass (*Micropterus salmoides*), smallmouth bass (*M. dolomieu*), and spotted bass (*M. punctulatus*) in Skiatook Lake, Oklahoma in 1997 and 1999 to assess inter-annual and size-related differences in food resource use. The diets of juvenile and adult largemouth bass consisted mainly of fish, but juveniles consumed a significant number of dipterans during both years. Smallmouth bass and spotted bass adult diets were similar to each other in both years; crayfish and fish were the predominant food items. Juvenile smallmouth bass and spotted bass were mainly insectivorous with fish and crayfish also making up a proportion of the diet. Mean diet overlap was greater in 1999 compared to 1997. These findings are consistent with the expanding population hypothesis that predicts increased niche overlap.

INTRODUCTION

Largemouth bass (*Micropterus salmoides*), smallmouth bass (*M. dolomieu*), and spotted bass (*M. punctulatus*) are ecologically similar species that inhabit the littoral zone of lakes and reservoirs and often occur sympatrically throughout the midwestern and southern regions of the United States. They are the most widespread of all the black bass species and are economically important as sportfishes (Robbins and MacCrimmon 1974). Consequently, there have been many studies on resource use by these species (Aggus 1972, Lewis 1976, Farquhar and Whiteside 1995, Scott and Angermeier 1998, Ward and Newmann 1998). Information on resource use provides insight into niche relationships among potentially competing species. Food is one of the resources that ecologically-similar species partition to avoid competition (Schoener 1974a). Partitioning of food resources is especially important for predators who feed on prey that are large in proportion to their own body size (Schoener 1974b), such as black bass.

Although the food habits of largemouth bass, smallmouth bass, and spotted bass are well known, most studies have examined the diets of these species in allopatry. Heidinger (1975) concluded that largemouth bass was mainly piscivorous, but also

[a] Current Address: South Carolina Department of Natural Resources, Freshwater Fisheries Research, 1921 VanBoklen Road, Eastover, SC 29044

consumed crayfish. Ward and Neumann (1998) found that the relative importance of fish to the diet of largemouth bass in Connecticut was highest during all seasons in Pickerel Lake, but that these results differed from those fish in Lake Lillinonah where insects dominated the diet. Coble (1975) reported that fish and crayfish were the primary prey of smallmouth bass. Farquhar and Whiteside (1995) found that smallmouth bass in Blanco River, Texas ate a greater proportion of aquatic insects than fish or crayfish. Additionally, they found that largemouth bass consumed fish more than any other prey item, followed by aquatic insects and crayfish. In contrast, spotted bass reportedly fed more heavily on crayfish and insects than on fish (Vogele 1975). Lewis (1976) found that the predominant prey item of spotted bass in West Virginia lakes was crayfish in Bluestone Reservoir and fish in Sutton Reservoir. These studies demonstrated that all three black bass species utilize similar prey resources, but that prey use is phenotypically plastic. However, they provide little information about how these three species differ in prey use when in sympatry.

Of the few studies that have examined prey use among sympatric black bass species, most have not documented prey use among all three species. Scott and Angermeier (1998) studied resource overlap between largemouth bass and spotted bass in the New River, Virginia and found prey overlap to be high; however, they concluded that habitat was the most significant variable that segregated these two species. Farquhar and Whiteside (1995) examined prey use among largemouth bass, smallmouth bass, and Guadalupe bass in the Blanco River, TX. They found that smallmouth bass and Guadalupe bass diets were more similar to each other than either were to largemouth bass. Aggus (1972) examined the diets of sympatric largemouth bass, smallmouth bass, and spotted bass in Bull Shoals Lake, Arkansas. He found that largemouth bass ate mostly fish, smallmouth bass mostly insects, and spotted bass mostly crayfish. Although differences in frequency of occurrence of fish in the diets of the three species were not statistically significant, differences in the frequency of crayfish between spotted bass and smallmouth bass, and insects between largemouth bass and smallmouth bass were significant.

A limitation of these studies on prey use among black bass species is that most reported the identities of prey items to very specific levels, yet they analyzed grouped data sets that consequently exhibited low statistical power. For example, Aggus (1972) identified prey items to the lowest taxonomic level (number of categories not reported) yet grouped and analyzed only five categories. Furthermore, Lewis (1976) and Farquhar and Whiteside (1995) did not statistically analyze their data, which consisted of six and five prey categories, respectively.

