Prey Community Responses to Bluegill and Gizzard Shad Foraging: Implications for Growth of Juvenile Largemouth Bass

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Abstract.—Bluegill *Lepomis macrochirus*, gizzard shad *Dorosoma cepedianum*, and largemouth bass *Micropterus salmoides* are common lentic species that may compete for invertebrate prey resources, and interactions among these species can have important consequences for aquatic community structure. Differential foraging behavior of bluegills and gizzard shad as juveniles, for example, may structure zooplankton and benthos communities and influence the growth of juvenile largemouth bass. We conducted a mesocosm experiment (1.6-m-diameter circular tanks) in which we allowed high and low densities of juvenile bluegills (70–100 mm total length [TL]) and gizzard shad (135–155 mm TL) to forage on established zooplankton and benthos communities for 6 weeks. After this period, we added juvenile largemouth bass (50–80 mm TL) to each tank for 4 weeks to examine growth and diets. Although foraging by bluegill and gizzard shad had limited effects on the total population densities of invertebrates, important taxon-specific effects were observed. At the time that largemouth bass were added to tanks, bluegill treatments exhibited a higher macrozooplankton density, higher turbidity, and lower density of larval hydrophilid coleopterans than did gizzard shad or control treatments. The growth of juvenile largemouth bass was strongly influenced by treatment; largemouth bass grew at similar rates in the gizzard shad and control treatments but lost weight in the bluegill treatments. We suggest that bluegills compete with juvenile largemouth bass for preferred prey items, thereby limiting largemouth bass growth. Further, our results demonstrate that the presence of larger gizzard shad may not have the negative implications observed in previous studies with smaller individuals. Knowledge of the relative, size-specific abundances of bluegills and gizzard shad should provide resource managers with valuable information for developing initiatives aimed at maximizing the growth of juvenile largemouth bass.

Complex interactions between fish and invertebrates can have important consequences for aquatic communities (e.g., Gilinsky 1984; Hambright et al. 1986; Turner and Mittelbach 1990; Nowlin and Drenner 2000) and include both direct and indirect pathways. For example, direct interactions like fish predation can influence the composition and abundance of invertebrates (e.g., Gilinsky 1984; Turner and Mittelbach 1990; Dettmers and Stein 1992; DeVries and Stein 1992). Alternatively, the number and type of invertebrate prey items available in a system can directly influence growth and abundance of fish species that depend on these prey resources (e.g., Mittelbach 1988; Mittelbach and Osenberg 1993; Olson et al. 1995; Aday et al. 2003). Indirect pathways may also be important. For example, the foraging activity of benthivorous or detritivorous fishes causes increased turbidity that can influence macrophyte abundance (a primary food item for benthic macroinvertebrates; e.g., Gilinsky 1984; Parkos et al. 2003) and the foraging ability of visually oriented fish predators (e.g., Vinyard and O'Brien 1976; Miner and Stein 1993), thereby indirectly influencing community composition. Despite these complexities, quantification of mechanisms associated with these interactions and their effects on aquatic communities is important for understanding factors that structure aquatic food webs and for managing competing fish species.

The intermediate trophic level of many freshwater lakes throughout North America (particularly in the midwestern and southeastern United States) is occupied by bluegill *Lepomis macrochi-*

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rus and gizzard shad *Dorosoma cepedianum*. As invertivores throughout their ontogeny, bluegills can have a direct influence on invertebrates, influencing density and diversity of both zooplankton and benthos (e.g., Gilinsky 1984; Turner and Mittelbach 1990). This influence may be mitigated, however, by such factors as habitat heterogeneity (Crowder and Cooper 1982). In addition, the size of prey items may be important; several experiments have illustrated size-specific foraging effects on zooplankton (e.g., Vanni 1986; Nowlin and Drenner 2000). Gizzard shad also can have a pronounced influence on invertebrate communities and have been shown to be a ''strong interactor'' in aquatic food webs (Stein et al. 1995). However, the mechanisms through which gizzard shad affect invertebrates may change throughout their ontogeny. As larvae and early juveniles, gizzard shad feed directly on zooplankton, and their influence on zooplankton density and composition has been well studied (e.g., Dettmers and Stein 1992, 1996; Welker et al. 1994; Garvey and Stein 1998b). As larger juveniles and adults, gizzard shad are primarily detritivorous but will feed on zooplankton when densities are high (Yako et al. 1996). Although gizzard shad do not normally consume benthic macroinvertebrates, they may indirectly affect benthos via alteration of nutrient dynamics (Vanni 1995; Schaus et al. 1997) and water quality (through the turbidity–macrophyte link described above, and through nutrient recycling; e.g., Vanni and Layne 1997). Clearly, the mechanisms through which bluegills and gizzard shad might influence invertebrate community structure can be quite different, particularly after the larval stage; bluegills would be expected to have primarily direct effects (predation), whereas gizzard shad effects might be manifested through indirect pathways (altering nutrients and water quality) as well. As a result, a variety of differences in the invertebrate communities of a particular lake or reservoir might be expected, depending on whether bluegills or gizzard shad dominate (e.g., Garvey and Stein 1998a; Kline 2000). One focus of this investigation was to examine how foraging by juvenile bluegills and gizzard shad influences zooplankton and benthos abundance and composition. We used experimental mesocosms in which natural variation can be reduced and direct quantification of foraging effects can be observed.

