

# Trophic Dynamics of Juvenile Largemouth Bass in Lucchetti Reservoir, Puerto Rico

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**Abstract:** The feeding dynamics of juvenile largemouth bass (*Micropterus salmoides*) were studied from March 1992 to December 1994 in Lucchetti Reservoir, Puerto Rico. Early piscivory by juvenile bass was aided by constant, but qualitatively variable, availability of fish prey items including threadfin shad (*Dorosoma petenense*), mozambique tilapia (*Tilapia mossambica*), redbreast tilapia (*T. rendalli*), and bluegills (*Lepomis macrochirus*). Threadfin shad was the primary food item for juvenile bass, supplemented by bluegills and tilapias when abundant. Insectivory was high in situations of low fish prey abundance and was accompanied by an increased occurrence of empty stomachs. Two temporal sub-cohorts (early and late) showed different food utilization. Insect consumption by early-hatched bass in Lucchetti Reservoir was consistently higher than for late-hatched bass; piscivory was lower for early-hatched bass than for late-hatched bass. Despite the artificial predator-prey community comprised of exotics, juvenile largemouth bass generally experienced adequate food supplies and rapid growth.

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Largemouth bass have been introduced as a sport fish worldwide (MacCrimmon and Robbins 1975). They were introduced in Puerto Rican reservoirs in 1954 (Erdman 1984) and have become a very popular sport fish (MacCrimmon and Robbins 1975, Corujo-Flores 1989).

Numerous studies have considered the feeding behavior of predatory species based on prey availability, selectivity, vulnerability, and size of prey. All agree that food is one of the most important factors controlling fish growth rates (Timmons et al. 1980, Barwick and Lorenzen 1984, Ryan 1985). For largemouth bass, availability

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of food items and prey size can influence the transition from planktivory to insectivory and from insectivory to piscivory. Inadequate abundance of suitable prey at a given developmental stage will delay the change in prey utilization. This may cause slow growth, increase predation and mortality, and delay the recruitment processes (Timmons et al. 1980, Keast and Eadie 1985, Jackson et al. 1990). Outgrowing prey species is essential for predators to maintain a fish diet. According to Shelton et al. (1979), the maximum size prey that a largemouth bass can consume is approximately 1/3–1/2 of its body length. Thus, in order to maintain a fish diet, bass need to keep growing at a rate 2 to 3 times faster than their prey. However, if the prey outgrow the predator, the availability of food will be limited and a shift to a less beneficial food source will reduce growth rate, jeopardizing survival (Shelton et al. 1979, Timmons et al. 1980, Phillips et al. 1995).

In Puerto Rico, most of the lacustrine freshwater species are introduced. As a result, juvenile bass are likely to experience variable prey supplies in a fish community comprised primarily of exotic predator and prey fishes. Periodic stocking of largemouth bass fingerlings produced at the local fish hatchery has been conducted in most reservoirs on the island. Although the food available for those fingerlings is seldom monitored, the fish are stocked in anticipation that they will survive and be recruited to the fishery.

The objectives of this study were focused on the feeding of juvenile largemouth bass ( $\leq 150$  mm total length, TL) and prey availability in a region outside its natural distribution. Emphasis is placed on the determination of seasonal and juvenile bass size-related patterns of prey utilization and changes in size and species utilization during the year. Stomach content analyses, as well as size frequency distributions of the prey base in electrofishing samples, were used to address these objectives.

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## Methods

Lucchetti Reservoir, an 108-ha water supply reservoir, is located in the southwestern mountains of Puerto Rico, approximately 3 km north of Yauco, at an elevation of 174 m above sea level (Corujo-Flores 1989). Water level fluctuates as much as 17 m annually (Churchill et al. 1995).

In addition to largemouth bass, the fish community includes mozambique tilapia, redbreast tilapia, channel catfish (*Ictalurus punctatus*), bluegill, marbled bullhead (*Ameiurus nebulosus marmoratus*), and the native bigmouth sleeper (*Gobiomorus dormitor*). Stocking has been employed since 1991 to enhance largemouth bass recruitment (Churchill et al. 1995).

