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Growth and Survival of Larval Fishes: Roles of Competition and Zooplankton Abundance

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Abstract.—Interactions among larval gizzard shad *Dorosoma cepedianum*, bluegills *Lepomis macrochirus*, and their zooplankton prey were examined in a controlled mesocosm experiment and by field sampling. In the mesocosm experiment, gizzard shad growth and survival were negatively correlated with gizzard shad density and positively correlated with macrozooplankton prey. Bluegill growth was positively correlated with prey availability, but survival was uniformly high despite differences in zooplankton abundance and fish density. Macrozooplankton and copepod biomasses were negatively correlated with fish density. In Lake Shelbyville, co-occurrence of larval gizzard shad and bluegills in the limnetic zone was limited to a 3-week period, and the period of greatest larval gizzard shad abundance preceded the appearance of bluegills. Zooplankton abundance declined greatly after the peak in larval gizzard shad abundance and remained low when bluegills were present. Growth rates of gizzard shad were highest early and declined throughout the summer, whereas bluegill growth was highest during mid to late summer. Growth rates of gizzard shad and bluegills in the field were not correlated with fish density. However, as in the mesocosm experiment, zooplankton biomass was negatively correlated with fish density, bluegill growth was correlated with the abundance of zooplankton prey, and bluegill survival was uniform through time and not related to fish density or zooplankton abundance. Diet overlap was substantial; gizzard shad and bluegills fed selectively on smaller prey items in June, switching to larger cladocerans and copepods by July. Our results suggest that growth and survival of planktivorous larval gizzard shad and growth of larval bluegills are affected by availability of zooplankton prey, which may become limiting when larval fish densities are high.

Knowledge of how larval fish growth and survival relate to prey availability is critical to understanding recruitment processes. Adequate densities of zooplankton prey are important to larval fish growth (Werner and Blaxter 1980; Mills et al. 1989; Papoulias and Minckley 1992) and also survival (Kashuba and Matthews 1984; Hart and Werner 1987). Fluctuations in zooplankton populations can occur both spatially and temporally (Threlkeld 1983) and may be caused, in part, by predation from planktivorous fishes (Post and McQueen 1987; Dettmers and Stein 1992; Lazarro et al. 1992). At low prey densities, intra- and interspecific competition may be important in reducing larval fish growth and survival.

Competition has been recognized as an important mechanism in structuring communities (Connell 1983; Schoener 1983). In aquatic ecosystems, recent studies have demonstrated that both intra- and interspecific competition can be important (Mittelbach 1988; Guest et al. 1990; Persson and Greenberg 1990). Although the majority of past research has centered on competition in the adult stage, more recent research has focused on early developmental stages (Prout et al. 1990; DeVries et al. 1991). Competition may be especially important during these stages, because larval fish are more susceptible to starvation (May 1974). During this critical period in development, larval fish have a short time period to initiate feeding before reaching a point of no return and, ultimately starving (Ehrlich 1974; Miller et al. 1988). If resources are limited during this critical period, growth and survival of larval fish may be reduced (Hart and Werner 1987; Prout et al. 1990).

We examined the potential effects of zooplankton abundance on growth and survival of larvae of two common fishes, gizzard shad *Dorosoma cepedianum* and bluegill *Lepomis macrochirus*, and how intra- and interspecific competition may result from food depletion. Gizzard shad are extremely prolific spawners, and thus their larval densities are high (Storck et al. 1978). They move

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from littoral areas to the limnetic zone shortly after hatching, where they are sight-feeding zooplanktivores until reaching a total length greater than 20 mm (Kutkuhn 1957; Cramer and Marzolf 1970; Jester and Jensen 1972). As larvae, gizzard shad can dramatically reduce macrozooplankton abundance and might adversely impact other planktivorous fishes through competition for resources (Dettmers and Stein 1992; DeVries and Stein 1992). Similarly, high densities of gizzard shad larvae and depressed resources may also lead to intraspecific competition, ultimately limiting their own growth and survival. Past studies have demonstrated that larval gizzard shad suffer high mortality rates (Houser and Netsch 1971; Mitzner 1980), which may be related to low zooplankton densities (Kashuba and Matthews 1984; Matthews 1984).

As with gizzard shad larvae, bluegill larvae move from shoreline nests after hatching to the limnetic zone, where they feed on zooplankton. At a total length of between 10 and 25 mm, they return to the littoral zone, where they feed on macroinvertebrates (Werner and Hall 1988). Bluegills begin spawning several weeks after gizzard shad, and their entry into the limnetic zone also follows that of gizzard shad (Storck et al. 1978; Beard 1982; DeVries and Stein 1992). Therefore, bluegills moving to limnetic areas may face competition for already depressed zooplankton resources, which would lead to reduction in growth and survival.

The objectives of this study were to quantify the impacts of larval fish density and zooplankton abundance on growth and survival of gizzard shad and bluegills, and the impacts of these fishes on their zooplankton prey. Patterns observed from field sampling in a large midwestern reservoir were compared with results of a controlled mesocosm experiment to test three specific hypotheses: (1) growth and survival of larval gizzard shad and larval bluegills are positively correlated with abundance of zooplankton prey; (2) larval gizzard shad and bluegills have the potential to reduce zooplankton density; and (3) both intra- and interspecific larval competition for food may occur as a result of resource depletion.

Methods

Mesocosm experiment.—To evaluate interactions among larval gizzard shad, larval bluegills and their zooplankton prey, an experiment was conducted in 750-L fiberglass tanks (the contents of which are hereafter referred to as mesocosms) during a 2-week period beginning in late June 1990. The duration was short so that environmental differences between mesocosms would be minimized. The experiment consisted of six treatments (three replicates per treatment) with varying densities of each fish species and a fishless control (Table 1). The range of larval fish densities used spanned the range of natural densities observed in Lake Shelbyville, central Illinois, and in other midwestern reservoirs (Dettmers and Stein 1992; DeVries and Stein 1992). Treatments were designed to detect intra- and interspecific competition, as well as the effects of increasing fish densities on zooplankton populations. The experimental design included low and high densities (35 and 70 fish$\cdot$m^{-3}) of either bluegills or gizzard shad alone. Two treatments included both species, one with low bluegill and low gizzard shad densities and the other with low bluegill and high gizzard shad densities (Table 1). A treatment of high bluegill and low gizzard shad densities was not included, because this situation had not been documented by our sampling and did not reflect naturally occurring conditions.