Our objective was to describe and compare the diets of sympatric populations of largemouth bass, smallmouth bass, and spotted bass in Skiatook Lake, Oklahoma to assess patterns in food resource use between two years. We accounted for the variability in food use that occurred among these species due to ontogenetic diet shifts by comparing similar size groups of each species. Finally, we used a multivariate method (canonical correspondence analysis) that considered all categories of identified prey.

METHODS AND MATERIALS

Study Area

Skiatook Lake is a 4,266-ha flood control impoundment of Hominy Creek in north-central Oklahoma that was formed in 1984. The lake has a mean depth of 9.7 m and a shoreline development index of 11.3. The upper end of the reservoir is more turbid than the lower end, with average spring Secchi depths of 0.1 m and 1.2 m, respectively (Long et al. 1999). The top of the conservation pool is 217.6 meters above mean sea level. Sportfish species in the lake consist mainly of largemouth bass, smallmouth bass, spotted bass, sunfish (*Lepomis* spp.), hybrid striped bass (*Morone saxatilis* X *M. chrysops*), walleye (*Stizostideon vitreum*), channel catfish (*Ictalurus punctatus*), and flathead catfish (*Pylodictis olivaris*).

Fish and Stomach Content Collection

We collected black bass from Skiatook Lake in the spring of 1997 and 1999 by electrofishing at night. Fish were captured and stored on ice. The following day, fish were identified, measured for total length, and dissected to remove all prey items from the stomach. Prey items were identified and enumerated. When possible, we identified remains of fish to genus, insects to order, and other invertebrates to class.

Since black bass exhibit ontogenetic diet shifts, resulting in larvae, juveniles, and adults feeding on different prey items (Matthews 1998), we separated the species into two size groups: juveniles and adults. Larvae were not vulnerable to our electrofishing gear and thus were not collected. Juveniles were those fish that were spawned in the previous year and vulnerable to our electrofishing in the spring. We classified each species as either juvenile or adult according to the respective mean sizes of age-one fish in Oklahoma waters, as reported by Carlander (1977). Thus, largemouth bass less than 205 mm, smallmouth bass less than 182 mm, and spotted bass less than 171 mm were considered juveniles.

Statistical Analyses

We used canonical correspondence analysis (CCA) with the CANOCO 4.0 (ter Braak and Šmilauer 1998) program to examine differences in diet among juveniles and adults of the three black bass species for each year. Canonical correspondence analysis is a multivariate, direct gradient analysis that ordinates species according to measured environmental variables (ter Braak 1986). We ordinated and ascertained the degree of association of prey items to the size classes of each species.

For the CCA, we used a square root transformation on the raw prey data to minimize the effects of large numbers of individuals in any one stomach. We also downweighted rare prey items (ter Braak and Šmilauer 1998). We conducted Monte Carlo randomization tests for the first and all combined canonical axes, with 1000 permutations, to determine the probability that the correlations among species occurrences could occur by chance alone.

Since the raw prey data contained many zeros and were not normally distributed, we normalized them with a square root plus one transformation and calculated Pearson correlation coefficients between the transformed prey data and the two size classes of the three black bass species for both years. We also calculated Pianka's (1973) niche overlap values for all possible pairs of size classes and species combinations for both years. This index ranges from 0 (no common resources) to 1 (complete resource overlap). We used a t-test to test whether the mean overlap values were the same between the two years.

RESULTS

Largemouth Bass Diet

Juvenile largemouth bass diet was significantly correlated with dipterans ($r = 0.219$) in 1997 and with dipterans ($r = 0.238$) and unidentified fish ($r = 0.160$) in 1999 (Table 1). Additionally, we found a significant, negative correlation for juveniles with crayfish ($r = -0.215$) in 1999. Adult largemouth bass diet, in contrast, was correlated with unidentified fish ($r = 0.300$) in 1997 and odonates ($r = 0.188$) in 1999. Adult largemouth bass was the only species to consume odonates in 1999, thus the significant correlation, but exhibited a diet mostly of unidentified fish and *Lepomis* spp.

Smallmouth Bass Diet

Juvenile smallmouth bass diet was correlated with unidentified insects in both years ($r = 0.308$ and 0.240, respectively; Table 1) although, numerically, they consumed more unidentified fish. Adult smallmouth bass diet was correlated with coleopterans in 1997 and 1999 ($r = 0.226$ and 0.174 respectively) and miscellaneous items ($r = 0.283$; miscellaneous items were usually some sort of fishing lure) in 1997. However, in 1997, adult smallmouth bass diet consisted mainly of crayfish and unidentified fish. Smallmouth bass was the only species to eat *Percina* spp. as adults and isopods as juveniles and adults.