Fish were sampled by electrofishing at 3-week intervals from March 1992 to

December 1994. Samples began at dusk at 5 fixed sites representative of littoral habitats. Shoreline electrofishing was conducted using a 240-volt, direct current, hand-held probe following procedures outlined by Jackson and Noble (1995). The sites were sampled with a maximum effort of 30 minutes or a total catch of 75 fish and 10 young largemouth bass ( $\leq 150$  mm TL). Threadfin shad were collected but not included in the counts due to their tendency to school and to be attracted to the light. All fish were held in ice for laboratory processing the following day.

Fish were identified, weighed in grams, and measured to the nearest millimeter TL. Sagittal otoliths and stomachs were removed from each bass. Otoliths were sent to the Age and Growth Laboratory at North Carolina State University to determine age in days. Stomachs were preserved in 10% formalin until analysis.

Bass stomachs were opened and presence or absence of food noted. Food contents were grouped into the following major categories: empty, zooplankton, insects, unidentified insect remains, fish species, unidentified fish remains, and other.

Yearly diet analyses in relation to time of cohort production, size of prey and species utilization were based on the percent frequency of occurrence of each item in food-containing stomachs. Analysis of variance (ANOVA) was used to test for similarity among years in relationships of frequency of occurrence to bass length. Analysis of covariance (ANCOVA) was used to determine yearly differences in the utilization of each particular food item (zooplankton, insects, and fish) in relation to bass length. For these analyses fish were pooled across sampling dates and grouped in 10-mm length classes.

Hatching of bass occurred over a period of approximately 6 months in Lucchetti Reservoir (Gran 1995). Two sub-cohorts were observed in 1992 and 1993. They were classified as early and late sub-cohorts based on hatching periods determined by otolith daily rings (Churchill et al. 1995). The 1994 cohort was arbitrarily divided into early and late sub-cohorts on the basis on size and age. Early and late sub-cohorts were compared by ANOVA to test for similarity among years in relationships of frequency of food item occurrence to bass length and by ANCOVA to determine differences in frequency of occurrence of food components among years.

Forage fish seasonal availability was determined by looking at mean TL and range (for individuals  $<100$  mm TL) in electrofishing samples over time. Abundance was estimated using CPUE based on electrofishing samples. Size composition of the prey base in regular electrofishing samples was used to determine annual fluctuation in prey availability. Statistical significance was accepted at  $P < 0.05$  in all tests.

## **Results**

A total of 1,272 stomachs of juvenile bass were analyzed. Annual sample sizes varied from 560 in 1992 to 316 in 1994 due to variations in sampling conditions and in bass abundance (Alicea 1995). Sample sizes were usually lower from October to April when cohorts were comprised mostly of bass  $> 150$  mm TL. Most stomachs contained food; annual percent empty stomachs ranged from 8.5 in 1994 to 17.9 in 1992.

### General Food Habits and Trends

Zooplankton consumption by juvenile bass was minimal and erratic during the study (Table 1) except in 1992, when zooplankton was common and occurrence reached 9.7% in bass 41–50 mm TL. Zooplankton in stomachs was comprised primarily of cladocerans, with occasional occurrence of copepods. Relative to bass size, zooplankton use was sporadic and did not reflect any pattern in utilization.

Insects occurred regularly in bass stomachs throughout the study (Table 1). Insects in stomachs were primarily immature stages of dipterans, but hemipterans, hymenopterans, and odonates also occurred commonly. Insect utilization showed a slight, but insignificant, decline in relationship to predator size each year. Insectivory was significantly higher in 1992 than in 1993 and 1994 (Fig. 1).

High rates of piscivory occurred throughout the study (Table 1). Piscivory was already high at sizes when bass first appeared in the samples (31–50 mm TL). Percent occurrence of fish in bass stomachs showed a general increase in relation to bass size for all years. Fish utilization differed significantly among years; fish consumption was similar in 1993 and 1994 and significantly higher than in 1992 (Fig. 1).

