

Diets and Factors Affecting Feeding Success of Age-0 Gizzard Shad

Paul H. Michaletz, Missouri Department of Conservation, 1110 South College Avenue, Columbia, MO 65201

Abstract: Diets, food selection, and factors affecting feeding success of small (5–9 mm total length, TL), medium (10–19 mm TL), and large (20–29 mm TL) larval and early juvenile gizzard shad (*Dorosoma cepedianum*) were examined in 2 large Missouri reservoirs. Diets and food selection shifted from mainly copepod nauplii and cyclopoids to rotifers and phytoplankton as fish grew. Mean length of ingested zooplankton rose slightly as gizzard shad grew from the small to medium length groups and then decreased for the large length group. Feeding success (feeding incidence and mean gut fullness) increased with fish size. Feeding incidences of small and medium gizzard shad were significantly higher at an upstream site than at a downstream site in 1 reservoir, but not in the other. Feeding incidence and, to a lesser degree, mean gut fullness of small and medium gizzard shad usually increased with food abundance, although correlations were weak. Feeding incidence and mean gut fullness were not usually correlated with secchi depth or temperature for any length group. These results indicate large shad are more efficient foragers than small shad and relations among feeding success, fish location, and food abundance may be complex and difficult to document in field studies.

Proc. Annu. Conf. Southeast. Assoc. Fish and Wildl. Agencies 50:182-191

Larval and early juvenile gizzard shad are numerically the most abundant planktivores in many midwestern and southern reservoirs. Because of their abundance and high consumption rates of zooplankton, they may be responsible for severe summer declines in zooplankton abundance in some reservoirs (DeVries and Stein 1992, Shadady 1993). The reduction or elimination of zooplankton may reduce recruitment of young of other species such as bluegill (*Lepomis macrochirus*) and, in turn, young piscivores such as largemouth bass (*Micropterus salmoides*) that rely on bluegills for food (DeVries and Stein 1992). Juvenile gizzard shad are also important prey for most piscivorous sport fishes (Noble 1981, Storck 1986, Johnson et al. 1988, Michaletz 1997). Hartman and Margraf (1992) and Michaletz (1997) found that growth of sport fishes was positively related to juvenile gizzard shad abundance in some aquatic systems.

The feeding ecology of larval and early juvenile gizzard shad is fairly well

documented. Larvae are particulate feeders and consume mainly small crustaceans and rotifers (Cramer and Marzolf 1970, Barger and Kilambi 1980, Van Den Avyle and Wilson 1980, Dettmers and Stein 1992). As they reach juvenile size (25–30 mm TL), they become filter feeders and consume phytoplankton and zooplankters that have poor escape abilities (Bodola 1965, Cramer and Marzolf 1970, Drenner et al. 1978, 1982). However, factors affecting feeding success of larvae and early juveniles have not been extensively studied. Because feeding success affects survival of young fishes (Crecco and Savoy 1987, Miller et al. 1992), feeding success of larval and juvenile gizzard shad may affect their potential as competitors and their availability as prey for sport fishes. Identifying factors affecting their feeding success would lead to a better understanding of gizzard shad population dynamics and their role in aquatic communities. In this paper, in addition to describing prey selection, I examine relations between feeding success and fish size, fish location, zooplankton abundance, temperature, and water clarity in 2 large reservoirs.

I thank D. Nicks for helping with all phases of this study and W. Mabee for processing the shad and zooplankton samples. I also thank C. Gale for statistical advice. J. G. Dillard, M. Colvin, S. Fischer, R. Luebke, G. Cada, and 2 anonymous reviewers provided useful critiques of various drafts of the manuscript. This study was funded through Federal Aid in Sport Fish Restoration, Project F-1-R, study I-28, provided to the Missouri Department of Conservation.

Methods

The study was conducted in 2 southwestern Missouri reservoirs, the Lindley Creek arm of Pomme de Terre Lake and the Sac River arm of Stockton Lake. Pomme de Terre Lake is a 3,167-ha Corps of Engineers reservoir used for flood control. Stockton Lake is a 10,072-ha Corps of Engineers reservoir used for both flood control and hydropower generation. These reservoirs are steep-sided, fairly deep (mean depth about 10 m), relatively clear (seasonal mean secchi depths >1.5 m), and moderately productive (chlorophyll *a*, 16.1 and 11.4 µg/liter; primary production, 3.9 and 2.9 mg oxygen/liter/day; for Pomme de Terre and Stockton lakes, respectively; Knowlton 1989). Both reservoirs are usually thermally stratified from late May through early September. Thermoclines develop at depths of 4–8 m and hypolimnia become oxygen deficient.