Table 1. Number of stomachs with prey items among juveniles and adults of largemouth bass (LMB), smallmouth bass (SMB), and spotted bass (SPB). Numbers in parentheses indicate sample size and an * indicates significance at the $\alpha = 0.05$ level for the correlation analyses. NA indicates that the prey item was not found in any of the stomach contents for that sample year.

	Juvenile LMB		Adult LMB		Juvenile SMB		Adult SMB		Juvenile SPB		Adult SPB	
Prey Item	1997 (6)	1999 (16)	1997 (15)	1999 (24)	1997 (5)	1999 (5)	1997 (9)	1999 (46)	1997 (26)	1999 (8)	1997 (26)	1999 (57)
Mollusca	0	NA	0	NA	0	NA	0	NA	0	NA	1	NA
Decapoda	0	0*	1	4	1	0	1	15	2	0	16*	29*
Lepomis spp.	0	3	2	5	0	0	1	7	1	2	1	7
Micropterus spp.	NA	0	NA	1	NA	0	NA	1	NA	0	NA	0
Dorosoma spp.	1	0	2	1	0	0	1	2	0	0	0	1
Percina spp.	NA	0	NA	0	NA	0	NA	1	NA	0	NA	0
Pimepheles spp.	NA	0	NA	1	NA	0	NA	0	NA	0	NA	1
Unidentified Fish	2	9*	9*	12	2	2	2	15	6	3	5	17
Amphipoda	0	NA	0	NA	0	NA	0	NA	1	NA	0	NA
Isopoda	NA	0	NA	0	NA	1	NA	1	NA	0	NA	0
Ephemeroptera	NA	1	NA	1	NA	1	NA	3	NA	1	NA	3
Trichoptera	0	NA	0	NA	1	NA	0	NA	8*	NA	2	NA
Diptera	3*	3*	0	1	1	1	1	1	9*	1	1*	3
Coleoptera	0	0	0	0	0	1	2*	4*	3	0	1	1
Odonata	0	0	0	1*	0	0	0	0	4*	0	0	0
Hemiptera	NA	0	NA	0	NA	0	NA	0	NA	0	NA	1
Unidentified Insect	0	0	1	0	1*	1*	1	1	7	0	2	1
Arachnida	0	NA	0	NA	0	NA	0	NA	2*	NA	0	NA
Miscellaneous	0	1	0	0	1	1	1*	4	1	2*	2	3

Spotted Bass Diet

Juvenile spotted bass diet was significantly correlated with dipterans ($r = 0.302$), trichopterans ($r = 0.341$), odonates ($r = 0.336$), and arachnids ($r = 0.235$) in 1997 but shifted to miscellaneous food items in 1999 ($r = 0.163$; Table 1). Numerically, the diet of juvenile spotted bass was also made up of unknown fish in 1997 and 1999 and of unidentified insects in 1999. Adult spotted bass diet was dominated by crayfish in 1997 and 1999 ($r = 0.499$ and 0.305 respectively) and exhibited a significant, negative correlation with dipterans in 1997 ($r = -0.220$).

