Feeding Preferences of Omnivorous Gizzard Shad as Influenced by Fish Size and Zooplankton Density

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Abstract.—In Ohio reservoirs, larval gizzard shad *Dorosoma cepedianum* less than 30 mm total length consume only zooplankton but frequently switch to detritus as they grow longer than 30 mm. However, in laboratory studies without detritus, gizzard shad longer than 30 mm consume crustacean zooplankton. To explore the composition of diets of omnivorous 30–100-mm gizzard shad, we completed 1-h laboratory feeding trials with different amounts of zooplankton and detritus and quantified the diets of gizzard shad in reservoirs. In both laboratory and field, gizzard shad ate primarily detritus but also ate zooplankton, consuming more as more became available, which demonstrates that this species is a facultative detritivore. In the field, zooplankton consumption declined as gizzard shad body size increased. We believe gizzard shad maximize growth by supplementing their low-protein detritus diet with more zooplankton as more becomes available. With this strategy, omnivorous gizzard shad may compromise the potential for food web manipulations based on the trophic cascade hypothesis in Ohio reservoirs.

Gizzard shad *Dorosoma cepedianum* often dominate fish communities in reservoirs (Jenkins 1967; Cramer and Marzolf 1970; Noble 1981; Johnson et al. 1988) and regulate summer zooplankton (Dettmers and Stein 1992; DeVries and Stein 1992; Dettmers and Stein 1996; Dettmers et al. 1996). As larvae less than 30 mm total length (TL), gizzard shad consume zooplankton almost exclusively (Bodola 1966; Cramer and Marzolf 1970; Dettmers and Stein 1992), reducing crustacean zooplankton to less than 20 individuals/L (Bremigan et al. 1991; DeVries and Stein 1992). By reducing crustacean zooplankton, gizzard shad exacerbate exploitative competition among reservoir fishes dependent on limited zooplankton (e.g., bluegill *Lepomis macrochirus*), perhaps compromising recruitment of these fishes (Guest et al. 1990; DeVries et al. 1991; Dettmers and Stein 1992; Stein et al. 1995).

Beyond 30 mm TL, gizzard shad become omnivorous pump-filter feeders consuming not only zooplankton, but also detritus (Bodola 1966; Cramer and Marzolf 1970; Drenner et al. 1982). Historically, this dietary shift has been attributed to low crustacean zooplankton availability because field evidence revealed that gizzard shad greater than 38 mm TL consumed primarily detritus (Mun-

dahl and Wissing 1987, 1988; Mundahl 1988, 1991), whereas gizzard shad 57–189 mm TL consumed crustacean zooplankton in laboratory pools without detritus (Drenner et al. 1982).

Composition of gizzard shad's diet probably influences the fishes' growth potential. Although gizzard shad can feed selectively on energy-rich detritus (Mundahl and Wissing 1988), detritus is low in protein and frequently compromises growth (Bowen et al. 1995). Hence, gizzard shad that consume more crustacean zooplankton may experience a growth advantage.

The potentially broad range of foods consumed by omnivorous gizzard shad greater than 30 mm may influence their impact on crustacean zooplankton resources, depending on whether gizzard shad alter their feeding preference when exposed to different crustacean zooplankton densities. Specifically, if gizzard shad greater than 30 mm are obligate detritivores, they will have little impact on crustacean zooplankton abundance. Conversely, as facultative detritivores, gizzard shad may continue to strongly influence crustacean zooplankton resources even beyond 30 mm. To determine whether omnivorous gizzard shad behave as obligate or facultative detritivores, we completed feeding trials with different densities of crustacean zooplankton and detritus, and then compared these results to age-0 gizzard shad diets in reservoirs.

Methods

Laboratory experiments.—Gizzard shad were collected by electrofishing from Kokosing Lake

(Knox County, Ohio; detailed description given later) during March and April 1992 and maintained in the laboratory with nauplii of *Artemia* spp. for at least 2 weeks before experiments began. Detritus was collected from the littoral zone of Kokosing Lake in March 1992, whereas crustacean zooplankton (hereafter zooplankton) was obtained from ponds at the Hebron State Fish Hatchery (Licking County, Ohio) during March and April 1992.