Effects on fish were evaluated by estimating growth and survival, whereas effects on zooplankton were assessed by monitoring changes in zooplankton density, biomass, and species composition in relation to the range of fish densities. Mesocosms were created with water pumped directly from Lake Shelbyville 1 week prior to the experiment to simulate natural zooplankton composition. Water was filtered through an ichthyoplankton net (500-μm mesh) to exclude any larval fish. Each replicate mesocosm was initially fertilized with 12–12–12 (P:N:K) fertilizer at a rate of 0.05 g$\cdot$L^{-1} to maintain productivity. Larval fish were collected from the lake at night by shining a handheld spotlight into a white, translucent bucket. Larval fish were transferred directly from the buckets to holding tanks to reduce handling mortality. After 24 h, live and dead fish in the holding tanks were counted to determine initial mortality; mortality rates were low for both gizzard shad (2%) and bluegills (0%). Mean total lengths (nearest 0.1 mm) and weights (nearest 0.1 mg) were recorded from subsamples of bluegills (N = 119) and gizzard shad (N = 100). Sizes of bluegills (mean $\pm$ 95% confidence interval = 12.3 $\pm$ 2.4 mm) and gizzard shad (15.8 $\pm$ 3.1 mm) closely resembled the sizes of larvae of these two species when they co-occur in the limnetic zone (Welker 1993).

Zooplankton densities in mesocosms were quantified immediately before fish were introduced and twice weekly thereafter with a 2 m long

TABLE 1.—Description of treatments in the 2-week mesocosm experiment. Factorial design was used to assess the potential for intra- and interspecific competition and effects of varying fish densities on zooplankton. There were three replicates per treatment.

Treatment				
Description (density, species)	Abbreviation	Number of gizzard shad	Number of bluegills	Larval fish density (number·m^{-3})
Low, bluegill	B	0	25	35
High, bluegill	BB	0	50	70
Low, gizzard shad	S	25	0	35
High, gizzard shad	SS	50	0	70
Low bluegill + low gizzard shad	BS	25	25	70
Low bluegill + high gizzard shad	BSS	50	25	105
Control (no fish)	C	0	0	0

× 7.5 cm diameter plexiglass tube sampler (DeVries and Stein 1991). Three replicate samples were taken from each mesocosm on each date, filtered through a Wisconsin-type zooplankton bucket (64-μm mesh), and preserved in a sucrose–10% formalin solution (Haney and Hall 1973). In the laboratory, samples were adjusted to a constant volume (100 mL) and subsampled in 1-mL aliquots. Zooplankton were identified to the lowest possible taxon and whole subsamples were counted until at least 200 organisms of each of the most common taxa were enumerated (Dettmers and Stein 1992). Abundant taxa, such as rotifers, were counted in 0.1-mL subsamples. Length frequencies were determined by measuring total body length (nearest 0.01 mm; excluding spines, helmets, and caudal rami) of 10 individuals from each rotifer taxon and 20 individuals from each crustacean taxon per replicate sample. A dissecting microscope (25× magnification) equipped with a drawing tube and electromagnetic digitizing tablet was used to take measurements. Zooplankton densities were converted to biomass by use of species-specific length–weight regressions for crustacean zooplankton (Culver et al. 1985) and rotifers (Dumont et al. 1975). Data from different species were combined for some analyses; total zooplankton included all rotifer and crustacean taxa, whereas macrozooplankton included only cladocerans, copepods, and copepod nauplii.

Light intensity, dissolved oxygen, and water temperature were monitored daily and chlorophyll *a* was checked twice weekly to track any environmental differences between mesocosms. Chlorophyll-*a* concentration was determined by filtering (through 45-μm pores) 1 L of water from zooplankton samples and measuring chlorophyll *a* with a Perkin-Elmers spectrophotometer (APHA et al. 1985). Mean values of these variables were not different between treatments (analysis of variance; $P > 0.05$).

Mesocosms were monitored daily for fish mortality. At the end of 2 weeks, final zooplankton samples were taken and all tanks were drained. Remaining fish were enumerated to determine survival, and were measured for total length (nearest 0.1 mm) and weighed (nearest 0.1 mg) to estimate growth.

Field study.—Field sampling was conducted on Lake Shelbyville, a flood control reservoir located on the Kaskaskia and West Okaw rivers in central Illinois (39°30′N, 88°45′W). The reservoir has a surface area of 4,500 ha and a maximum depth of 18 m (Storck et al. 1978). During 1990 sampling, the water level rose to 5 m above normal pool.

To assess the abundance and growth of larval fishes, as well as monitor zooplankton abundance and limnological conditions, we established five sampling stations along the length of Lake Shelbyville. Larval fishes were collected weekly from April through September in the open-water regions of each station by using paired 0.5-m-diameter conical ichthyoplankton nets (0.5-mm mesh). Nets were towed from a boat with individual bridles on both sides of the bow and were attached 1.5 m above a terminal depressor. Larval tows each lasted 5 min and were done at the surface, and at 1-m depth intervals to a maximum depth of 4 m, at a uniform speed (1.5 m·s^{-1}). The volume of water filtered in each collection was determined with calibrated flowmeters that were suspended in the mouth of each net. Larval fish densities at each depth were calculated and expressed as the number of fish collected per cubic meter of water filtered. Densities were averaged across depths at each station to provide a measure of total fish density (Storck et al. 1978).

Zooplankton and chlorophyll *a* were sampled and Secchi disk visibility and temperature–dissolved oxygen profiles were recorded immediately after larval tows at each station and on each date. Two replicate zooplankton samples were taken by vertically hauling from the bottom a 0.5-m-diameter (64-μm-mesh) zooplankton net. Integrated water samples for chlorophyll-*a* analysis were collected from the surface to within 0.5 m of the thermocline (0.5 m of bottom if no thermocline was present) with a clear polyethylene tube sampler (25.4-mm diameter). Zooplankton and chlorophyll-*a* samples were preserved and analyzed as described for the mesocosm experiment.

To relate changes in zooplankton abundance over time to larval fish abundances and zooplankton fecundities, we calculated changes between sampling dates as total zooplankton biomass on date $x + 1$ minus biomass on date x for each sampling interval at each station. These changes were then paired with larval fish densities and mean zooplankton fecundities on date x from the same stations.

We estimated growth rates for larval gizzard shad and larval bluegills by using daily growth increments found on otoliths (Davis et al. 1985). To ensure that we could obtain reliable age estimates, two readers aged a separate set of known-age otoliths. No differences were found between estimated and known ages of larval gizzard shad and bluegills from 2 to 71 d old (paired t-tests; $P > 0.05$). Sagittal otoliths were removed from larval fishes ($N = 50$ per date, station, and species; maximum of 5 per 1-mm size-interval) and mounted on microscope slides, and daily rings were counted by two readers. Age estimates from the two readers were averaged (Davis et al. 1985). If reader counts did not agree within 10% for a specimen, the otolith was reexamined until a consensus was reached, or the fish was eliminated from the data set. Growth rates for each species on each date were then estimated by the slope of the regression of larval length versus age in days.