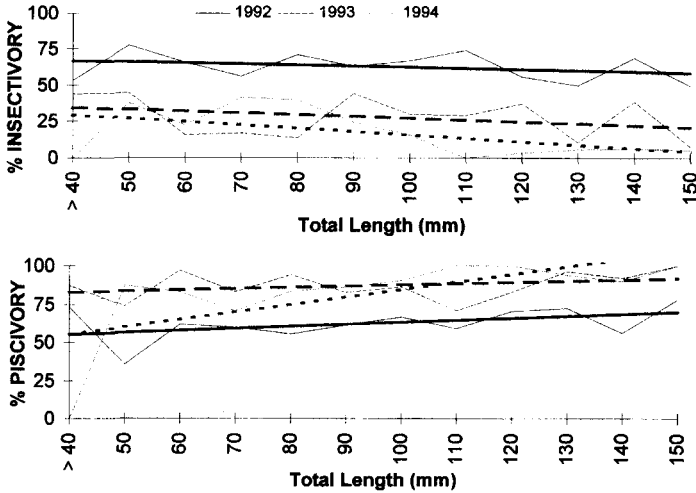
Piscivory and insectivory varied inversely among years. A higher percent occurrence of fish was observed in bass stomachs during 1993 and 1994, when a lower utilization of insects occurred. Likewise, there was a lower incidence of empty stomachs during the years of high piscivory. In 1992, a lower occurrence of fish in the diet was associated with a higher percent occurrence of insects as well as a higher percent of empty stomachs.

### Cohort Timing and Food Habits

*Insects.*—Insectivory was consistently higher for early-hatched bass across the size classes (Fig. 2). Insect utilization by early and late sub-cohorts was significantly

**Table 1.** Percent occurrence of food items in the diet of juvenile largemouth bass by length classes, Lucchetti Reservoir, Puerto Rico. *N* = number of bass stomachs examined.

TL (mm)	1992 <i>N</i> = 560			1993 <i>N</i> = 396			1994 <i>N</i> = 316		
	Zooplankton	Insects	Fish	Zooplankton	Insects	Fish	Zooplankton	Insects	Fish
31–40	6.7	53.3	73.3	0.0	43.8	87.5	0.0	0.0	0.0
41–50	9.7	77.4	35.5	3.7	44.4	74.1	0.0	37.5	87.5
51–60	3.6	65.5	61.8	0.0	15.6	96.9	0.0	22.2	83.3
61–70	5.3	56.0	60.0	4.2	16.7	83.3	0.0	41.2	70.6
71–80	3.1	70.8	55.4	0.0	13.5	94.2	0.0	39.5	83.7
81–90	1.4	62.9	61.4	0.0	43.9	82.9	3.5	24.1	86.2
91–100	0.0	66.7	66.7	0.0	29.7	86.5	0.0	15.6	90.6
101–110	3.7	74.1	59.3	3.2	29.0	71.0	0.0	0.0	100.0
111–120	2.9	55.9	70.6	0.0	37.5	83.3	0.0	3.6	100.0
121–130	0.0	50.0	72.7	0.0	10.7	96.4	0.0	5.9	94.1
131–140	0.0	68.8	56.3	0.0	38.5	92.3	0.0	6.4	90.3
141–150	7.1	50.0	78.6	0.0	7.7	100.0	0.0	5.6	100.0

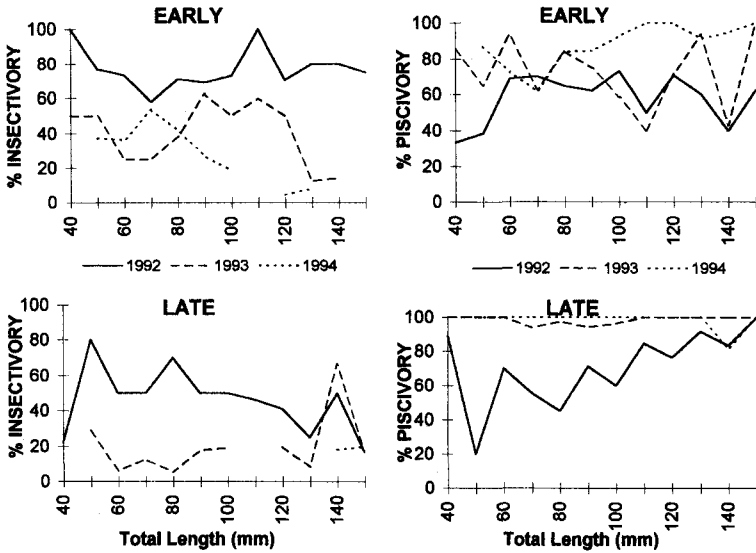


**Figure 1.** Percent frequency-of-occurrence (curves) and linear models (lines) of percent occurrence of insects (top) and fish (bottom) in the diet of juvenile largemouth bass ( $\leq 150$  mm TL), Lucchetti Reservoir, Puerto Rico, 1992–1994. Model Equations—Insects, 1992:  $Y = 0.73X + 67.37$ ,  $R^2 = 0.08$ ; 1993:  $Y = -1.22x + 35.51$ ,  $R^2 = 0.10$ ; 1994:  $Y = -2.26x + 31.50$ ,  $R^2 = 0.27$ . Fish, 1992:  $Y = 1.37X + 53.73$ ,  $R^2 = 0.019$ ; 1993:  $Y = 0.81X + 82.10$ ,  $R^2 = 0.10$ ; 1994:  $Y = 4.90X + 50.35$ ,  $R^2 = 0.42$ .