We established four treatments: (1) high zooplankton (100 zooplankters/L; biomass about 100 μg/L) only (HZPO; $N = 5$ replicates), (2) high zooplankton and detritus (HZPD; $N = 5$), (3) low zooplankton (20 zooplankters/L; biomass about 20 μg/L) and detritus (LZPD; $N = 5$), and (4) detritus only (DO; $N = 3$). Both HZPO and HZPD reflect zooplankton densities in Clark Lake (see below). We chose LZPD because gizzard shad frequently drive zooplankton below 20/L in reservoirs (DeVries et al. 1991; Dettmers and Stein 1992; DeVries and Stein 1992) and matched densities in Kokosing Lake.

Mean total lengths of gizzard shad in experiments were HZPO ($N = 10$), 101.60 ± 5.36 mm (mean ± 1 SE); HZPD ($N = 10$), 105.00 ± 5.18 mm; LZPD ($N = 10$), 103.30 ± 2.40 mm; and DO ($N = 6$), 74.17 ± 1.99 mm. Gizzard shad in the DO treatment were smaller than fish in other treatments (analysis of variance [ANOVA]: $F = 5.31$, df = 3,14, $P = 0.01$; Tukey's multiple comparisons, $P < 0.05$); hence, all comparisons among treatments were evaluated as micrograms of zooplankton or detritus (dry weight) consumed per gram of wet body weight of gizzard shad to correct for absolute differences in amount of food in guts.

Detritus (3–5 cm) and zooplankton were added to 114-L aquaria 4 d and 24 h, respectively, before experiments began. Zooplankton were dominated by *Bosmina* spp. but also contained nauplii and copepods. Organic plus inorganic material comprised detritus; the organic fraction included both fine and coarse particulates, whereas the inorganic fraction consisted of silt, clay, and sand. We maintained zooplankton in experimental aquaria with algae and did not remove shed zooplankton carapaces from the tanks between trials; hence, carapaces and algae occurred in all treatments and were considered part of the detritus.

During experiments, two gizzard shad, starved for 24 h to permit complete gut evacuation, were added to an aquarium, allowed to feed for 1 h, and then removed, measured (nearest millimeter total length), and frozen for later analysis. During each replicate, we recorded feeding behavior of one randomly chosen gizzard shad. Position in the water column (upper, midlevel, bottom) was recorded every 30 s; feeding activity was recorded every 3 min as the number of feeding gulps during 1 min. After each replicate, zooplankton remaining were estimated with a tube sampler (30-mm inside diameter; $N = 3$ hauls/aquarium; total volume sampled, ~600 mL); zooplankton densities were then increased to original treatment levels in preparation for the next replicate. Replicates of each treatment were run at intervals of at least 24 h to permit settling of detritus.

To quantify gizzard shad diets, we removed both pharyngeal pockets, the foregut, and the gizzard (hereafter, collectively called the gut). We examined gut contents with a dissecting microscope, measured all intact zooplankters (nearest 0.01 mm) when possible, and converted length to dry biomass (Dumont et al. 1975; Bottrell et al. 1976; Culver et al. 1985). When possible, damaged zooplankters within each gut were identified and assigned a total length equal to the mean length of their taxon. Zooplankton carapaces found in guts were considered part of the detritus because they had been shed from zooplankters before ingestion. Gut contents were dried for 24 h at 60°C. We calculated total zooplankton dry weight in each gut by summing individual zooplankton weights. Detritus dry weight was the difference between calculated zooplankton weight and weight of the gut contents.

Gizzard shad wet weights were calculated as per Johnson et al. (1988):

$$\log_e(W) = 3.357 \log_e(L) - 12.97;$$

W = wet body weight (g), and L = total length (mm).

We analyzed overall treatment effects using one-way ANOVA and used Tukey's multiple comparisons to examine treatment differences.