Larval fish diets were compared by analyzing the stomach contents of 15 fish (1–2 per 1-mm size-interval) of each species at each station on three dates (June 15, June 27, and July 12). Stomach contents were removed and individual zooplankton prey items were identified to the lowest possible taxon and measured as described above. An index of feeding selectivity, Chesson's α (Chesson 1978, 1983), was calculated for each prey taxon. Alpha values for zooplankton taxa were compared against values expected if prey were eaten in direct proportion to their abundance. Positive selection was defined as an α value greater than the reciprocal of the number of prey taxa available in the lake on that date (Chesson 1983). Diet overlap between gizzard shad and bluegills was estimated by the Schoener index (Wallace 1981). In addition, gut fullness was calculated as the dry weight (g) of prey items in the stomach divided by the wet weight (g) of the fish.

To determine the effects of larval gizzard shad densities on recruitment of bluegills, juvenile bluegills were collected by seining from littoral-zone areas adjacent to each station during September 1990. At each station, 30 randomly selected fish were measured, and their otoliths were removed to determine age in days. Sagittal otoliths were removed, ground on 600-grit sandpaper, and polished, and rings were counted under a microscope with oil immersion. Each otolith was read by two readers. If counts were within 10%, values were averaged. Juvenile bluegill ages determined from daily otolith rings were used to identify first-feeding dates, from which we could infer the period of maximum recruitment success (i.e., the larval period resulting in the greatest recruitment of juvenile bluegills to the littoral zone). To evaluate relative survival of bluegill larvae, we considered first-feeding dates of juvenile bluegills recruiting to the littoral zone in the fall and larval bluegill abundance estimated from summer ichthyoplankton tows. The distribution of first-feeding dates "back-dated" from juveniles was divided into groups corresponding to larval sampling dates, such that the sampling dates were the midpoints. These frequencies were then compared with larval bluegill abundance by using Spearman's rank correlation.

Statistical analyses.—Larval fish growth and survival data, and zooplankton abundance data, from the mesocosm experiment and field study were analyzed with analysis of variance (ANOVA) to compare differences among treatments. Tukey's multiple-comparisons test was used to detect differences between treatments and the control and among treatments. Correlation analysis was used to determine relationships between several variables: fish growth, fish survival, fish density, zooplankton abundance, zooplankton biomass, and chlorophyll-*a* concentration. Regression equations were generated to define several of the significant correlations. Survival data (proportions, p) were transformed as arcsine ($p^{0.5}$) prior to analyses, and growth and zooplankton abundance data were analyzed untransformed.

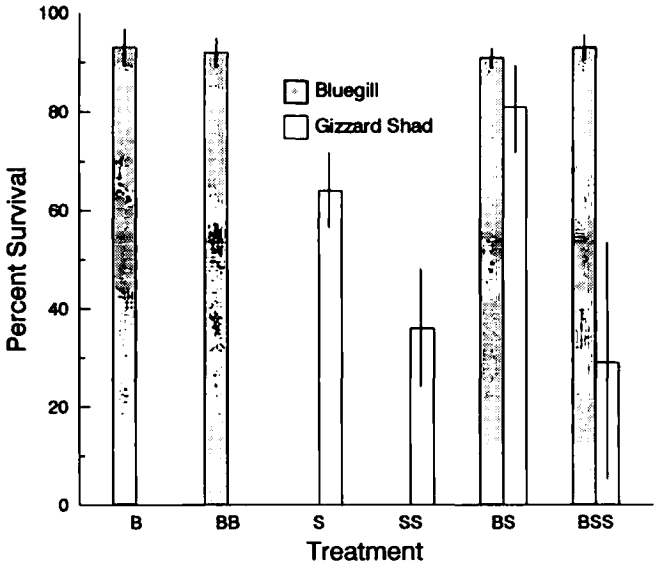

FIGURE 1.—Percent survival (mean ± 95% confidence interval) of larval gizzard shad and bluegills in different mesocosm experiment treatments (see Table 1). Percentages shown are untransformed; proportions (p) were transformed (arcsine[$p^{0.5}$]) for analysis.

Field study data were analyzed with ANOVA. As in the mesocosm experiment, correlation analysis was used to examine relationships between variables and regression equations were generated to define significant correlations. Survival (proportions) was transformed as arcsine($p^{0.5}$) and zooplankton abundance (a) was transformed as $\log_{10}$(a) to conform with assumptions and conventions of ANOVA and parametric correlation analysis. All analyses were performed with general linear models (GLM) and correlation (CORR) procedures (SAS Institute 1991).

Results

Survival and Growth of Larval Fish in Mesocosms

Survival of gizzard shad varied considerably among and within treatments, whereas bluegill survival was uniformly high across treatments (Figure 1). Survival of gizzard shad was high in the low-density treatments (S and BS) and reduced in the high-density treatments (SS and BSS); however, these differences were not significant because of variability among replicates (ANOVA: $F = 2.84$; df = 3, 8; $P = 0.10$). Bluegill survival was uniform among treatments (ANOVA: $F = 0.18$; df = 3, 8; $P = 0.90$). Growth of gizzard shad was somewhat higher in low-density treatments (S and BS) than in high-density treatments (SS and BSS), but these differences were not significant (ANOVA: $F = 1.58$; df = 3, 8; $P = 0.26$). Growth of bluegill during the experiment was highest in the two bluegill-only treatments (B and BB) and lowest in treatments containing gizzard shad (BS and BSS). As was the case with gizzard shad growth, differences in bluegill growth between treatments were not significant (ANOVA: $F = 1.94$; df = 3, 8; $P = 0.20$). Variation in gizzard shad survival between replicate treatments and uncontrollable differences in initial zooplankton biomass among replicates obscured the distinction between the treatment levels. Accordingly, growth and survival of fish, and responses of zooplankton prey, were examined as correlations across the entire set of mesocosms.

Gizzard shad survival was positively correlated with total zooplankton biomass per fish (Figure 2), and was more strongly correlated with macrozooplankton per gizzard shad ($r = 0.84$, $P = 0.0005$) and with gizzard shad density ($r = -0.68$, $P = 0.015$). Conversely, bluegill survival was not correlated with total zooplankton biomass per fish (Figure 2), with abundance of any of the zooplankton groups, or with fish density.