Sampling

Larval and early juvenile gizzard shad (<30 mm TL), hereafter referred to as shad, and zooplankton were collected offshore at an upstream (upper) and downstream (lower) site in each reservoir from 1988 through 1991. The 2 sites were about 9 km apart in Pomme de Terre Lake and 5 km apart in Stockton Lake. Sampling was conducted weekly in May and June and biweekly thereafter, until sampling ended when sufficient numbers of shad were no longer collected for food-habit analysis (late June to early August). Shad and zooplankton collections were made during midday (1100–1300 hours for Pomme de Terre Lake, 1500–1700 hours for Stockton

Lake) which correspond with peak shad feeding periods (Hayward and Hiebert 1993). Shad were collected with paired 1-m² frame trawls equipped with 500- μ m mesh. Trawls were towed at a speed of 1 m/sec for about 1 minute at 0.5-, 2.5-, 4.5-, 6.5-, and 8.5-m depths (midpoints of trawls) before being obliquely retrieved. Zooplankton were collected from 9 m to the surface with a vertical tow of an 80- μ m Wisconsin plankton net. Both trawl and zooplankton samples were preserved in 10% formalin. Temperature and dissolved oxygen were measured at 1-m intervals from the surface to 9 m at the trawling locations. Secchi depths also were measured. Mean epilimnetic temperature was computed by averaging temperatures measured at 1-m intervals in the epilimnion.

Zooplankton

In the laboratory, zooplankton samples were rinsed and diluted to 10–45 ml. Three, 1- or 2-ml subsamples were withdrawn with a large-bore pipette and all zooplankton within the subsample were identified and counted. Zooplankton were identified as rotifers, copepod nauplii, cyclopoid copepods, calanoid copepods, or to genus for cladocerans. Subsample counts were averaged and used to estimate the density of zooplankton (N/m^3).

Zooplankton of 100 randomly selected individuals were measured (nearest 0.1 mm) according to the procedures of Culver et al. (1985). Measured individuals were usually identified to species, and their dry weights were estimated using length-dry weight equations for the same species or nearest congener (Dumont et al. 1975, Rosen 1981, Culver et al. 1985). Dry weights were adjusted for preservation effects (Giguère et al. 1989). Average individual dry weights of each taxon were multiplied by the corresponding density estimates to determine biomass of each taxon. Dry weights of each taxon were summed to estimate total zooplankton biomass.

Feeding

Entire digestive tracts were excised from at least 15 randomly-selected shad from each site when possible, and food contents were removed. All zooplankton were counted and total numbers of phytoplankton were estimated based on counts of subsamples in Sedgewick-Rafter cells. Zooplankton were identified and measured and their dry weights were estimated as described for zooplankton samples. Phytoplankton were identified to phylum.

To describe changes in diets with shad size, the mean percentage (by N) of zooplankton taxa, the mean size of zooplankton, and the mean number of phytoplankton consumed were computed for small (5–9 mm TL), medium (10–19 mm TL), and large (20–29 mm TL) shad pooled over all dates for each reservoir. A linear food selection index (Strauss 1979) was used to depict trends in food preferences over sizes of shad. The linear index (L) was calculated as

$$L = r_i - p_i$$

where r_i is the proportion of prey item i consumed and p_i is the proportion of prey item i in the environment. The index ranges from -1 to $+1$ with negative values

indicating avoidance or inaccessibility and positive values indicating preference of prey items. The index was calculated for each shad, and the mean index value was calculated for each length group.

Feeding incidence (% of fish with food) and mean gut fullness (food dry weight in mg/fish wet weight in g) were computed for small, medium, and large shad. Food weights were estimated by summing the estimated dry weights of zooplankton in the guts of individual fish. Wet weights of shad were estimated by a length-weight equation (Michaletz 1997). Phytoplankton were not included in food weight calculations. Feeding incidence was compared between sites and among length groups within reservoirs (all dates combined) with chi-square tests. Correlation analyses were used to relate feeding incidence [$\arcsin(X^{0.5})$ transformed] and mean gut fullness for the length groups of shad to site-specific estimates of mean epilimnetic temperature, secchi depth, and zooplankton biomass. Only dates when ≥ 10 shad were examined for food for a length group were included in the correlation analyses. Zooplankton biomass was adjusted to account for gape-limitation by shad. Only zooplankton that were small enough to be ingested by shad in each length group were included in zooplankton biomass estimates. Mouth gape for the midpoint of each length group (7.5, 15, and 25 mm TL), estimated from a total length-mouth gape equation in Michaletz et al. (1987), was used to determine the sizes of zooplankton available to different length groups of shad. Significance level was set at $P \leq 0.05$ for all statistical tests.

