Bioenergetic Values of Shads and Sunfishes as Prey for Largemouth Bass

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Abstract: We conducted laboratory and field investigations to determine the relative value of shads (*Dorosoma* spp.) and sunfishes (*Lepomis* spp.) as prey for largemouth bass (*Micropterus salmoides*). In the laboratory, we examined the energy content of gizzard shad (*D. cepedianum*) and bluegill (*L. macrochirus*) and digestibility by largemouth bass. Although the ratios of proximate components in the 2 prey species differed, total energy contents as calories per gram were equal. The rates at which gizzard shad and bluegill were digested were similar at feeding rates <1.5%–2.0% of largemouth bass body weight, but gizzard shad were digested increasingly faster than bluegill at progressively higher feeding rates: maximum rate of digestion occurred at about 5% of the largemouth bass body weight for gizzard shad, and about 3% for bluegill. We examined the food of largemouth bass of the 1984 year class during 1984 and 1985 in 2 reservoirs with different densities of shads and sunfishes, and related the food to vital statistics of the largemouth bass populations. Largemouth bass ate more fish (mainly shads), grew faster, and had lower mortality in a reservoir where shads and sunfishes were about equally available than in a reservoir where sunfishes were the most readily available and most important forage. We attributed these differences to differences in diet. Vital statistics of the population with a shad-dominated diet were superior because the largemouth bass were able to obtain larger rations, digest food and empty the stomach at a faster rate, and possibly locate and capture prey more easily.

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In reservoirs of the southeastern United States, the principal food items in the diet of piscivorous largemouth bass are shads and sunfishes. Relative dietary

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importance of the 2 prey taxa has been reported to be a function of availability, season, and largemouth bass size (Aggus 1973, Pasch 1975, Hubert 1977, Timmons et al. 1981). Presence of threadfin shad (*D. petenense*) in the largemouth bass diet has been found to increase growth and condition (von Geldern and Mitchell 1975, Davies et al. 1979; but see Range 1972), but few studies have investigated the energetic relationships between largemouth bass dietary composition and population characteristics. These data are important for interpreting observed diets and rates of growth, developing strategies for manipulating predator-prey interactions, and predicting results of management inputs.

We examined in the laboratory the relative nutritional value (i.e., difference in proximate composition, caloric content, and digestibility) of gizzard shad and bluegill to largemouth bass. We also examined the diet of the 1984 year class of largemouth bass during 1984 and 1985 in 2 reservoirs with different availabilities of shads and sunfishes, and related diet composition to largemouth bass population statistics. We then used field and laboratory observations to investigate the value of shads and sunfishes as prey of largemouth bass.

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Methods

Laboratory Study

Largemouth bass, gizzard shad, and bluegill used in the laboratory study were collected by electrofishing nearshore areas of Columbus Lake, Mississippi, during fall 1985. Fish were transported live to the laboratory and maintained in 950-liter circular tanks at 24° ± 1° C with continuous water exchange.

Gizzard shad and bluegill used in proximate analyses were placed on ice immediately after capture, and at the laboratory were analyzed for moisture, protein, fat, and ash contents (Williams 1984). Nitrogen-free extract was regarded as carbohydrate, and proportions of carbohydrate, fat, and protein in whole fish were multiplied by their energy contents (4.1, 9.45, and 4.8 kcal/g, respectively) and added to estimate total energy content of a prey item (Brett and Groves 1979).

Because shads are more elongated than sunfishes, they probably provide more food per capture than do sunfishes of equal body depth. We examined this relation by regressing $\log_{10}$-transformed measurements of depth and weight for each prey species and testing for differences in slopes and intercepts (Neter and Wasserman 1974:161).

The nutritive value of a prey species is also determined by the rate at which it can be digested by the predator. We investigated rates at which the 2 prey species are digested by largemouth bass by measuring reduction in prey body weight in the stomach during a 12-hour period. Largemouth bass were deprived of food for 2–3 days, anesthetized in water with 10 mg/liter quinaldine, force-fed a gizzard shad or bluegill, and 12 hours later induced to regurgitate by injecting hydrogen peroxide into the stomach (Miranda 1986*a*). Water temperature was maintained at 24° ± 1° C. Total length (TL) and weight of the predator and weight of the prey were recorded before the feeding; the prey fish was then reweighed after regurgitation.