Both gizzard shad growth and bluegill growth in mesocosms were positively correlated with total zooplankton biomass per fish (Figure 3). Gizzard shad growth was also negatively correlated with gizzard shad density ($r = -0.57$, $P = 0.05$). In contrast, bluegill growth was not related to ei-

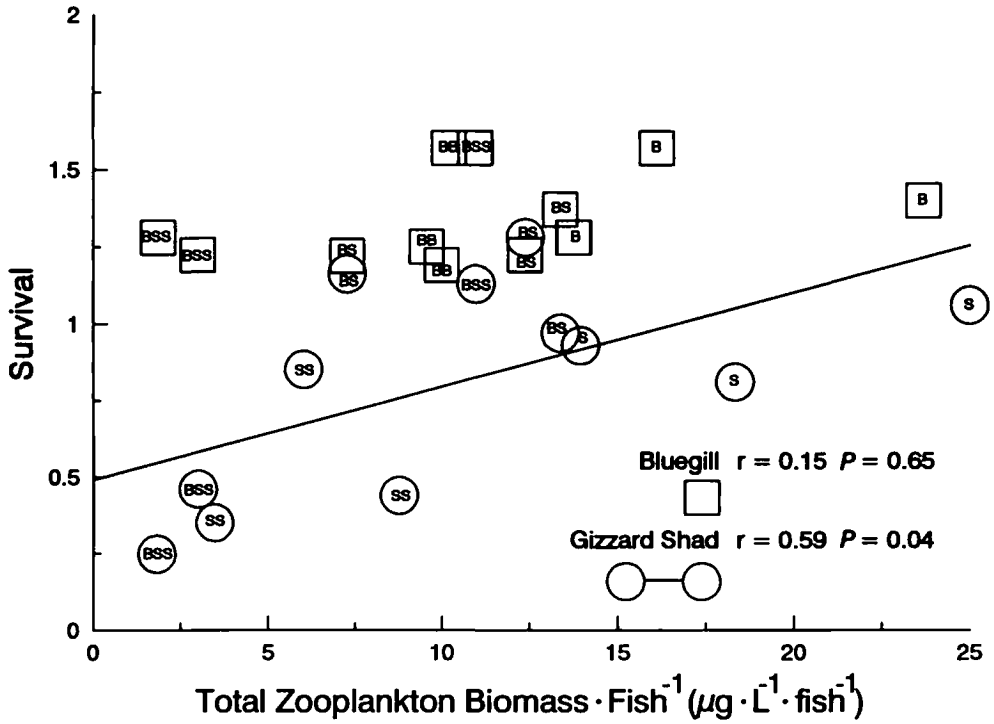

FIGURE 2.—Relationship of larval fish survival (arcsine[$p^{0.5}$]) with total zooplankton biomass per fish (initial biomass·initial fish density^{-1}) in the mesocosm experiment. Treatment abbreviations, defined in Table 1, are given within symbols. The regression equation for gizzard shad is $Y = 0.49 + 0.03X$.

ther total fish density or gizzard shad density ($r = -0.54$, $P = 0.07$; $r = -0.53$, $P = 0.07$).

Effects of Larval Fish on Zooplankton in Mesocosms

Zooplankton populations were monitored to determine the impact of fish density on zooplankton abundance and species composition. Overall, treatments resulted in significant changes in macrozooplankton biomass (ANOVA: $F = 5.01$; df = 6, 14; $P = 0.006$) and copepod biomass (ANOVA: $F = 5.09$; df = 6, 14; $P = 0.006$) with respect to fishless controls. Macrozooplankton were reduced in the treatment with high bluegill density and in the treatment with low bluegill and low gizzard shad densities, and copepods were reduced in most treatments ($P < 0.05$, Tukey's multiple comparisons; Table 2). No other zooplankton groups had significant changes in abundance in any of the treatments. Changes in macrozooplankton and copepod biomass were positively correlated with fish densities at the end of the experiment (Figure 4). Among individual zooplankton taxa, only the copepod *Acanthocyclops vernalis* was reduced in treatments relative to the fishless control (ANOVA: $F = 3.84$; df = 6, 14; Tukey's multiple comparisons, $P < 0.05$). Reductions of *A. vernalis* were primarily responsible for the dramatic declines in copepod and macrozooplankton biomass.

Limnological Conditions in Lake Shelbyville

Limnological conditions throughout the summer sampling period in Lake Shelbyville ranged as follows: Secchi disk visibility, 41–117 cm; chlorophyll *a*, 1.7–8.9 mg·L^{-1}; temperature, 15.9–26.8°C; and dissolved oxygen, 5.5–11.1 mg·L^{-1} (Welker 1993). Differences in these values were detected on both temporal and spatial scales. Chlorophyll-*a* concentrations were different among dates, being highest during mid-July and lowest during mid-May (two-way ANOVA: $F = 2.44$; df = 10, 39; $P = 0.02$). Differences in temperature were also detected among dates (two-way ANOVA: $F = 79.14$; df = 10, 39; $P = 0.0001$), with the highest values recorded during late July. No significant spatial differences were detected for these variables. Secchi disk visibility was lower at uplake stations (two-way ANOVA: $F = 41.65$; df = 4, 39; $P = 0.0001$), a reflection of the considerable sediment load of inflowing rivers, and also