Results

Diets and food selection of shad were similar in both reservoirs and shifted from mainly copepod nauplii and cyclopoid copepods to rotifers and phytoplankton as fish grew (Fig. 1). The contribution to the diets and selection of copepod nauplii declined with increasing fish size; the opposite trend occurred for rotifers. The importance of cyclopoid copepods was greatest for medium shad. *Daphnia* were most important as food for large shad. Calanoid copepods never composed more than 1% of the diet (by numbers of organisms) for any length group and were not preferred food items (L ranged from -0.11 to -0.02).

Mean length of zooplankton ingested by shad rose slightly as the fish grew from small to medium sizes and then declined for large fish (Fig. 1). The length range of zooplankton consumed by gizzard shad increased as shad grew larger.

Feeding incidence varied with fish size in both reservoirs and with site in Pomme de Terre Lake. Feeding incidence increased with fish size (Table 1) and was significantly different among length groups for both reservoirs ($P < 0.001$). Only 17%–36% of small shad contained food while about 70% of large shad contained food in each reservoir. Feeding incidence was significantly higher at the upper site than at the lower site in Pomme de Terre Lake for small and medium shad ($P < 0.001$), but there were no significant site differences for Stockton Lake.

Feeding incidence was sometimes related to food abundance and temperature. Feeding incidence was significantly correlated with zooplankton biomass for small ($r = 0.39$, $P = 0.046$, $N = 27$) and medium shad ($r = 0.48$, $P = 0.004$, $N = 34$) in

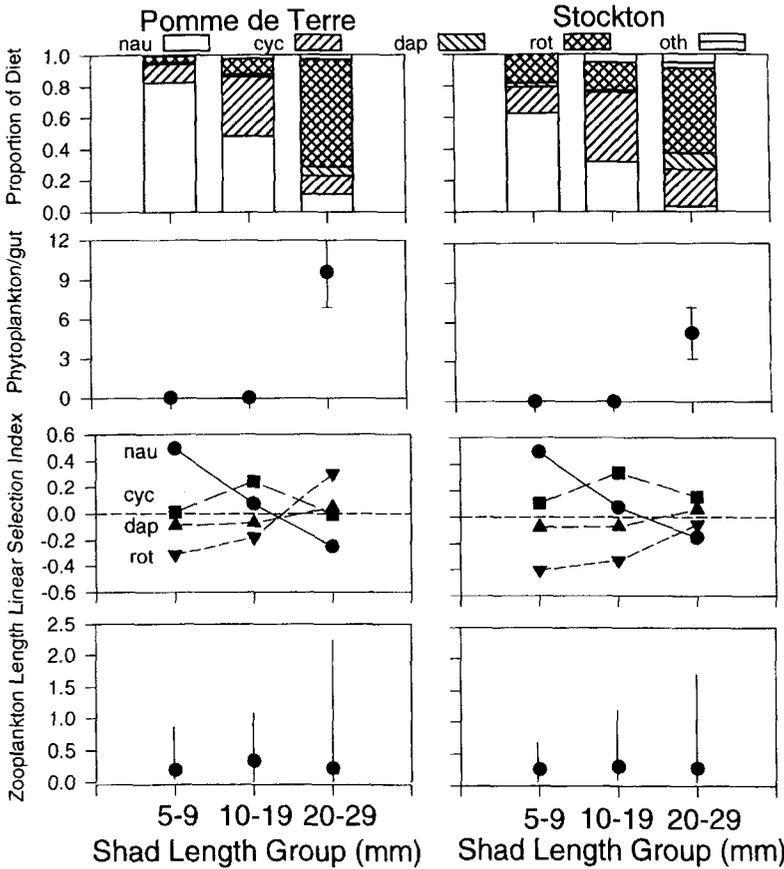


Figure 1. Diet composition (percent by number, excluding phytoplankton), mean N (1,000s) phytoplankton/gut (\pm SE), linear selection index values, and mean total length (mm, TL) and range of ingested zooplankton for length groups (mm) of age-0 gizzard shad collected from Pomme de Terre and Stockton lakes, 1988–1991. Abbreviations are copepod nauplii (nau), cyclopoid copepods (cyc), *Daphnia* (dap), rotifers (rot), and others (oth). The others category was composed of *Bosmina*, *Diaphanosoma*, *Chydorus*, *Leptodora*, and calanoid copepods. The numbers of fish examined with food contents were 147 (5–9 mm TL), 439 (10–19 mm TL), and 95 (20–29 mm TL) for Pomme de Terre Lake and 80 (5–9 mm TL), 371 (10–19 mm TL), and 81 (20–29 mm TL) for Stockton Lake. Standard errors for linear selection index values usually were <0.02 and all were <0.05 .