Differences in rate at which the 2 prey species were digested by largemouth bass were tested by regression analysis. Digestion ratio was computed as weight reduction of prey during the 12-hour period/initial weight of prey, and feeding ratio as initial weight of prey/initial weight of predator. Then, for each prey species, feeding ratio was regressed on $\log_e$(digestion ratio/(1 - digestion ratio)). This logistic transformation produced an S-shaped antisymmetrical curve, with an inflection point (maximum slope) corresponding to the fastest digestion rate and occurring exactly half-way between the 2 asymptotes. We felt that this logistic curve better reflected the digestion ratio by implying that some digestion occurred regardless of how large the food was, that the food was never completely digested, and that there was an optimum feeding ratio. The 2 resulting equations were tested for differences in slopes and intercepts (Neter and Wasserman 1974:161).

Field Study

The field study was conducted in the Divide Section of the Tennessee-Tombigbee Waterway in northeastern Mississippi. The Divide section encompasses 2,670-ha Bay Springs Lake (Bay Springs) to the south, the 1,170-ha Yellow Creek Arm of Pickwick Lake (Yellow Creek) to the north, and the 35-km navigation canal connecting the 2 reservoirs. Yellow Creek was impounded in the Tennessee River basin in 1938, and Bay Springs in the upper Tombigbee River basin in 1983 by releasing water from Yellow Creek through the connecting canal. Bay Springs and Yellow Creek average 10.7 and 6.7 m in depth, respectively, and are maintained at 126 m above mean sea level except for a 2-m winter drawdown.

The fish assemblage of Bay Springs was dominated by adult gizzard shad, sunfishes (primarily bluegill), and largemouth bass, with a total standing stock of about 270 kg/ha in 1984 and 1985 (Miranda 1986*b*). The fish assemblage in Yellow Creek is older and more diverse, and was dominated by gizzard and threadfin shad, sunfishes (primarily bluegill and longear *L. megalotis*), and black basses (spotted *M. punctulatus*, smallmouth *M. dolomieui*, but primarily largemouth), with a total standing stock of about 490 kg/ha in 1984 and 1985 (Miranda 1986*b*).

Largemouth bass of the 1984 year class were collected by electrofishing at 2-week intervals from March to early May 1985, and mid-October in 1984 and 1985, in areas randomly selected along the shore of Bay Springs and Yellow Creek. All largemouth bass collected were held on ice and at the end of each sampling day measured (TL) to the nearest millimeter, weighed to the nearest gram, and dissected to remove the stomach. Stomach contents were identified when possible, and TL of prey fish were recorded. The length of partly digested prey often had to be estimated. Weight of fish prey were estimated using length-weight tables (Swingle and Shell 1971). We expressed ration as the percentage of the predator's weight consisting of fish prey present in the stomach. Although a crude estimate of ration, we felt it was sufficient for comparing rates of food intake. We computed relative weights of largemouth bass (Anderson and Gutreuter 1983) and quantified diets in terms of percent frequency of occurrence and size of prey fish consumed. The year class was identified primarily from length-frequency modes, but ages of large fish were verified from scale annuli.

Fish standing crops were estimated from cove-rotenone samples as described by Davies and Shelton (1983). Three coves in each reservoir, totaling 2.02 ha in Bay Springs and 1.21 ha in Yellow Creek, were sampled during the last week of July and the first week of August in 1984 and 1985. Fish were collected for 2 consecutive days in each cove, sorted by species into 25-mm TL groups, and counted and weighed by length group. Largemouth bass were measured in 10-mm TL groups. The AP/P model (Jenkins and Morais 1978) was used to calculate the ratio of available prey (shads and sunfishes) biomass to predator (largemouth bass of the 1984 year class) biomass.

Results and Discussion

Laboratory Study

Correlation analyses indicated that the ratios of moisture, protein, fat, and carbohydrate in each of the prey species did not change with size of the prey fish ($P > 0.05$). Ash ratio increased with size in both prey species, probably due to an increase in the density of bones and scales. Analyses of variance indicated that average moisture, ash, and carbohydrate contents did not differ significantly between the 2 prey species ($P > 0.05$); however, protein content was significantly higher in bluegill and fat content significantly higher in gizzard shad (Table 1). The amount of protein in the 2 prey species exceeded the 40% dietary crude

Table 1. Main tissue constituents of gizzard shad and bluegill collected from Columbus Lake, Mississippi, October 1985. Standard errors are shown in parentheses.[a]

Tissue constituent	Gizzard shad (N = 10)	Bluegill (N = 10)
Moisture (%)	74.71 (0.73)	74.61 (0.46)
Protein (%)	14.16 (0.34)	16.44 (0.26)[b]
Fat (%)	5.28 (0.60)	3.45 (0.20)[b]
Ash (%)	4.78 (0.35)	4.68 (0.22)
NFE[c] (%)	1.07 (1.40)	0.82 (1.20)
Kcal/g (wet-weight basis)	1.22 (0.07)	1.16 (0.03)

[a] TL ranges of gizzard shad and bluegill were 99–272 and 47–175, respectively.