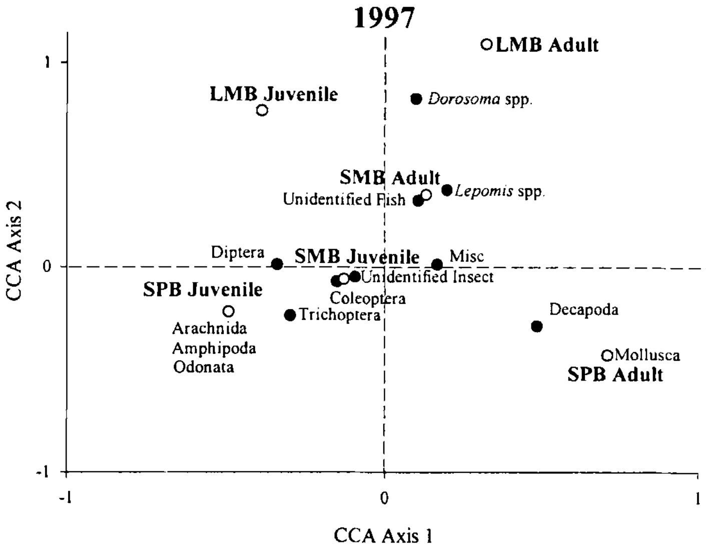
Prey Overlap

The distribution of prey items among all three black bass species and size classes was significantly different from random for the first CCA axis ($P = 0.014$) and all combined axes ($P = 0.005$) in 1997 but not for either axis in 1999 ($P = 0.156$ and 0.366 respectively). The first and second axes of a CCA (Figure 1) represented the most important gradients that influenced the distribution of the prey items. The first CCA axis explained 39.4% of the variation in prey item distribution among the two size classes of the three species in 1997 (eigenvalue = 0.365) and 52.0% of the variation in 1999 (eigenvalue = 0.167) and separated prey items of juveniles from adults. The second CCA axis explained an additional 30.0% of the variation in 1997 (eigenvalue = 0.279) and 24.9% of the variation in 1999 (eigenvalue = 0.080) and separated prey items of juvenile and adult largemouth bass from both size classes of the other two black bass species. The third CCA axis was not interpreted (or plotted) for either year because the amount of explainable variation for this axis was low (14.7% in 1997 and 12.7% in 1999).

The proximity of a particular prey item to any predator in a CCA is related to the magnitude of association between the prey and predator (ter Braak 1995; Figure 1). For example, in 1997 molluscs were in close proximity to spotted bass adults and were only found in the stomachs of that species. Also in 1997, arachnids, amphipods, and odonates were found only in the stomachs of juvenile spotted bass and were found in close proximity to this size and species in the CCA. Decapods (crayfish) were located between adults of spotted bass and smallmouth bass in 1997 and 1999, indicating that this was an important prey item for both of these species. Moreover, Figure 1 illustrates the groups of predators with similar diets. For example, the two size classes of smallmouth bass had very similar diets in 1997, but not in 1999. In 1999, adult spotted bass and smallmouth bass had very similar diets.

Figure 1 also illustrates a difference in the degree of mean diet overlap of all possible pairs of black bass species between 1997 and 1999. In 1997, most prey items were concentrated around black bass species, but in 1999 prey items were clustered near the center of the CCA diagram. Accordingly, mean overlap in 1999 (0.914) was greater than mean overlap in 1997 (0.560; $P = 0.016$).

The similarity of diets among species from the CCA was confirmed with the overlap values (Table 2), with the exception of the high overlap between largemouth bass adults and smallmouth bass juveniles in 1997. The three highest overlap values in 1997 were between juvenile smallmouth bass and spotted bass (0.797), adult smallmouth bass and juvenile smallmouth bass (0.713), and adult largemouth bass and juvenile smallmouth bass (0.699). The three highest overlap values in 1999 were between adult smallmouth bass and adult spotted bass (0.944), adult and juvenile largemouth bass (0.914), and juvenile largemouth bass and juvenile spotted bass (0.890).



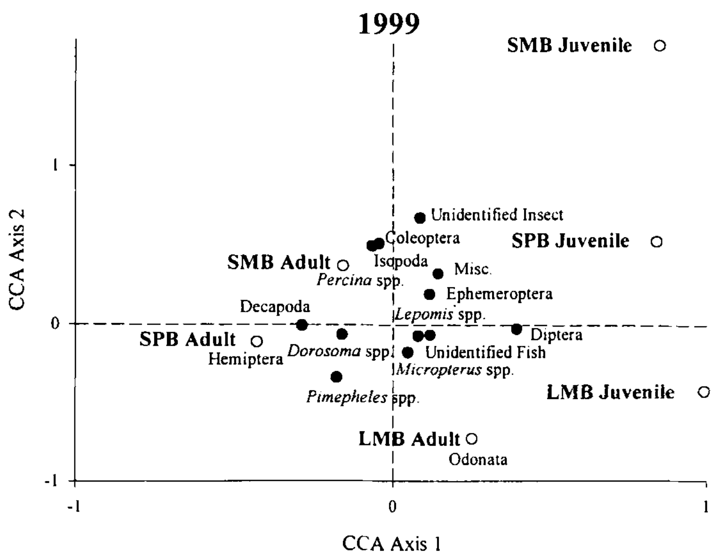


Figure 1. Bi-plots of the first two canonical correspondence analysis axes relating prey items to juvenile and adult largemouth bass (LMB), smallmouth bass (SMB), and spotted bass (SPB) in 1997 and 1999. Solid circles indicate species (prey items) scores and open circles indicate environmental (bass size and species) centroids.

Table 2. Pianka's (1973) resource overlap values for size classes of largemouth bass (LMB), smallmouth bass (SMB), and spotted bass (SPB) in 1997 (upper triangular matrix) and 1999 (lower triangular matrix).