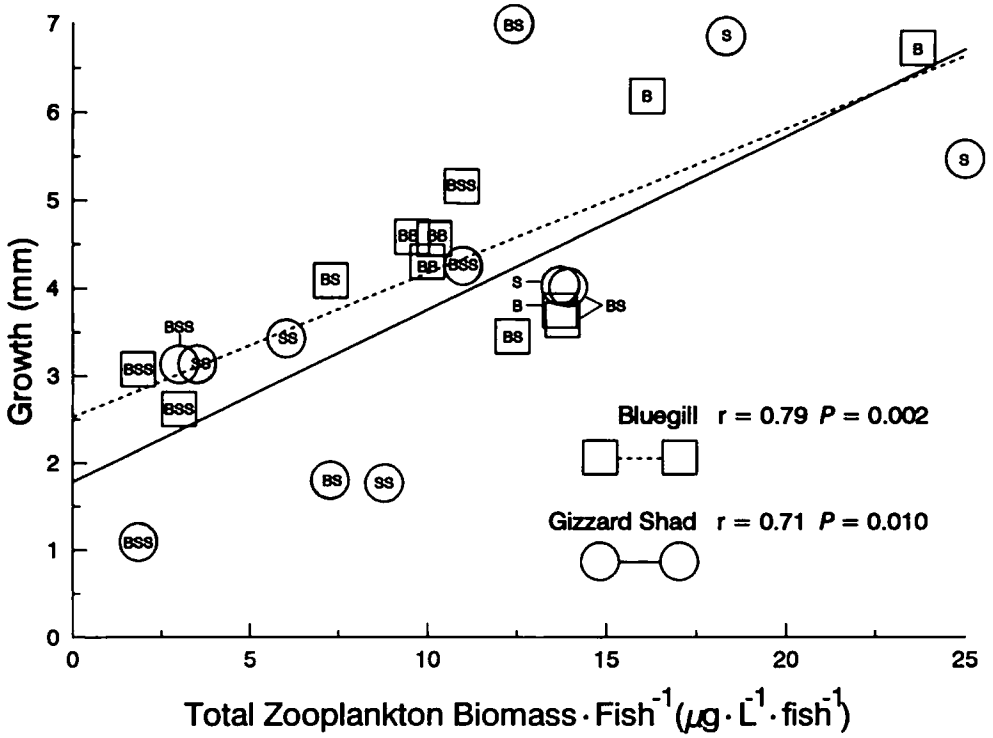

FIGURE 3.—Relationship of growth (in total length) of gizzard shad and bluegills with total zooplankton biomass per fish (initial biomass·initial fish density^{-1}) in the mesocosm experiment. Treatment abbreviations, defined in Table 1, are given within symbols. The regression for bluegills is $Y = 2.52 + 0.16X$; the regression for gizzard shad is $Y = 1.78 + 0.20X$.

differed over time (two-way ANOVA: $F = 3.72$; df = 10, 39; $P = 0.001$), being higher later in the season. Dissolved oxygen concentrations differed over time (two-way ANOVA: $F = 7.56$; df = 10, 39; $P = 0.0001$) and space (two-way ANOVA: $F = 15.06$; df = 4, 39; $P = 0.0001$), being highest downlake and during June and July.

Abundance, Growth, and Survival of Larval Fish in Lake Shelbyville

Larval gizzard shad were first collected in late April (Figure 5). Abundance of larval gizzard shad increased through May, peaking during early June (ANOVA: $F = 2.46$; df = 10, 54; $P = 0.02$). Densities declined rapidly thereafter and gizzard shad larvae were absent from limnetic ichthyoplankton tows by late July. In contrast, larval bluegills were first collected in mid-June and densities peaked in mid-July (Figure 5; ANOVA: $F = 8.28$; df = 10, 54; $P = 0.0001$). Thus, temporal overlap between larval gizzard shad and bluegill was limited to a 3-week period. Bluegill densities were lower than gizzard shad densities by two orders of magnitude on all dates.

Growth of gizzard shad was not different among stations (two-way ANOVA: $F = 2.53$; df = 4, 10; $P = 0.11$) but varied through time (two-way ANOVA: $F = 4.80$; df = 3, 10; $P = 0.03$), being highest early in the year and declining throughout the summer. Growth was not correlated with gizzard shad density ($r = 0.27$, $P = 0.28$) or with total larval fish density ($r = 0.27$, $P = 0.29$). Similarly, bluegill growth was not different among stations (two-way ANOVA: $F = 0.38$; df = 4, 12; $P = 0.82$) but varied among dates (two-way ANOVA: $F = 8.12$; df = 3, 12; $P = 0.003$). Growth of larval bluegill was highest during mid-July and early August, after abundance of gizzard shad declined, and was slowest during June, when larval gizzard shad were abundant in the limnetic zone. However, across all sites and dates, bluegill growth was not significantly correlated with gizzard shad density ($r = -0.32$, $P = 0.11$) or total larval fish density ($r = -0.29$, $P = 0.15$).

As in the mesocosm experiment, larval bluegill

TABLE 2.—Mean change (95% confidence intervals in parentheses) in biomass of zooplankton groups in treatments from the mesocosm experiment. Changes were calculated as final minus initial biomass (dry weight, $\mu g \cdot L^{-1}$) for each replicate mesocosm. Asterisks indicate means that were significantly different from controls ($P < 0.05$*). Treatments are described in Table 1.

Zooplankton group	Control	Treatment					
		B	BB	S	SS	BS	BSS
Total zooplankton	145.7	573.6	93.9	−248.0	−155.4	−287.7	−292.6
	(173.0)	(1,162.3)	(315.0)	(365.0)	(17.6)	(527.0)	(399.0)
Macrozooplankton	55.6	−172.9	−367.9*	−211.9	−114.2	−326.1*	−194.8
	(174.0)	(111.0)	(74.5)	(86.2)	(23.3)	(65.0)	(207.0)
Copepods	134.7	−70.4	−145.8*	−131.9*	−43.5	−151.6*	−99.5*
	(137.0)	(62.7)	(50.9)	(105.6)	(10.3)	(39.2)	(117.6)
Copepod nauplii	−80.5	−96.1	−206.6	−69.4	−67.4	−171.1	−82.2
	(37.0)	(45.0)	(77.0)	(28.6)	(35.9)	(86.0)	(94.0)
Cladocerans	1.3	−6.4	−15.5	−10.1	−3.2	−3.4	−12.6
	(24.0)	(6.9)	(30.7)	(11.9)	(17.0)	(1.8)	(11.3)
Rotifers	90.1	746.5	445.2	−36.6	−41.3	−38.4	−97.8
	(47.7)	(1,058.4)	(405.0)	(351.3)	(6.9)	(499.0)	(219.0)

growth was positively correlated with total zooplankton biomass per fish (Figure 6). In addition, there were slightly stronger correlations between larval bluegill growth and both macrozooplankton biomass per fish ($r = 0.54$, $P = 0.005$) and copepod biomass per fish ($r = 0.53$, $P = 0.006$). In contrast, gizzard shad growth was not related to either total zooplankton biomass per fish or any other zooplankton group or taxon. Bluegill growth was positively correlated with gut fullness (Figure 7), but no relationship between gizzard shad growth and gut fullness was observed ($r = -0.12$, $P = 0.60$). Bluegill growth was not correlated with temperature ($r = -0.07$, $P = 0.61$), whereas gizzard shad growth exhibited a negative relationship with temperature ($r = -0.59$; $P = 0.01$).