[b] Mean values for gizzard shad and bluegill are significantly different ($P \leq 0.05$).

[c] Nitrogen-free extract is regarded here as carbohydrate.

protein requirement (dry weight) of largemouth bass determined by Anderson et al. (1981). The total caloric contents of gizzard shad and bluegill were not significantly different ($P > 0.05$).

The relation between weight and body depth was best described by a power curve (Fig. 1). Gizzard shad were heavier than bluegill of equal body depth (slopes and intercepts were different, $P < 0.05$). Within the range of sizes examined, a largemouth bass would get roughly 30%–40% more food from a gizzard shad than from a bluegill of equal body depth.

Digestion ratios were determined for 15 gizzard shad and 32 bluegill fed to largemouth bass at rates ranging from 0.007 to 0.065 of largemouth bass weight. When higher feeding rates were attempted, the prey was immediately regurgitated. The relation between feeding ratio and digestion ratio was inverse and highly significant in both prey species, indicating that the time required for digestion is longer for a large meal than for a small one. Largemouth bass digested the 2 prey species at similar rates when fed at low ratios (Fig. 2); as feeding ratio was increased, however, the rates of digestion diverged and gizzard shad were digested faster than bluegill (slopes of the 2 lines were significantly different ($P < 0.05$) but the intercepts were not). Force feeding has been reported to decrease the rate of digestion, in comparison with the rate for food consumed voluntarily (Fange and Groves 1979), but this complication may not be of great concern when the results are used in a comparative sense.

The points of inflection in the relations between feeding ratio and digestion ratio (Fig. 2) represent maximum rates of digestion and optimum meal size. These points occur at the 0.5 digestion ratio, revealing a maximum rate of digestion at about 0.05 of the largemouth bass body weight for gizzard shad and about 0.03 for bluegill. These optimum weight ratios correspond to length ratios of roughly 40% for gizzard shad and 30% for bluegill (Swingle and Shell 1971). The S-shaped relationship between feeding ratio and digestion ratio for gizzard shad was statisti-

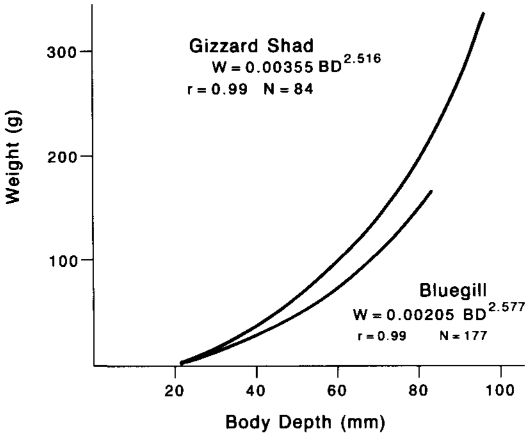

Figure 1. Relation between body depth (BD) and weight (W) of gizzard shad and bluegill collected from Bay Springs Lake and the Yellow Creek Arm of Pickwick Lake, Mississippi, October 1985.

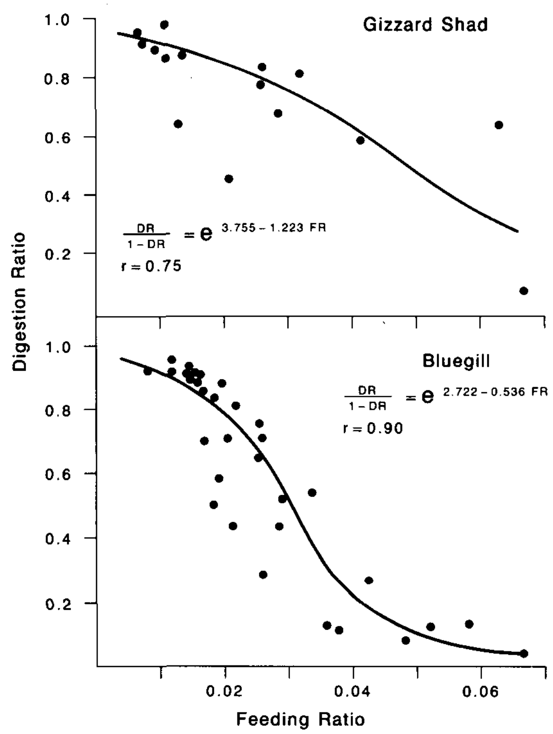

Figure 2. Relation between feeding ratio (FR, expressed as a proportion of the predator's weight) and digestion ratio (DR, expressed as the proportion of a meal evacuated from the stomach in a 12-hour period at 24° ± 1° C) of gizzard shad and bluegill force-fed to largemouth bass.

cally significant but weak, possibly because of a small sample size at high feeding ratios; thus, estimates of optimum ratios for gizzard shad are imprecise.