Field pattern.—Kokosing Lake was a 65-ha reservoir with 7.5 km of shoreline, a mean depth of 2.0 m (maximum depth = 4.9 m), and Secchi depths typically less than 1 m. Neither submersed nor emergent vegetation was abundant. Clark Lake (Clark County, Ohio) was a 40-ha reservoir with 4.5 km of shoreline, a mean depth less than 1.0 m (maximum depth = 2.0 m), and typical Secchi depths from 25 to 75 cm. Emergent vegetation (*Typha* spp.) occupied about 25% of the shoreline. Fish communities in both lakes included gizzard shad, largemouth bass *Micropterus salmoides*,
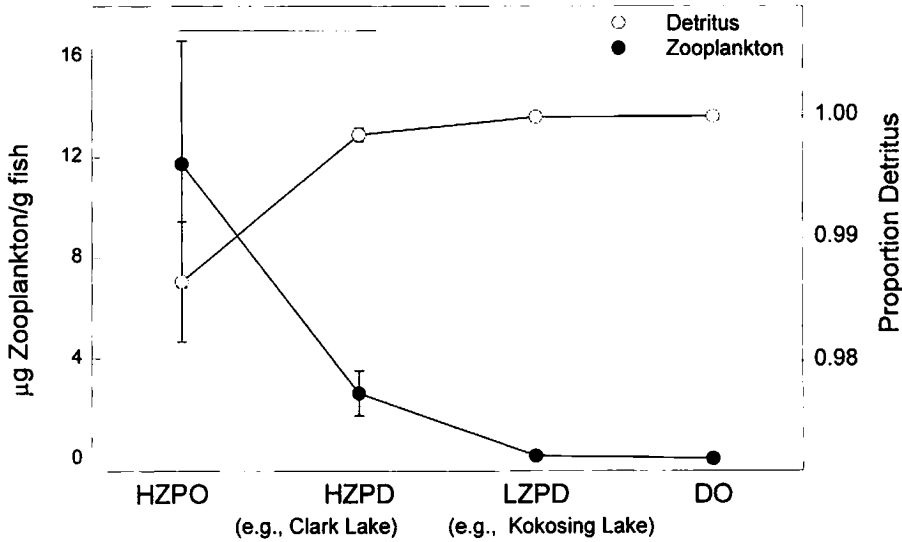
FIGURE 1.—Mean crustacean zooplankton dry biomass (±1 SE) consumed per gram wet body weight of gizzard shad (left y-axis; solid circles) and mean percent detritus in gizzard shad guts (right y-axis; open circles) during experiments in 114-L aquaria. We used 10 replicate fish in each aquarium treatment, except for DO, in which only 6 fish were used; HZPO, zooplankton only; HZPD, high zooplankton plus detritus; LZPD, low zooplankton plus detritus; DO, detritus only. The horizontal line in the upper left signifies similar zooplankton consumption, as determined by Tukey's multiple comparisons (P > 0.05).

white crappie *Pomoxis annularis*, bluegill *Lepomis macrochirus*, and common carp *Cyprinus carpio*.

We collected age-0 gizzard shad by electrofishing or seining from Kokosing Lake on six dates during June through November and from Clark Lake on seven dates during July through August 1992. Fish were immediately placed on ice. Gut contents of 7–15 fish collected from each date and lake were quantified as described earlier.

While seine samples were being taken, zooplankton samples (16–33 L per sample, $N = 3$ sites per date) were collected with a tube sampler (2 m long, 72 mm inside diameter). Each sample was then filtered through a 54-μm mesh net, preserved in 70% ethyl alcohol, and counted as per Stahl and Stein (1994). Up to 20 individuals of each taxon in a sample were measured (nearest 0.01 mm), allowing us to calculate biomass using taxon-specific, length–dry weight regressions (Dumont et al. 1975; Bottrell et al. 1976; Culver et al. 1985).

We evaluated weight-specific zooplankton consumption (μg zooplankton dry weight/g fish wet weight) by age-0 gizzard shad using regression analysis. Data were log-transformed to satisfy normality assumptions.