Stockton Lake and for medium shad ($r = 0.44$, $P = 0.005$, $N = 39$) in Pomme de Terre Lake. Feeding incidence of medium shad was also significantly correlated with temperature ($r = -0.44$, $P = 0.005$, $N = 39$) in Pomme de Terre Lake. No other correlations were significant. Sample sizes were insufficient to test for correlations with large shad using the ≥ 10 shad/date criteria.

Table 1. Percent of digestive tracts that contained food for total length groups (mm) of age-0 gizzard shad collected in Pomme de Terre and Stockton lakes, 1988–1991. N = number of fish. Significant differences ($P \leq 0.05$) between sites within a length group and reservoir are indicated by different capital letters.

Length	Site	N	Percent
Pomme de Terre Lake			
5–9	Upper	142	49A
	Lower	186	26B
	Combined	328	36
10–19	Upper	362	62A
	Lower	310	48B
	Combined	672	56
20–29	Upper	40	70A
	Lower	11	55A
	Combined	51	67
Stockton Lake			
5–9	Upper	260	18A
	Lower	192	16A
	Combined	452	17
10–19	Upper	317	49A
	Lower	280	54A
	Combined	597	51
20–29	Upper	7	71A
	Lower	8	75A
	Combined	15	74

Mean gut fullness also increased with fish size but was not usually correlated with environmental conditions. Mean gut fullness of large shad was about 2 to 6 times higher than that of small shad (Table 2). Only mean gut fullness of medium shad was positively correlated with zooplankton biomass for Stockton Lake ($r = 0.40$, $P = 0.020$, $N = 33$). No other correlations were significant. As before, sample sizes were insufficient for large shad.

Discussion

Diets and food selection of larval and early juvenile gizzard shad were similar to that reported by Kutkuhn (1957), Cramer and Marzolf (1970), Barger and Kilambi (1980), Van Den Avyle and Wilson (1980), and Dettmers and Stein (1992). Small larvae were restricted by their mouth gape (Michaletz et al. 1987, Bremigan and Stein 1994) to feeding on very small organisms such as copepod nauplii, cyclopoid copepodites, and rotifers. As they grew, larger organisms such as adult cyclopoids and *Daphnia* were included in their diet. As they became juveniles and switched from particulate to pump-filter feeding (Drenner et al. 1982), phytoplankton and rotifers

Table 2. Mean gut fullness (food dry weight in mg/fish wet weight in g) for total length groups (mm) of age-0 gizzard shad collected from Pomme de Terre and Stockton lakes, 1988–1991. *N* = number of dates.

Length	<i>N</i>	Mean gut fullness	
		Mean	Range
Pomme de Terre Lake			
5–9	24	0.14	0–0.58
10–19	30	0.15	0–0.73
20–29	15	0.32	0–2.05
Stockton Lake			
5–9	22	0.05	0–0.20
10–19	29	0.16	0–0.57
20–29	10	0.31	0–1.02

dominated their diets. Calanoid copepods were never important in larval or juvenile shad diets, probably because of their good escape abilities (Drenner et al. 1978).

Mean length of prey ingested by shad changed very little as shad grew. There was a slight increase in mean zooplankton prey length as shad grew from small to medium sizes followed by a slight decrease for large shad. These results support the work of Bremigan and Stein (1994) who reported larval shad continue to select for small zooplankton prey even though they are morphologically capable of eating larger prey.

Feeding incidence and mean gut fullness data clearly indicated that foraging efficiency increased with fish size as reported by others (Miller et al. 1988, 1992; Hirst and DeVries 1994, Welker et al. 1994). Most small shad had empty digestive tracts during the afternoon when peak feeding usually occurred (Hayward and Hiebert 1993), documenting their relatively poor feeding success. Feeding incidence of small and medium shad usually increased with food abundance. Too few large shad were sampled to allow for statistical analysis, but most contained food, suggesting they were more successful at using the existing food resources than were small and medium shad.