Field Study

Rotenone sampling in late July and early August 1984 estimated average abundance of age–0 largemouth bass at 594 and 416/ha in Bay Springs and Yellow Creek, respectively. Age–0 largemouth bass averaged 86-mm TL in Bay Springs and 83-mm TL in Yellow Creek. The standing crops (kg/ha) of shads and sunfishes, respectively, were 61 and 104 in Bay Springs, and 100 and 62 in Yellow Creek. In Bay Springs, virtually all the shad biomass was contributed by gizzard shad, and 75% of the sunfish biomass by bluegill; in Yellow Creek, 89% of the shad biomass consisted of gizzard shad, and 84% of the sunfish biomass of bluegill and longear sunfish.

Not all the biomass of shads and sunfishes was available as prey to age–0 largemouth bass. In Bay Springs young sunfishes were more abundant than shads, whereas in Yellow Creek young shads were more abundant than sunfishes. Survival of shad larvae in Bay Springs was limited, perhaps by low phytoplankton production (Boggs 1985). AP/P ratios in Bay Springs and Yellow Creek, respectively, averaged 0.0 and 10.2 for shads, and 8.7 and 3.8 for sunfishes. Thus, prey available to age–

0 largemouth bass was almost exclusively sunfishes in Bay Springs, but both shads and sunfishes in Yellow Creek.

Foods of the 1984 year class of largemouth bass differed considerably. In fall 1984, age–0 largemouth bass in Bay Springs fed primarily on invertebrates and sunfishes, and only 35% of the stomachs with food contained fish (Table 2). In Yellow Creek, the most common food items were shads and invertebrates, and 75% of the stomachs with food included fish. Relative weight for the year class averaged 100 in Bay Springs and 101 in Yellow Creek, which was unexpected considering dietary differences and higher caloric content in fish relative to invertebrates (Cummins and Wuycheck 1971). We speculate that an ample supply of invertebrate food for age–0 largemouth bass existed on the abundant submerged terrestrial vegetation present in Bay Springs during the first year of impoundment, compensating for the reduced caloric content of the diet.

Food use in Bay Springs in spring 1985 was similar to that in the previous fall (Table 2), although total fish consumption increased slightly. In Yellow Creek, shad consumption was reduced in spring; perhaps because availability was diminished by winter mortality (Adams et al. 1982), number and size of schools were reduced due to dispersal (Dendy 1946), supply was exhausted by intensive predation during the previous fall, or shad grew beyond largemouth bass predatory capabilities. Body condition decreased considerably during winter and relative weights averaged 83 in both reservoirs by spring.

Rotenone sampling in 1985 indicated that the 1984 year class had been reduced to 61 age–1 largemouth bass/ha in Bay Springs (10% annual survival) averaging 218 mm TL, and to 136/ha in Yellow Creek (33% annual survival) averaging 234 mm TL. Shad reproduction in Bay Springs remained low in 1985, although age–0 shads were slightly more abundant than in 1984. AP/P ratios in Bay Springs and Yellow Creek, respectively, averaged 0.2 and 4.2 for shads and 4.2 and 3.4 for sunfishes. Thus, sunfishes composed the bulk of prey available to age–1 largemouth

Table 2. Stomach contents as percent frequency of occurrence in largemouth bass of the 1984 year class in Bay Springs Lake (BSL) and the Yellow Creek Arm of Pickwick Lake (YCA), Mississippi, 1984 and 1985. Total length ranges (mm) are given in parentheses.

	Fall 1984		Spring 1985		Fall 1985	
Food	BSL $N = 133$ (75–212)	YCA $N = 150$ (74–218)	BSL $N = 462$ (96–243)	YCA $N = 558$ (104–247)	BSL $N = 44$ (172–307)	YCA $N = 218$ (194–338)
Shads	1	23	1	13	16	81
Sunfishes	11	3	11	4	16	1
Other fishes	1	4	3	6	2	1
Unidentified fishes	8	12	16	13	23	5
Crayfish	0	2	0	2	0	1
Other invertebrates	39	12	38	20	0	0
Empty	40	44	31	42	43	11

bass in Bay Springs, whereas in Yellow Creek shads and sunfishes remained the most abundant prey.