Results

Laboratory Experiments

Gizzard shad consumed zooplankton in all treatments with zooplankton. Zooplankton biomass

consumed differed significantly among treatments (ANOVA: $F = 3.52$, df = 3,14, $P = 0.04$; Figure 1). Gizzard shad in the HZPO and HZPD treatments consumed similar amounts of zooplankton but more zooplankton than gizzard shad in the LZPD treatment (Tukey's multiple comparisons, $P = 0.05$; Figure 1).

Gizzard shad in all treatments consumed primarily detritus. Detritus consumed did not significantly differ among treatments (ANOVA: $F = 0.59$, df = 3,14, $P = 0.63$). Percent detritus in gizzard shad guts varied from 98.6% in the HZPO treatment to 100% in the DO treatment (Figure 1).

Gizzard shad in all treatments spent 86% of their time swimming in the water column. Most feeding activity (>85%) occurred in midwater rather than near the bottom because gizzard shad frequently approached very close to the bottom, sending clouds of detritus into the water where they could filter it from the water column. Number of feeding gulps per minute did not significantly differ among treatments (ANOVA: $F = 0.09$, df = 3,14, $P = 0.97$).

Field Pattern

Zooplankton in Clark Lake were dominated by nauplii, with *Diaphanosoma* spp. secondarily important. In Kokosing Lake, zooplankton were
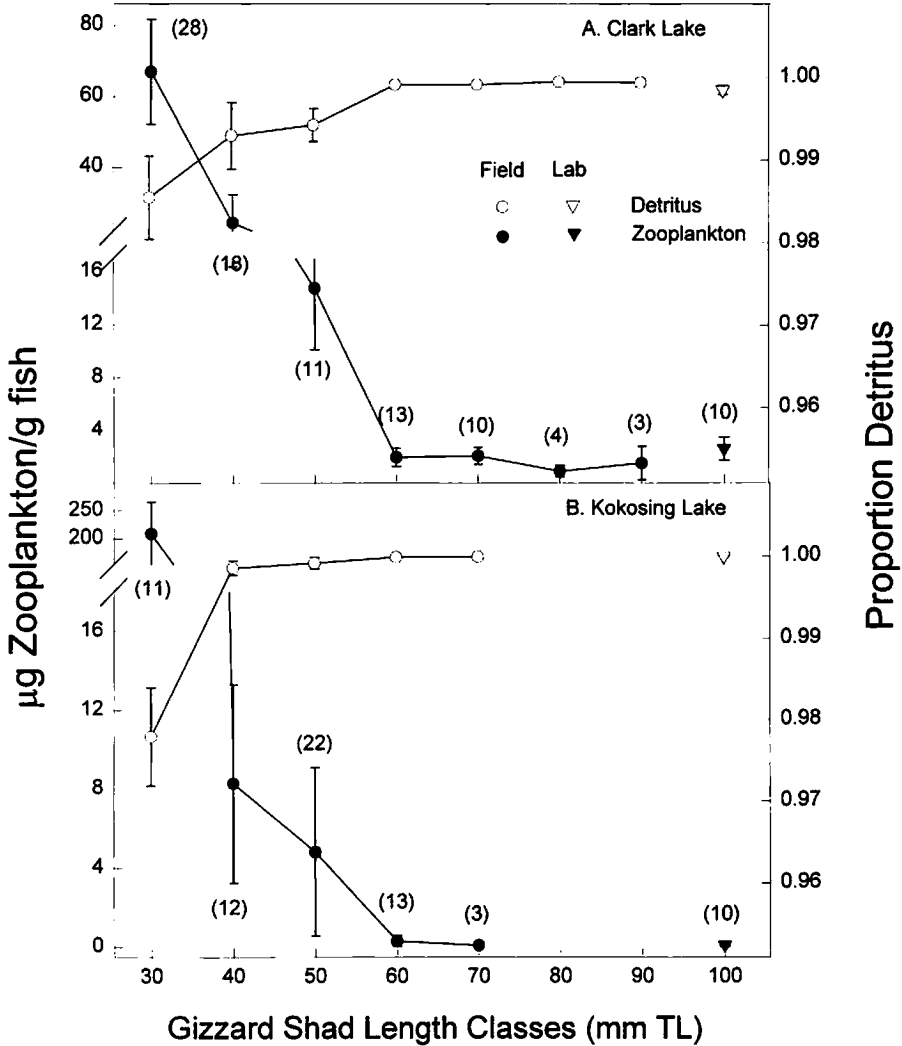
FIGURE 2.—Mean crustacean zooplankton dry biomass (± 1 SE) consumed per gram wet body weight of gizzard shad (left y-axis) and mean percent detritus in gizzard shad guts (right y-axis), as for 10-mm size-classes in (**A**) Clark Lake and (**B**) Kokosing Lake, Ohio, during June–November 1992. Numbers in parentheses reflect sample sizes for each size-class.