Correlations between mean gut fullness or feeding incidence of shad with zooplankton biomass were usually weak ($r < 0.50$). Relationships between abundance of food and food amounts in guts of young shad may be at a finer temporal and spatial scale than the methods used in this study could detect. Both shad and zooplankton are patchily distributed in space and time, and interactions between them are probably very complex and difficult to document in field studies.

Feeding success was higher at the upper site than at the lower site in Pomme de Terre Lake, but not in Stockton Lake. The 2 sites in Stockton Lake were more similar in depth and other characteristics than were the 2 sites for Pomme de Terre Lake. For Pomme de Terre Lake, the upper site was considerably shallower and more riverine

than the lower site, providing a greater contrast in potential feeding conditions. Upper portions of reservoirs are usually more productive (Kimmel et al. 1990) and may have higher zooplankton biomass (Marzolf 1990) than lower portions, consequently feeding success should be higher.

Only 1 correlation between either feeding incidence or mean gut fullness with secchi depth and temperature was significant. Secchi depths almost always exceeded 0.7 m at individual locations, higher than those of the turbid inflows (<0.5 m) reported by Matthews (1984) which resulted in starvation of larval shad. Water clarity in the 2 study reservoirs likely did not inhibit feeding of young shad. Although temperature affects many aspects of feeding, including gut evacuation, I found no consistent relation between temperature and feeding success of shad.

In summary, feeding success of young shad was affected by fish size and sometimes by zooplankton biomass and location within a reservoir. Because feeding success affects survival (Crecco and Savoy 1987, Miller et al. 1992), these factors may affect the abundance and size distribution of age-0 shad present in reservoirs. In turn, the abundance and size distribution of age-0 shad affect their potential as competitors (Dettmers and Stein 1992) and their availability as prey for sport fishes (Michaletz 1997). Because feeding success may vary with reservoir location, survival of shad may also differ spatially which could ultimately lead to spatial differences in sport fish growth via differing prey abundances. Because of the importance of age-0 shad and their feeding success to reservoir community dynamics, future research should focus on more clearly defining the temporal and spatial relations among shad, their feeding success, and their prey.

Literature Cited

- Barger, L. E. and R. V. Kilambi. 1980. Feeding ecology of larval shad, *Dorosoma*, in Beaver Reservoir. Pages 136–145 in L. A. Fuiman, ed. Proc. 4th Annu. Larval Fish Conf. U.S. Fish and Wildl. Serv. FWS/OBS-80/43, Washington, D.C.
- Bodola, A. 1965. Life history of the gizzard shad, *Dorosoma cepedianum* (LeSueur), in western Lake Erie. U.S. Fish and Wildl. Serv. Bull. 65:391–425.
- Bremigan, M. T. and R. A. Stein. 1994. Gape-dependent larval foraging and zooplankton size: implications for fish recruitment across systems. Can. J. Fish. and Aquat. Sci. 51:913–922.
- Cramer, J. D. and G. R. Marzolf. 1970. Selective predation on zooplankton by gizzard shad. Trans. Am. Fish. Soc. 99:320–332.
- Crecco, V. and T. Savoy. 1987. Effects of climatic and density-dependent factors on intra-annual mortality of larval American shad. Pages 69–81 in R. D. Hoyt, ed. Proc. 10th Annu. Larval Fish Conf. Am. Fish. Soc. Symp. 2, Bethesda, Md.
- Culver, D. A., M. M. Boucherle, D. J. Bean, and J. W. Fletcher. 1985. Biomass of freshwater crustacean zooplankton from length-weight regressions. Can. J. Fish. and Aquat. Sci. 42:1380–1390.
- Dettmers, J. M. and R. A. Stein. 1992. Food consumption by larval gizzard shad: zooplankton effects and implications for reservoir communities. Trans. Am. Fish. Soc. 121:494–507.
- DeVries, D. R. and R. A. Stein. 1992. Complex interactions between fish and zooplankton-