As the top fish predator in many of the same aquatic systems occupied by bluegills and gizzard shad, largemouth bass *Micropterus salmoides* will be influenced throughout their ontogeny by the outcome of these two species' foraging activities. As juveniles, largemouth bass undergo ontogenetic diet shifts from invertebrates to fish (see Olson 1996 and citations therein), thereby making them potential competitors with species that will ultimately become prey resources. Because largemouth bass are an important sport fish species, myriad management initiatives have been directed at increasing and maintaining populations with large individuals. A considerable body of literature on growth and foraging by largemouth bass, particularly during the piscivorous stage, has been generated (e.g., Noble 1981; Kirk and Davies 1987; Hambright et al. 1986; Michaletz 1998a, 1998b). Much of the focus of investigations at early life stages has been directed at understanding the availability and relative importance of appropriate-sized larval bluegills and gizzard shad when young-of-year largemouth bass first become piscivorous (e.g., Garvey and Stein 1998a; Michaletz 1998a, 1998b; Allen et al. 1999). Little consideration has been given to the potential for larger bluegills and gizzard shad to alter growth rates of pre-piscivorous largemouth bass through their effects on zooplankton and benthos communities (but for bluegills, see Gilliam 1982; Olson et al. 1995; Olson 1996).

In this investigation, we quantify the influence of age-1 bluegills and gizzard shad on zooplankton and benthic macroinvertebrates (important forage items for all three species) and subsequently determine the influence of any species-specific foraging patterns on the growth of juvenile largemouth bass. We hypothesized that (1) the abundance and composition of zooplankton and benthic macroinvertebrates would differ in treatments with bluegills versus gizzard shad because of species-specific foraging preferences and (2) growth of juvenile largemouth bass would vary according to the availability of preferred prey resources and the degree of competition with bluegills and gizzard shad.

Methods

The experiment was conducted in 20 circular tanks (1.6 m in diameter × 0.46 m deep) located outdoors at the Kaskaskia Biological Station, Sullivan, Illinois. Each tank received 0.16 m^3 of sediment from Lake Shelbyville, Illinois, mixed with 9 kg of organic peat. Tanks were filled with conditioned tap water in April and were seeded with zooplankton and phytoplankton from Ridge Lake, Coles County, Illinois, because of the abundance of zooplankton and diversity of taxa found in the

lake. Zooplankton and phytoplankton populations were allowed to develop and benthic macroinvertebrates were allowed to colonize for 8 weeks. During this time, water was periodically exchanged among tanks to keep species composition and abundance of zooplankton similar.

Phase 1: bluegill and gizzard shad effects on invertebrate communities.—After the 8-week colonization period, juvenile bluegills or gizzard shad were added to experimental tanks. Four replicates were used for each of five treatments (low biomass of bluegills [LB]; high biomass of bluegills [HB]; low biomass of gizzard shad [LG]; high biomass of gizzard shad [HG]; no-fish control [NO]). Juvenile age-1 bluegills (70–100 mm total length [TL]; 6–10 g) were obtained from Wood Lake, Shelby County, Illinois, and a brood pond at the Sam Parr Biological Station, Kinmundy, Illinois (individuals were mixed prior to the experiment and were added randomly to appropriate tanks). Juvenile age-1 gizzard shad (135–155 mm TL; 17–31 g) were collected from Lake Shelbyville. To maintain similar biomass between bluegill and gizzard shad treatments, we added three bluegills or one gizzard shad per tank to the low-biomass treatments and 10 bluegills or three gizzard shad per tank to the high-biomass treatments. These densities yielded low-biomass (mean ± SE, 24.2 ± 3.3 g) and high-biomass (71.5 ± 2.9 g) treatments that were within the range of biomass levels commonly found in natural systems (Hackney 1979; Johnson et al. 1988). Mortality was relatively low (2% for bluegills, 19% for gizzard shad), but dead fish were removed and replaced with similar-sized live fish.

Water samples were taken to quantify nutrients, chlorophyll *a* (chl *a*), and turbidity by means of an integrated tube-sampler (46 cm long, 5.1-cm inside diameter). Water samples for nutrient analyses were taken on the day of fish introduction and again before largemouth bass were added. Total phosphorus (TP) and soluble reactive phosphorus (SRP) were analyzed with the molybdenum blue–ascorbic acid method (APHA 1992), and total nitrogen (TN) was analyzed with a persulfate digestion spectrophotometric method (Reveh and Avnimelech 1979). All three nutrient analyses were performed with a Spectronic 20-Genesis spectrophotometer. Chlorophyll-*a* samples were taken three times (beginning, middle, and end) during phase 1 of the experiment. Chlorophyll *a* was determined by filtering 150 mL of water through a glass-fiber filter (1.2-μm pore size) and analyzing according to U.S. Environmental Pro-

tection Agency method 445.0 (USEPA 1992) by means of a Turner Designs TD-700 fluorometer. Turbidity (nephelometric turbidity units [NTU]) was measured weekly during the experiment by use of a turbidimeter (Hach model 8391–40).