dominated by nauplii, *Diaphanosoma* spp., and calanoid copepods. Mean crustacean zooplankton density and biomass differed significantly between lakes (*t*-tests, *P* = 0.0001). Clark Lake zooplankton density and biomass persisted at high levels during 2 July–9 September, maintaining density at 64–158/L and biomass at 90–196 μg/L. Kokosing Lake zooplankton density and biomass remained low during 25 June–9 September, declining to zero on 15 July and never increasing above 25/L and 27 μg/L, respectively.

Total lengths of gizzard shad from Clark (*N* = 87) and Kokosing (*N* = 62) lakes were 52.6 ± 1.9

mm (mean ± SE) and 51.8 ± 11.7 mm, respectively. Gizzard shad from Kokosing and Clark lakes consumed primarily detritus (Figure 2). Weight-specific detritus consumption did not significantly differ between lakes (paired *t*-test, *P* = 0.88). No other trends in detritus consumption were evident, either between lakes or across fish size. Gizzard shad always consumed more than 97% detritus (Figure 2).

Weight-specific zooplankton consumption declined as gizzard shad grew from 30 to 60 mm in both reservoirs (Figure 2). Gizzard shad from 60 to 100 mm maintained constant, low zooplankton

TABLE 1.—Regressions predicting the weight-specific amount of zooplankton in age-0 gizzard shad guts (μg/g) during June–November 1992 in Clark and Kokosing lakes combined. The regression model for both reservoirs was $\log_e$ (zooplankton biomass in gut) = a + $b(\log_e$gizzard shad size) + $c(\log_e$zooplankton biomass in reservoir). Partial r^2 refers to the partial coefficient of determination; one interprets it as the reduction in error by adding the given variable, assuming the other is already in the model. Zooplankton biomass available in each lake is denoted by ZP.

Dependent variable	Regression coefficients			Sum of squares (regression)	Sum of squares (error)	Adjusted R^2	Partial r^2
	a	b	c				
Size and ZP	9.34	−2.77	0.68	41.04	22.98	0.62	
Size	11.36	−2.60		23.28	40.73		0.53
ZP	−1.00		0.62	14.80	49.22		0.44

consumption. Regression analysis with data from both reservoirs revealed that zooplankton consumption declined with increasing gizzard shad size, but increased as zooplankton biomass increased (Table 1; Figure 3). In fact, zooplankton consumption by gizzard shad declined as a function of body size at similar rates in both lakes (test for homogeneity of slopes, $F < 0.01$; df = 1,26; $P = 0.99$), but was always greater in Clark Lake (test for equal intercepts, $F = 16.98$, df = 1,26, $P = 0.0003$). Despite the decline of zooplankton consumption with size, this decline did not affect the capacity of gizzard shad to consume more zooplankton if more was available. However, the stronger determinant of overall gizzard shad consumption was gizzard shad size (Table 1).
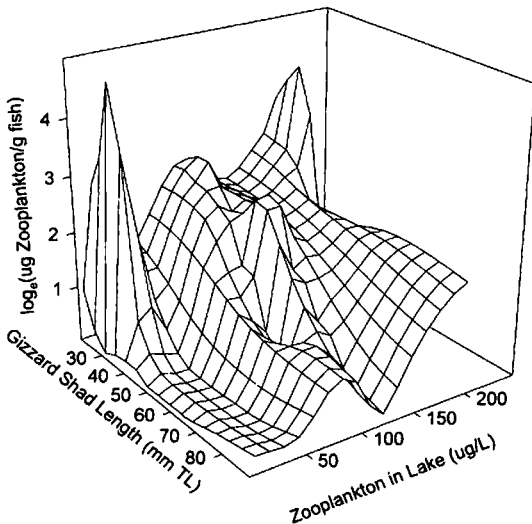