First-feeding bluegills were present in the limnetic zone from mid-June through late August and

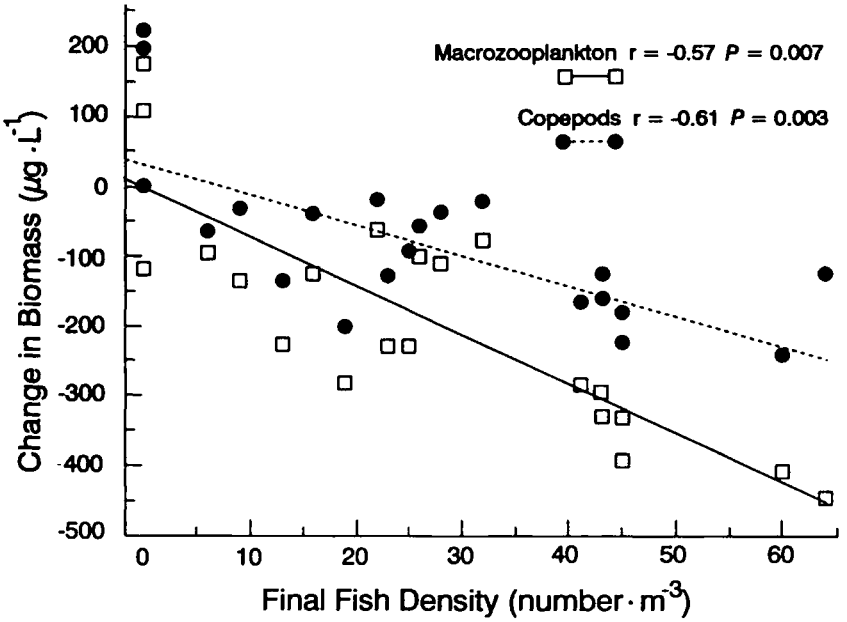

FIGURE 4.—Relationship of changes in macrozooplankton and copepod biomass with fish density at the end of the mesocosm experiments with gizzard shad and bluegill larvae. Changes in macrozooplankton and copepod biomass were calculated as final minus initial biomass. The regression for macrozooplankton is $Y = 4.2 - 7.0X$; the regression for copepods is $Y = 35.1 - 4.0X$.

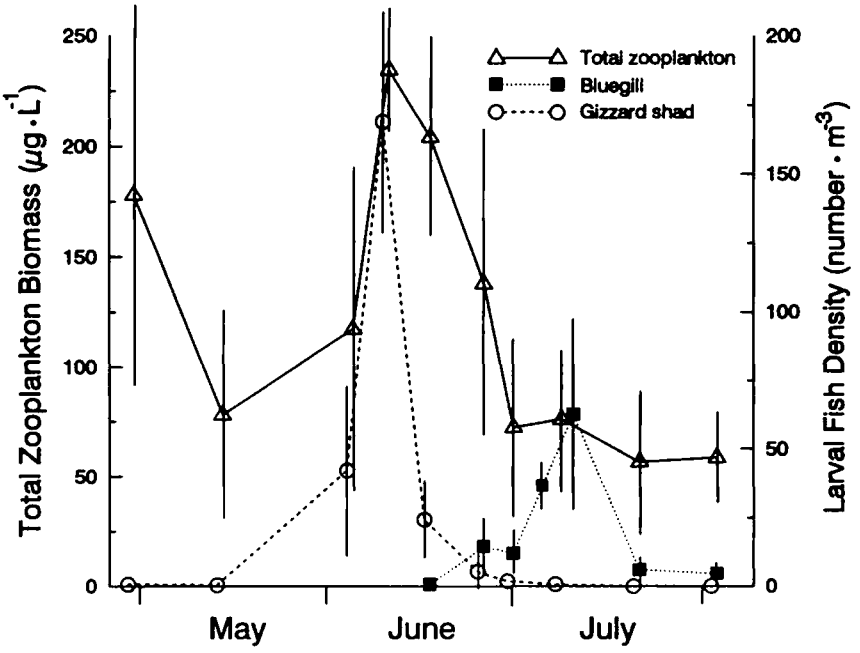

FIGURE 5.—Mean densities of larval gizzard shad (density × 1) and bluegills (density × 100) and mean total zooplankton biomass in Lake Shelbyville, 1990. Mean bluegill densities never exceeded 1 fish/m^3 and were multiplied by 100 for presentation. Means were averaged across stations; vertical lines represent 95% confidence intervals.

showed periodic peaks in density throughout the summer (Figure 8). The period of first feeding resulting in greatest juvenile recruitment occurred during early July, at a time when larval bluegill abundance was high. The median date of first larval feeding (see arrow in Figure 8) occurred almost simultaneously with the period of greatest larval bluegill abundance. The distribution of first feeding dates was positively correlated with larval bluegill abundance (Spearman's rank correlation,

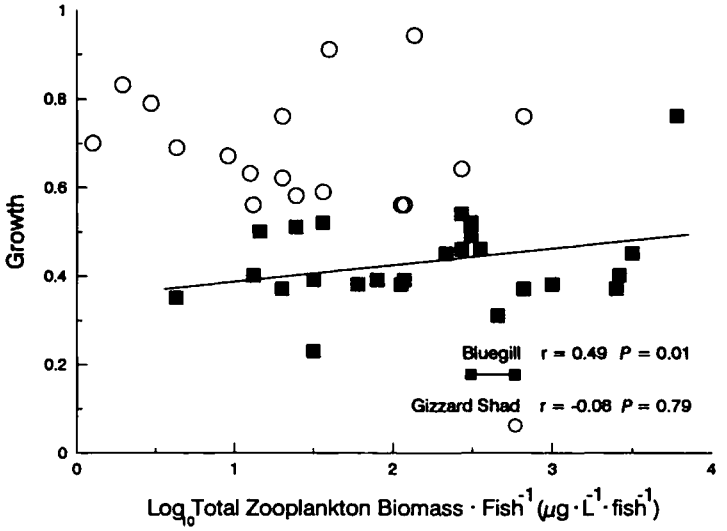

FIGURE 6.—Relationship of growth of larval gizzard shad and bluegills with total zooplankton biomass per fish in Lake Shelbyville, 1990. The regression for bluegills is $Y = 0.35 + 0.04X$.

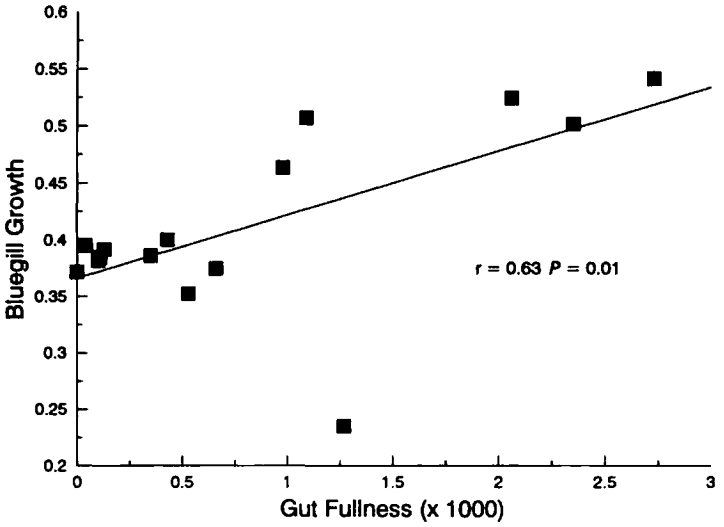

FIGURE 7.—Relationship of growth of larval bluegills in Lake Shelbyville with gut fullness, 1990. The regression is $Y = 0.38 + 0.20X$.