different for cohorts produced in 1992 and 1993. No significant difference was observed between sub-cohorts in 1994 ( $P = 0.48$ , Fig. 2), but data were limited for the late 1994 cohort. In 1994, insect consumption by early-hatched bass was high and occurred in most length classes. Late-hatched bass did not rely on insects as much as early-hatched bass; insects only comprised 20% of the diet for fish 140–150 mm TL.

A significant difference in insect utilization by early cohorts was observed between 1992 and 1993 but no difference was observed between 1993 and 1994 ( $P = 0.15$ ). Similar results were obtained for late cohorts. Insect consumption was higher in 1992 than in 1993; no significant difference between late cohorts during 1992 and 1994 ( $P = 0.94$ ) was observed. The extremely limited occurrence of insects in the stomachs of late-hatched bass in 1994 may account for these results. ANOVA indicated similar relationships of insect frequency of occurrence and TL of bass among years and ANCOVA showed no difference in utilization of insect taxa among sub-cohorts. Dipterans (chironomids and ceratopogonids), hymenopterans (braconids), odonates (libellulids), and hemipterans (corixids) comprised the principal food items for both sub-cohorts during 1992 and 1994. In 1993, hemipterans were the dominant insects in bass stomachs.

*Fish.*—Comparisons of early and late cohorts indicated significantly different utilization of fish as a food source during 1992 and 1993 (Fig. 2). No significant difference was observed between cohorts in 1994 ( $P = 0.10$ ). During 1993 and 1994,



**Figure 2.** Percent frequency-of-occurrence of insects and fish in the diet of early- (top) and late-hatched (bottom) largemouth bass ( $\leq 150$  mm TL), Lucchetti Reservoir, Puerto Rico, 1992–1994.

occurrence of fish in the stomachs was almost 100% for all length classes of late-hatched bass. During 1992, fish consumption was relatively lower, but both sub-cohorts exhibited an increase in fish utilization as they grew.

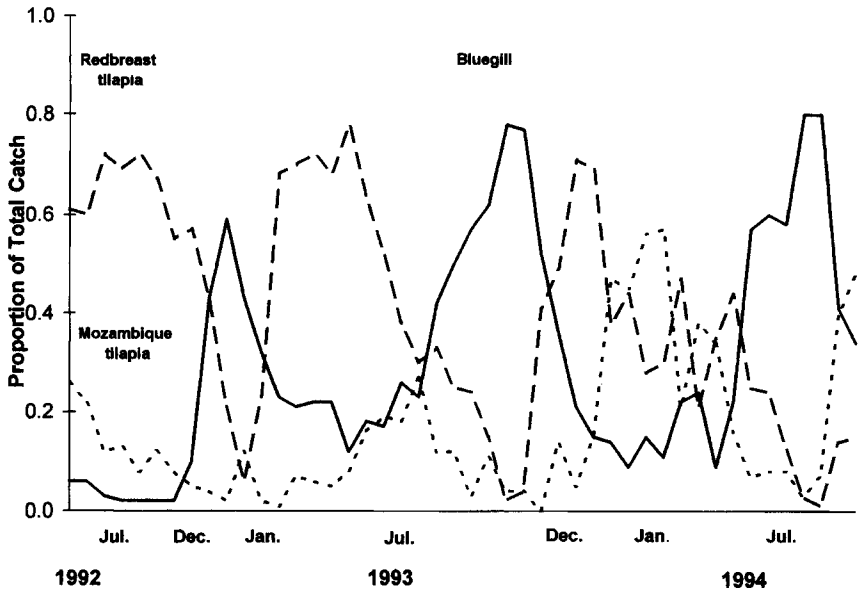
Differences in fish utilization among early cohorts were observed every year. Highest mean frequency of occurrence value was obtained during 1994 ( $88.17 \pm 4.4$ ) and the lowest in 1992 ( $57.78 \pm 4.2$ ). Late cohort piscivory was significantly different between 1992 and 1993, and between 1992 and 1994. No significant difference ( $P = 1.00$ ) was observed between 1993 ( $98.44 \pm 4.21$ ) and 1994 ( $98.48 \pm 4.21$ ).