By fall of 1985, the 1984 year class was eating chiefly fish in both reservoirs. In Bay Springs, shads and sunfishes were eaten in equal proportions (Table 2), but because sunfishes of suitable size were much more abundant than shads, largemouth bass apparently selected shads. Similarly, availability of shads and sunfishes was roughly similar in Yellow Creek, but shads were eaten more often (Table 2).

Total length of prey eaten by the 1984 year class of largemouth bass in the 2 reservoirs averaged 39% of predator length for shads and 29% for sunfishes, below the maximum size that largemouth bass can generally swallow (50% of the largemouth bass length for shads and 40% for sunfishes; Lawrence 1958, Timmons and Pawaputanon 1981). In stomachs containing shads or sunfishes, the average number of shads per stomach (1.8) was greater than the number of sunfishes (1.2), particularly in Yellow Creek. Thus, largemouth bass that fed on shads had larger rations (4.6% of body weight for shads and 3.7% for sunfishes). Regression of largemouth bass length on ingested prey length indicated no significant relationship with shads ($P > 0.05$), but a positive significant relationship with sunfishes in both lakes, suggesting that larger largemouth bass generally selected larger sunfishes but the size of shads was not selected.

Conclusions and Implications

The largemouth bass population in Yellow Creek, with greater recruitment to age–1 and faster growth, would be more desirable from a management perspective than the Bay Springs population. We believe differences in diet made the Yellow Creek largemouth bass population more desirable. Prey-predator plots indicated that both reservoirs had abundant small prey although different prey composition. Food analyses showed more use of fish prey, particularly shads, in Yellow Creek. It is thus apparent that prey types and vulnerability, instead of total available prey, are of critical importance in largemouth bass-prey dynamics. These conclusions lead to the question of why shads are better than sunfishes as forage for largemouth bass in reservoirs.

Proximate analyses showed some differences in the proportion of nutrients available in equal weights of gizzard shad and bluegill, but no real difference in total energy content. Metabolizable energy is slightly less than the total energy content. Beamish (1972) fed emerald shiners (*Notropis atherinoides*) to largemouth bass and found assimilation efficiency to be around 90%, but no information is available on the assimilation efficiency of energy from shads or sunfishes. Because chemical composition of the 2 prey species differ, assimilation efficiency may vary, but probably not enough to cause the differences observed between largemouth bass populations in Bay Springs and Yellow Creek.

The amount of food ingested could be responsible for observed differences in growth between the 2 populations. Lengths of shad and sunfishes eaten by largemouth bass averaged near the optimum feeding ratios estimated from our digestion studies except in Yellow Creek, where suboptimal size shads were used regularly. Largemouth bass that fed on shads, however, averaged larger rations because they often had more than a single shad in their stomachs. Because largemouth bass in Bay Springs ate mainly sunfishes and those in Yellow Creek mainly shads, differences in ration size could have contributed to the observed differences in largemouth bass growth.

Rate of digestion may have also contributed to differences between largemouth bass growth rates. Gizzard shad were digested faster than bluegill when eaten at ratios exceeding 0.015–0.02 of body weight. Faster breakdown by gastric juices can result in an increased rate of food absorption and emptying of the stomach. Emptying would stimulate appetite resulting in more frequent feeding and larger quantities of food processed. Growth rate could be fastest when the fish feed on shad of sizes closer to the optimum 5% of body weight or 40% of TL.

Vulnerability to predation may influence differential use of shads and sunfishes. Sunfishes normally use vegetation and submerged structures to reduce or avoid predation (Savino and Stein 1982), making them harder to capture and thus energetically less valuable. Bluegill, by remaining motionless, seeking cover, and dispersing, were less susceptible to predation by tiger muskellunge (*Esox masquinongy* x *E. lucius*) than fathead minnows (*Pimephales promelas*) which schooled and remained in open water (Moody et al. 1983). Shads are found in more open habitats and are usually in motion and schooling (Miller 1960); consequently, they are more readily discernible and likely to be attacked by largemouth bass (Howick and O'Brien 1983). Based on the regularity of multiple shad occurrences in largemouth bass stomachs and the lack of size selectivity, we speculate that largemouth bass struck shad schools. Schools of age–0 shad usually provided prey of suboptimal size, but because they were highly vulnerable, they possibly provided the opportunity to capture more than 1 fish.

Our study confirmed that shads are an important food in largemouth bass in large reservoirs. Biomass of shads in reservoirs, however, is often excessive and composed of fish too large to serve as prey. Management programs designed to increase production of largemouth bass should include manipulation of shad populations to maintain adequate stocks within size ranges vulnerable to this predator.

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