$r_s = 0.74$; $P = 0.04$), further suggesting that there was no strong pattern of differential survival of bluegill larvae to the juvenile stage.

Diets of Larval Fish in Lake Shelbyville

Proportions of prey items found in the stomachs of larval gizzard shad and bluegills changed dramatically during the time when both species inhabited the limnetic zone. In gizzard shad stomachs, copepods, rotifers, and copepod nauplii made up the the majority of identified contents during the first part of the period, and the proportions of cladocerans and copepods increased through time. Similarly, bluegill stomachs early in the year contained mostly smaller rotifers and copepod nauplii, and the prey composition shifted to copepods and cladocerans later in the year.

Gizzard shad positively selected rotifers and the copepods *A. vernalis* and *Diaptomus siciloides* during early June (Table 3). By late June gizzard shad were selecting the rotifers *Brachionus* sp., the copepod *A. vernalis*, and the cladocerans *Bosmina longirostris*, *Diaphanasoma leuchtenbergianum*, and *Daphnia* spp. During July, gizzard shad were selecting exclusively the cladocerans *Moina micrura* and *Ceriodaphnia reticulata*. Bluegills were also positively selecting *Brachionus* spp. and *A. vernalis* during early June, in addition to copepod nauplii. In July, their diets shifted from smaller nauplii and rotifers to larger-bodied prey items, as indicated by positive selectivity values for *A. vernalis*, *B. longirostris*, *D. leuchtenbergianum*, *M. micrura*, and *C. reticulata*. Diet overlap (Schoener's index) between the two species was high (0.89–0.98) throughout their period of co-occurrence in the limnetic zone.

Mean gut fullness ranged from near 0 to 0.0024 (prey dry weight·fish wet weight^{-1}; weights measured in grams) for gizzard shad and from 0 to 0.0028 for bluegills. Gut fullness of gizzard shad differed among dates (two-way ANOVA: $F = 38.33$; df = 2, 202; $P = 0.0001$), being highest during mid-July. Similarly, gut fullness of bluegill was highest during the same time period (two-way ANOVA: $F = 28.95$; df = 2, 191; $P = 0.0001$). Bluegill gut fullness averaged slightly higher at stations in the upstream end of the reservoir (two-way ANOVA: $F = 2.82$; df = 4, 191; $P = 0.03$); gizzard shad gut fullness did not vary significantly across stations. Gut fullness of neither gizzard shad nor bluegill was correlated with fish density across sites or dates. Gut fullnesses of both bluegill ($r = 0.36$, $P = 0.0001$) and gizzard shad ($r = 0.33$, $P = 0.0001$) were correlated with fish size.

Larval Fish and Zooplankton Relationships in Lake Shelbyville

Total zooplankton biomass in Lake Shelbyville increased from May to early June, peaking during the first week in June (Figure 5). Peak biomass was followed by a precipitous decline shortly after larval gizzard shad densities peaked. When gizzard shad densities in the limnetic zone fell to near

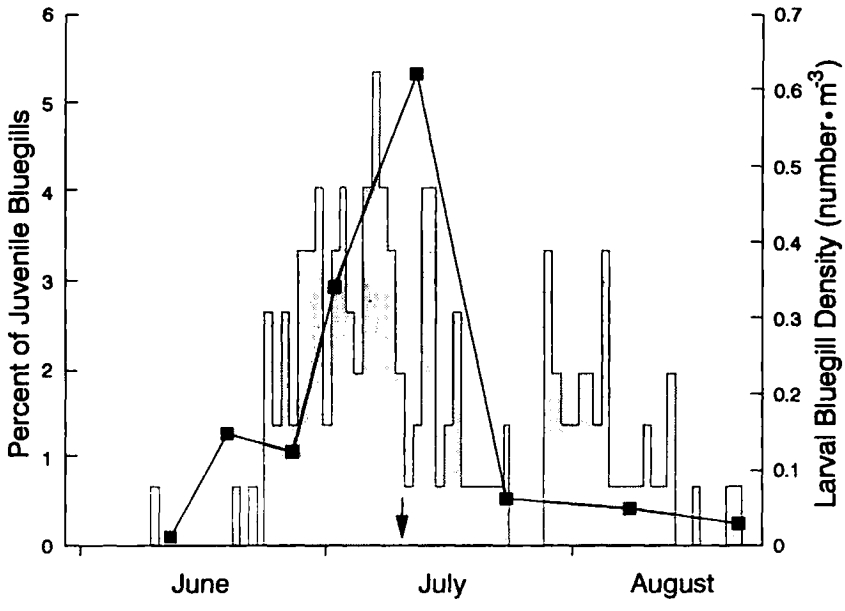

FIGURE 8.—Comparison of first-feeding dates of juvenile bluegills collected in the littoral zone with larval bluegill densities in Lake Shelbyville, 1990. The distribution of first larval feeding dates (histogram) was estimated by counting daily rings on otoliths from juvenile bluegills collected from the littoral zone in September 1990. Mean larval bluegill densities (solid squares) were determined from limnetic ichthyoplankton tows. The arrow indicates the median day of first feeding.

zero in late June, zooplankton biomass apparently stabilized at the lower levels (Figure 5).

Changes in zooplankton biomass were weakly correlated with fish density ($r = -0.29$, $P = 0.03$, $N = 54$) across all dates; however, the correlation was somewhat stronger ($r = -0.53$, $P = 0.02$, $N = 20$) for June and early July, when larval fish densities were highest. Correlations of zooplankton biomass changes with chlorophyll-*a* concentrations were not significant ($P > 0.05$). Declines in total zooplankton biomass were largely due to declines in copepod biomass ($r = 0.65$, $P = 0.0001$), upon which both larval gizzard shad and bluegill fed heavily (Tables 2, 3). No relationship was observed between zooplankton fecundity (mean number of eggs per zooplankter) and changes in zooplankton biomass ($r = -0.10$, $P = 0.5$).

Discussion

Our study suggests that larval fish can have significant negative effects on populations of their zooplankton prey. In mesocosms, reductions in macrozooplankton and copepod biomass were observed in all treatments relative to the fishless control. Similarly, zooplankton biomass declined precipitously in Lake Shelbyville after larval fish densities peaked, and apparently stabilized as larval fish densities declined. These changes in zooplankton biomass may have been due to predation, but may also have been related to changes in zooplankton fecundity.

We did not quantify fecundity in the mesocosm experiment, but the short duration of the experiment should have minimized the effects of fecundity. We did observe a significant relationship between changes in zooplankton biomass and fish density. In Lake Shelbyville, we found no relationship between zooplankton fecundity and biomass. Although changes in zooplankton biomass were only weakly linked to fish densities over the entire sampling period, a stronger negative correlation was observed during June and July when larval fish densities were highest. These results suggest that declines in zooplankton biomass resulted from planktivory by larval fish and are supported by previous studies that have linked the presence of planktivorous fish to shifts in zooplankton abundance, and species composition and size distribution of zooplankton communities (Lazzaro 1987; Post and McQueen 1987; Dettmers and Stein 1992).