**Seasonal Prey Base Variability**

Littoral electrofishing samples were dominated by tilapias during the first half of each year and by juvenile bluegills during late summer and fall (Fig. 3). These trends corresponded with size distributions of prey  $< 100$  mm TL (Fig. 4). However, ranges of minimum length for all prey species typically included individuals small enough to serve as prey for young bass.

Mean bluegill size in electrofishing samples during the first half of 1992 was relatively large for juvenile bass to utilize as prey (Fig. 4). Bluegill abundance increased in the summer and fall months of each year. Identifiable bluegills first appeared in bass stomachs in mid-1993.

Threadfin shad were present in the littoral areas, but no pronounced reproduction pulse was evident (Fig. 4). Their small size (mean TL usually  $< 55$  mm TL) and



**Figure 3.** Proportion of total catch of forage fishes in electrofishing samples at 5 sites, Lucchetti Reservoir, Puerto Rico, 1992–1994.

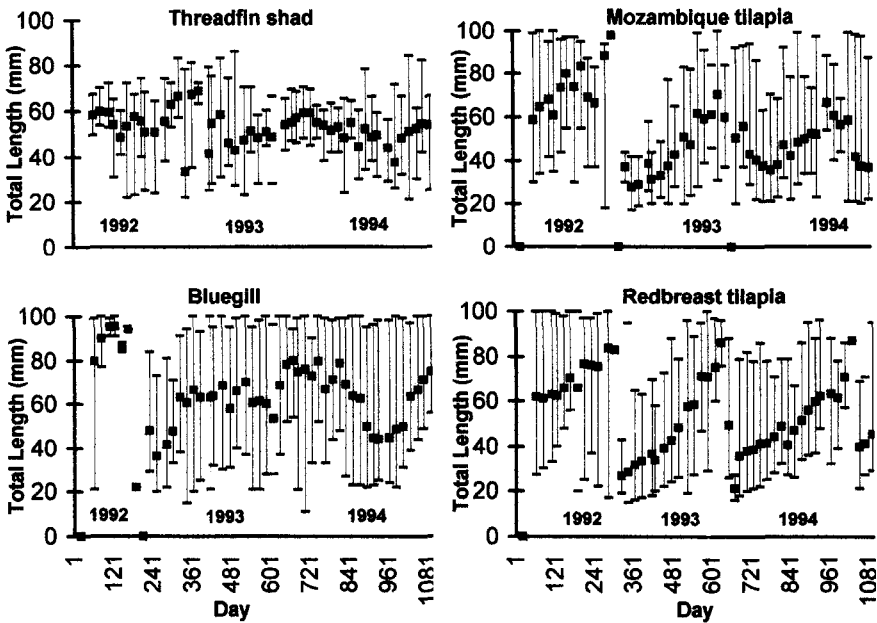
year-around availability made them suitable prey. Nevertheless, most identifiable shad were observed in stomachs during the spring and summer.

Tilapias showed the most marked annual cycle of reproduction (Fig. 4). They were abundant in the early part of the year when bluegills were too big to be used by early-hatched bass. Tilapias comprised about 65% of the fish diet of early-hatched juvenile bass during 1992 and 45% in 1994, but their utilization was lower for late-hatched bass.

**Discussion**

Food habit studies of fishes serve as a partial baseline to interpret population interactions and constitute an important tool for resource management decisions. Lucchetti Reservoir bass fingerlings are stocked to promote sport fishing and stocked bass contribute to the population. Sampling intensity over several years in Lucchetti Reservoir has provided insight on the interaction between juvenile bass and their prey base in this artificial community.