FIGURE 3.—Response curve of dry biomass of mean crustacean zooplankton consumed per gram wet body weight of gizzard shad versus lakewide zooplankton biomass available and gizzard shad size-class in Clark and Kokosing lakes, Ohio, during June–November 1992.

Discussion

With laboratory and field data, we have described the response of 30–100-mm gizzard shad to variable amounts of zooplankton. In both short-term laboratory experiments and in reservoirs, gizzard shad consumed more zooplankton if more became available. Regardless of zooplankton density in the field, weight-specific zooplankton consumption by gizzard shad declined 1–3 orders of magnitude as gizzard shad grew from 30 to 90 mm.

When zooplankton biomass exceeded 90 μg/L (HZPD treatment and Clark Lake), 60–100-mm gizzard shad consumed 1–3 μg zooplankton/g fish, whereas when zooplankton biomass fell below 27 μg/L (LZPD treatment and Kokosing Lake), 60–100-mm gizzard shad ate 0.1–0.3 μg zooplankton/g fish. Interestingly, zooplankton consumption declined by an order of magnitude as zooplankton biomass declined by 70% from Clark to Kokosing Lake.

This dietary pattern of gizzard shad is consistent with that reported in the literature. Although zooplanktivorous as larvae, larger gizzard shad consume zooplankton, phytoplankton, and detritus (Miller 1960; Bodola 1966), frequently feeding primarily on detritus (Mundahl 1988). This decline in zooplankton in diets of gizzard shad greater than 30 mm likely reflects reduced requirements for protein as growth slows because protein frequently limits growth in detritivores (Bowen et al. 1995). To maintain high growth as larvae, when essential amino acids are required for tissue development, gizzard shad consume only zooplankton (Dettmers and Stein 1992; DeVries and Stein 1992). Because protein becomes less limiting as growth slows, omnivorous gizzard shad greater than 30 mm can still generate sufficient caloric intake by increasing detritus consumption, thus compensating for reduced food quality (Bowen et al. 1995).

We conclude that gizzard shad are facultative, rather than obligate, detritivores. Although gizzard

shad do consume less zooplankton as they grow, they also eat more zooplankton if more becomes available. To ensure high growth rates, thus reducing their vulnerability to piscivores (Johnson et al. 1988), gizzard shad should seek to consume as much protein-rich invertebrate prey as possible.

This pattern of zooplankton consumption by omnivorous gizzard shad may have important implications for reservoir food webs. For instance, omnivorous gizzard shad can persist at very low zooplankton abundance (Mundahl 1991), whereas recruitment success of sport fishes with zooplanktivorous larvae requires zooplankton densities exceeding 100/L (Werner and Blaxter 1980; Eldridge et al. 1981; Li and Mathias 1982). Conceivably, when gizzard shad feed primarily on detritus, zooplankton abundance will increase if conditions are favorable for growth and reproduction of zooplankton, again permitting recruitment by zooplanktivores. However, our results suggest that any tendency for increased zooplankton abundance may be offset by increased zooplankton consumption by omnivorous gizzard shad, depending on their size, their population density, and zooplankton productivity (Dettmers and Stein 1996; Dettmers et al. 1996). In our view, successfully manipulating reservoir food webs by the trophic cascade specifically to increase zooplankton is unlikely in the presence of omnivorous gizzard shad.

Acknowledgments

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