Our mesocosm experiment revealed that larval fish growth was related to prey availability. A similar pattern between bluegill growth and prey

TABLE 3.—Diet selection (Chesson's α) for zooplankton taxa by larval bluegills and gizzard shad in Lake Shelbyville, Illinois, 1990. For a given prey taxon, α can range from 0 (absent from diet) to 1 (all items in diet). An asterisk (*) indicates positive selection (α greater than the reciprocal of the number of prey taxa available). Size ranges (total lengths) of fish present are given for each date.

	Bluegills			Gizzard shad		
Zooplankton taxon	Jun 15 (4–8 mm)	Jun 27 (6–11 mm)	Jul 12 (6–23 mm)	Jun 15 (5–16 mm)	Jun 27 (6–27 mm)	Jul 12 (10–28 mm)
Rotifers	0.82*	0.08*	0.0	0.30*	0.08*	0.0
Diaptomus siciloides	0.0	0.0	0.01	0.24*	0.01	0.0
Acanthocyclops vernalis	0.06*	0.20*	0.08*	0.43*	0.10*	0.03
Copepod nauplii	0.11*	0.07*	0.0	0.01	0.01	0.0
Bosmina longirostris	0.0	0.65*	0.06*	0.0	0.67*	0.02
Daphnia spp.	0.0	0.0	0.05	0.0	0.06*	0.01
Diaphanasoma leuchtenbergianum	0.0	0.0	0.11*	0.0	0.07*	0.02
Moina micrura	0.0	0.0	0.14*	0.0	0.0	0.09*
Ceriodaphnia reticulata	0.0	0.0	0.36*	0.0	0.0	0.83*

availability was also documented in the field study. Although gizzard shad growth in the field study was not correlated with zooplankton abundance, growth tended to be higher early in the season, when zooplankton abundance was high, than later when zooplankton abundance was declining. Numerous studies have documented similar influences of prey abundance on larval fish growth (Werner and Blaxter 1980; Papoulias and Minckley 1992). In addition, many of the factors regulating larval fish survival are size dependent (Miller et al. 1988). Therefore, reduced growth rates might be expected to ultimately result in increased mortality.

Our mesocosm experiment demonstrated that survival of larval gizzard shad was related to prey availability, as has been determined for other larval fishes (Werner and Blaxter 1980; Kashuba and Matthews 1984; Hart and Werner 1987; Freeberg et al. 1990). Although we did not quantify gizzard shad survival in the field, our mesocosm experiment and results of previous studies (Houser and Netsch 1971; Mitzner 1980; Kashuba and Matthews 1984; Matthews 1984) predicted that gizzard shad survival would be lower during periods of reduced zooplankton abundance. In contrast, we found no evidence that bluegill survival was related to prey abundance in either the mesocosms or in the field. Although we would certainly expect reduced bluegill survival in cases of extreme food limitation, this situation evidently did not occur in our studies. Apparently, larval bluegills are less susceptible to mortality by starvation than gizzard shad at zooplankton densities occurring in our studies. The well-known variation in year-class strength of gizzard shad (Willis 1987) relative to other reservoir species may be, in part, a consequence of prey availability.

Overlap in resource use between gizzard shad and bluegills was high in our field study. Both species selected similar prey items and diet overlap was high throughout the summer. In our work and in previous studies, both species selected smaller-sized prey such as copepod nauplii and rotifers early in the year, and shifted to larger cladocerans and copepods later in the year (Mayhew 1977; Beard 1982; Lemly and Dimmick 1982; Mallin et al. 1987; DeVries et al. 1991). Because of the high degree of diet overlap between these two species, interspecific competition could occur during periods of limited prey availability. The timing of occurrence of these species in the limnetic zone (gizzard shad and then bluegills) would favor gizzard shad if such competition were to occur, but the imbalance would be offset somewhat by the apparently lower susceptibility of bluegill larvae to starvation.

Competition between larval gizzard shad and bluegills has been implied in recent studies (Dettmers and Stein 1992; DeVries and Stein 1992); these studies have demonstrated the ability of gizzard shad to strongly depress zooplankton populations and suggest that this should negatively affect other fish species. Indeed, we did find evidence for intraspecific competition among larval gizzard shad in both our mesocosms and in Lake Shelbyville. However, despite documenting very high gizzard shad densities and high diet overlap, our study does not support the suggestion that gizzard shad strongly suppress bluegill via competition. We found evidence that gizzard shad can deplete zooplankton, and that growth of bluegill was related to zooplankton abundance. However, these effects in our study were less dramatic than those predicted by previous studies (DeVries and Stein 1992; Dettmers and Stein 1992). Furthermore, we

found no evidence of differential survival of larval bluegills of different ages recruiting to the littoral zone in the fall as juveniles. The available evidence to date suggests that gizzard shad do affect zooplankton and could potentially compete with bluegills and other species with pelagic larvae, but that the strength of competitive interactions may vary considerably among systems. Gizzard shad may have their greatest impact in small, relatively closed systems without rapid throughflow or renewal of nutrients (Dettmers and Stein 1992). In larger systems, like Lake Shelbyville, with rapid flushing time, high year-to-year and seasonal variability of limnological conditions, and complex morphometry, these effects may be less pronounced (McQueen et al. 1986).

A current model of trophic interactions in aquatic ecosystems suggests that communities may be controlled by top-down forces (Carpenter et al. 1985; Northcote 1988), by bottom-up forces (McQueen et al. 1986), or by a combination of both types of forces (McQueen et al. 1989). Recently the idea that gizzard shad can regulate community structure via "middle-out" processes has been proposed (DeVries and Stein 1992) as an alternative to the conventional top-down and bottom-up models. This hypothesis centers on the idea that gizzard shad, which are of roughly intermediate position in aquatic food webs and are frequently immune to piscivory because of their rapid growth, can affect other planktivores and even young piscivores via competition for zooplankton, thus exhibiting intermediate regulation of community structure. Although this idea has potential utility, it should be considered cautiously until the strength of control by gizzard shad is determined more precisely. Interactions among larval fish and their zooplankton prey are key components to understanding growth and survival patterns in fish. However, these interactions are complex and further studies will be necessary to document competition within and between these species, as well as their effects on zooplankton populations. Pinpointing these interactions and the underlying mechanisms involved will greatly enhance our understanding of the dynamics of planktivorous fish and zooplankton in aquatic systems.

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