In general the occurrence of zooplankton in the diet of juvenile bass was minimal for fish as small as 31–40 mm TL. This can be associated with low densities of cladocerans and copepods in Lucchetti Reservoir. In contrast, zooplankton has been described as an important food item for bass < 40 mm TL in southeastern temperate reservoirs (Shelton et al. 1979, Jackson et al. 1990, Phillips et al. 1995). Zooplankton composition in Lucchetti Reservoir was dominated mainly by rotifers for most of the



**Figure 4.** Size distribution (mean and range) of forage species < 100 mm TL in electrofishing samples, Lucchetti Reservoir, Puerto Rico, 1992–1994.

year, while copepods and cladocerans did not reach densities > 75 individuals/liter (Churchill et al. 1995). However, both insects and fish were available and well-utilized as prey for the smallest bass sampled.

Insectivory was primarily represented by immature stages of dipterans and hemipterans. A direct relationship between insectivory and proportion of empty stomachs was found. Limited prey availability has been described as playing an important role in the diet shifts of juvenile largemouth bass (Timmons et al. 1980). When fish prey are insufficient, juvenile bass feed on insects for prolonged periods of time or they shift back to insects from a fish diet (Shelton et al. 1979, Phillips 1994). Juvenile bass diets in Lucchetti Reservoir showed a low occurrence of insects throughout the size classes, but when insects comprised most of the diet (1992) a high percent (17.9) of empty stomachs was observed. Insectivory and piscivory were inversely correlated in Lucchetti Reservoir, following the same patterns observed in a southeastern U.S. reservoir (Phillips et al. 1995). In Lucchetti Reservoir, insectivory was low during 1993 and 1994 (< 40%), and at the same time piscivory was high (> 70%).

High piscivory in Lucchetti Reservoir was related to the annual cycles of reproduction of the prey species (bluegills, threadfin shad, and tilapias) leading to their respective seasonal availabilities. Seasonal changes in prey composition were observed



in electrofishing samples and were reflected in the occurrence of prey in the diet of juvenile bass. Threadfin shad were abundant for most of the year, tilapias during the first part of the year, followed by bluegills later (Alicea 1995). However, our sampling method did not provide a reliable estimate of the relative abundance of tilapias and threadfin shad in the reservoir.

Continual spawning of threadfin shad made them a dependable food for juvenile bass throughout the year. Shad were supplemented with tilapias during the first part of the year and with bluegill the last part of the year. This was accentuated when the diet of the 2 bass sub-cohorts were analyzed individually. A combination of tilapias and threadfin shad was observed for early-hatched bass and a combination of bluegills and shad by late-hatched bass.

Time of cohort production plays an important role in the growth and survival of juvenile bass. Goodgame and Miranda (1993) and Phillips et al. (1995) found that bass which hatched earlier utilized the fish prey base earlier, thus increasing their growth and probability of survival. If fish prey are the optimal forage for juvenile bass, early-hatched bass in Lucchetti Reservoir had a prey-availability disadvantage compared to those hatched later due to reproduction regimes of the prey species. Early-hatched bass fed primarily on insects; the percent occurrence of insects in the diet was consistently higher for early-hatched bass than for late-hatched bass.

Despite the among-year variations in diet and prey availability, there is no evidence for limitations of prey availability on growth of juvenile bass in Lucchetti Reservoir. According to Churchill et al. (1995), young bass in Lucchetti Reservoir exhibited rapid growth rates (1.1 mm/day) regardless of year or time of year. Apparently shifts from 1 prey type to another occurred within the range of bass densities and prey abundances without substantial bioenergetic compromise.

Growth rates of Lucchetti Reservoir juvenile largemouth bass were similar to those of bass in Cuban reservoirs. According to Guerra-Padrón et al. (1980, 1983), a growth rate of 1 mm/day during the first 5 months was a typical rate in Cuban reservoirs. Cuban studies did not describe the community composition nor the diet of juvenile bass.

The trends observed in Lucchetti Reservoir generally followed the findings in temperate and southern reservoirs. In general, trophic stages in juvenile bass have been divided into zooplanktivory (< 40 mm), insectivory (40–60 mm) and piscivory (> 60 mm). Our data suggest that zooplanktivory is not particularly important for bass > 31 mm TL.

Micro-tagged largemouth bass fingerlings periodically stocked in Lucchetti Reservoir comprised 4.5%–20.0% of the population (Churchill et al. 1995). Based on our findings, these stocked fish apparently did not experience intra-specific competition for food resources and, due to the fact that early-hatched bass had no foraging advantage, stocking fingerlings earlier in the year (before natural spawning) would appear to be less advantageous than stocking later (after natural spawning), when piscine prey are more abundant and naturally-reproduced bass have grown to larger sizes.

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