	Adult LMB	Juvenile LMB	Adult SMB	Juvenile SMB	Adult SPB	Juvenile SPB
Adult LMB	1.000	0.560	0.672	0.699	0.395	0.418
Juvenile LMB	0.914	1.000	0.571	0.624	0.202	0.639
Adult SMB	0.871	0.705	1.000	0.713	0.527	0.623
Juvenile SMB	0.595	0.724	0.594	1.000	0.638	0.797
Adult SPB	0.755	0.540	0.944	0.409	1.000	0.381
Juvenile SPB	0.797	0.890	0.695	0.725	0.508	1.000

DISCUSSION

We found largemouth bass in Skiatook Lake to be mainly piscivorous, which confirms the results of Aggus (1972), Heidinger (1975), and Ward and Neumann (1998). However, we found that juvenile and adult largemouth bass in Skiatook Lake had similar diets. Wanjala et al. (1986) reported similar diets for three size classes of largemouth bass (<25 cm, 25.1 - 30.5 cm, and 30.6 - 55.9 cm); all size classes consumed predominately shad. Although juvenile largemouth bass exhibited positive correlations with dipteran prey in both years, the frequency of occurrence of fish prey was numerically greater than that of insect prey.

Smallmouth bass and spotted bass in Skiatook Lake both had similar diets within each size class. Adults of these two species consumed mostly crayfish and insects while juveniles consumed insects and fish. These results also confirm previous studies in that both species eat insects and crayfish (Aggus 1972, Coble 1975, Vogele 1975, Lewis 1976, Farquhar and Whiteside 1995, Scott and Angermeier 1998).

Our results also demonstrate differences in prey partitioning between years. Resource overlap for prey was significantly greater in 1999 than in 1997, resulting in a switch from a more specific feeding mode in 1997 to a more generalist feeding mode in 1999. Two competing hypotheses of competition and niche segregation can be used to explain these differences. In the first hypothesis, the "superabundant resource hypothesis," resource levels become superabundant and mitigate exploitative competition, which results in increased overlap among species for these resources (Wootton 1990, Matthews 1998). Unpublished data obtained from the Oklahoma Department of Wildlife Conservation refute this hypothesis. Those data show decreasing trends in the relative abundance of the major forage fish of all three black bass species (gizzard shad [*Dorosoma cepedianum*] and bluegill) in Skiatook Lake from 1997 to 1999. Conversely, non-native threadfin shad (*Dorosoma petenense*) recently has been found in this lake and may be increasing in abundance; however, the shad was not documented until 1998 when only two individuals were captured; and in 1999 only 19 individuals were captured (Oklahoma Department of Wildlife Conservation, unpublished data). Therefore, threadfin shad was probably not abundant enough in Skiatook Lake to be a major source of prey in 1999 or to lead to an increased food base and a concomitant increase in diet overlap.

A more probable hypothesis is that an increase in black bass abundance created a condition of increased niche breadth and thus increased diet overlap. Under conditions of an expanding population, niche breadth tends to increase and species utilize a wider variety of resources (Pianka 1994, Matthews 1998). This is termed the "expanding population hypothesis." We documented an increase in the electrofishing catch rates of largemouth bass and smallmouth bass from 1997 to 1999 in Skiatook Lake while the electrofishing catch rates of spotted bass have remained constant (Long et al. 1999). Therefore, total black bass abundance has increased, which has resulted in increased diet overlap. However, the expanding population hypothesis has traditionally been used for models of intraspecific competition. Given the relatedness of these three species, this hypothesis might still be plausible, especially for prey resources. Miller (1975) reported that these three species typically eat the same food items, varying only in the proportions of these items depending on season and year. Based on this information, these three species could be treated as the same "ecological species" with regard to food and this hypothesis would then work as an "intrageneric" model of competition.

Prey partitioning as a means to avoid competition and allow long-term coexistence might be only marginally important for black bass in Skiatook Lake. Other resources, such as habitat, might be partitioned and allow for high prey overlap thereby mitigating competition for prey. Others have noted that habitat tends to be a more significant segregating force than food (Schoener 1974b, Werner and Hall 1977, Janssen 1996, Scott and Angermeier 1998). Unpublished data from Skiatook Lake indicate that smallmouth bass and spotted bass segregate habitat within the lake, resulting in smallmouth bass being more abundant in the lower section of the reservoir and spotted bass being most abundant in the upper section. Thus, significant overlap in prey use among black bass species in Skiatook Lake may be relatively unimportant. Nonetheless, our results provide evidence for the "expanding population hypothesis" leading to increased diet overlap. Furthermore, these results suggest that prey partitioning under these circumstances exists among these three black bass in a manner previously unreported.

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