- quantifying the role of an openwater planktivore. *Can. J. Fish. and Aquat. Sci.* 49:1216–1227.
- Drenner, R. W., J. R. Strickler, and W. J. O'Brien. 1978. Capture probability: the role of zooplankton escape in the selective feeding of planktivorous fish. *J. Fish. Res. Board Can.* 35:1370–1373.
- , F. de Noyelles, Jr., and D. Kettle. 1982. Selective impact of filter-feeding gizzard shad on zooplankton community structure. *Limnol. and Oceanogr.* 27:965–968.
- Dumont, H. J., I. Van de Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda, and Rotifera from the plankton, periphyton, and benthos of continental waters. *Oecologia* 19:75–97.
- Giguère, L. A., J.-F. St-Pierre, B. Bernier, A. Vézina, and J.-G. Rondeau. 1989. Can we estimate the true weight of zooplankton samples after chemical preservation? *Can. J. Fish. and Aquat. Sci.* 46:522–527.
- Hartman, K. J. and F. J. Margraf. 1992. Effects of prey and predator abundances on prey consumption and growth of walleyes in western Lake Erie. *Trans. Am. Fish. Soc.* 121:245–260.
- Hayward, R. S. and J. F. Hiebert. 1993. Low-effort regression estimation of average daily food weight in fishes: application to larval gizzard shad. *Trans. Am. Fish. Soc.* 122:834–844.
- Hirst, S. C. and D. R. DeVries. 1994. Assessing the potential for direct feeding interactions among larval black bass and larval shad in two southeastern reservoirs. *Trans. Am. Fish. Soc.* 123:173–181.
- Johnson, B. M., R. A. Stein, and R. F. Carline. 1988. Use of a quadrat rotenone technique and bioenergetics modeling to evaluate prey availability to stocked piscivores. *Trans. Am. Fish. Soc.* 117:127–141.
- Kimmel, B. L., O. T. Lind, and L. J. Paulson. 1990. Reservoir primary production. Pages 133–193 in K. W. Thornton, B. L. Kimmel, and F. E. Payne, eds. *Reservoir limnology*. John Wiley and Sons, New York, N.Y.
- Knowlton, M. F. 1989. Limnological features of midwest lakes and their relations to sport fish yield. Ph.D. Diss., Univ. Mo., Columbia. 396pp.
- Kutkuhn, J. H. 1957. Utilization of plankton by juvenile gizzard shad in a shallow prairie lake. *Trans. Am. Fish. Soc.* 87:80–103.
- Marzolf, G. R. 1990. Reservoirs as environments for zooplankton. Pages 195–208 in K. W. Thornton, B. L. Kimmel, and F. E. Payne, eds. *Reservoir limnology*. John Wiley and Sons, New York, N.Y.
- Matthews, W. J. 1984. Influence of turbid inflows on vertical distribution of larval shad and freshwater drum. *Trans. Am. Fish. Soc.* 113:192–198.
- Michaletz, P. H. 1997. Influence of abundance and size of age-0 gizzard shad on predator diets, diet overlap, and growth. *Trans. Am. Fish. Soc.* 126:101–111.
- , D. G. Unkenholz, and C. C. Stone. 1987. Prey size selectivity and food partitioning among zooplanktivorous age-0 fishes in Lake Francis Case, South Dakota. *Am. Midl. Nat.* 117:126–138.
- Miller, T. J., L. B. Crowder, J. A. Rice, and E. A. Marschall. 1988. Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Can. J. Fish. and Aquat. Sci.* 45:1657–1670.
- , ———, ———, and F. P. Binkowski. 1992. Body size and the ontogeny of the functional response in fishes. *Can. J. Fish. and Aquat. Sci.* 49:805–812.
- Noble, R. L. 1981. Management of forage fishes in impoundments of the southern United States. *Trans. Am. Fish. Soc.* 110:738–750.

- Rosen, R. A. 1981. Length-dry weight relationships of some freshwater zooplankton. *J. Freshwater Ecol.* 1:225–229.
- Shahady, T. D. 1993. Impact of larval *Dorosoma* predation on *Daphnia parvula* dynamics. *Freshwater Biol.* 30:279–287.
- Storck, T. W. 1986. Importance of gizzard shad in the diet of largemouth bass in Lake Shelbyville, Illinois. *Trans. Am. Fish. Soc.* 115:21–27.
- Strauss, R. E. 1979. Reliability estimates for Ivlev's electivity index, the forage ratio, and a proposed linear index of food selection. *Trans. Am. Fish. Soc.* 108:344–352.
- Van Den Avyle, M. J. and J. R. Wilson. 1980. Food habits and feeding selectivity of larval *Dorosoma* spp. in Center Hill Reservoir. Pages 146–156 in L. A. Fuiman, ed. *Proc. 4th Annu. Larval Fish Conf. U.S. Fish and Wildl. Serv. FWS/OBS-80/43*, Washington, D.C.
- Welker, M. T., C. L. Pierce, and D. H. Wahl. 1994. Growth and survival of larval fishes: roles of competition and zooplankton abundance. *Trans. Am. Fish. Soc.* 123:703–717.