Macrozooplankton (total zooplankton, excluding rotifers and nauplii) were sampled four times during the first phase of the experiment. Zooplankton were collected in three pooled samples of an integrated tube-sampler (7.5-cm inside diameter; DeVries and Stein 1991), filtered through a 64-μm-mesh net, and preserved in 4% Lugol's solution. Organisms were later identified to either family or genus (depending on taxon) and counted. Benthic macroinvertebrates were sampled at the time of fish introduction and again 6 weeks later (when largemouth bass were added) by pressing a polyvinyl chloride pipe (10.2-cm inside diameter) into the substrate of the tank. All substrate within the pipe was suctioned into a wet/dry shop vacuum. Samples were preserved with a 70% rose bengal and ethanol solution, and the organisms were later identified to family and enumerated.

Phase 2: influence on largemouth bass diet and growth.—Six weeks after the addition of bluegills or gizzard shad, one juvenile largemouth bass was weighed (g), measured (mm), and added to each tank. Largemouth bass (50–80 mm TL; 1–5 g) were obtained from a rearing pond at the Sam Parr Biological Station. After 4 weeks, largemouth bass were removed from tanks, weighed, measured, and euthanatized. Stomachs were removed from each largemouth bass, and stomach contents were preserved in 40% ethanol. Stomach fullness for each individual was determined by calculating the difference in wet weight of the stomach before and after diet items were removed and dividing that value by the wet weight of the largemouth bass (with stomach intact). Stomach contents were identified to the lowest taxonomic level possible. Diet items were measured for up to 10 randomly selected individuals of each prey type from each largemouth bass; we then used length–weight regressions to estimate the average pre-digestion biomass of each prey type consumed (invertebrates: Smock 1983; Sample et al. 1993; zooplankton: Dumont et al. 1975; spiders: Sage 1982). Diet data were calculated as percent composition by both weight and number. Separate one-factor analyses of variance (ANOVAs) were used to test for among-treatment differences in weight change and stomach fullness of largemouth bass.

Zooplankton, benthic macroinvertebrates, TP, SRP, and TN were sampled as described above at

TABLE 1.—Mean (SE) soluble reactive phosphorus (SRP), total phosphorus (TP), and total nitrogen (TN) in 20 tanks (1.6 m^3) that contained gizzard shad and bluegills at high (71.5 g) and low (24.2 g) biomass during 10 weeks (4 tanks/treatment). The end of phase 1 describes conditions at the time of largemouth bass introduction to the tanks (week 6); the end of phase 2 describes conditions 4 weeks after largemouth bass introduction (week 10).

	SRP (mg/L)			TP (mg/L)	
Treatment	Initial	End of phase 1	End of phase 2	Initial	End of phase 1
High bluegill	0.21 (0.03)	0.54 (0.07)	0.18 (0.03)	0.49 (0.02)	1.08 (0.21)
High gizzard shad	0.17 (0.05)	0.35 (0.09)	0.14 (0.04)	0.52 (0.07)	1.13 (0.21)
Low bluegill	0.24 (0.05)	0.55 (0.13)	0.19 (0.01)	0.49 (0.03)	1.09 (0.18)
Low gizzard shad	0.20 (0.03)	0.48 (0.13)	0.15 (0.03)	0.51 (0.02)	0.96 (0.15)
Fishless control	0.27 (0.02)	0.44 (0.16)	0.20 (0.01)	0.48 (0.02)	1.17 (0.17)

the beginning and end of phase 2 of the experiment. Turbidity and chl *a* were measured three times (beginning, middle, and end) during phase 2.

Nutrients, chl *a,* turbidity, zooplankton, and benthos abundance were analyzed by repeated-measures ANOVAs; each tank was treated as a repeated subject measured on multiple dates. Because the tanks started with the same values at the beginning of phase 1, both main treatment effects and treatment × date interactions indicated changes that were attributable to treatment conditions. However, in analyses of phase 2 (weeks 6–10, when largemouth bass were present), initial conditions differed among treatments because of the foraging effects from phase 1. Therefore, a separate analysis was used to test for phase-2 effects. For phase 2, main effects only indicate that initial differences were maintained, whereas treatment × date interactions indicate that changes during weeks 6–10 were due to differences among treatment conditions (i.e., the pattern of change through time was affected by treatments). Repeated-measures ANOVA was also used to test for significant differences among treatments for zooplankton and benthos taxa that contributed at least 5% of the total on at least one sample date (zooplankton: *Daphnia*, calanoid copepods, *Bosmina*, cyclopoid copepods, and chydorids; benthos: chironomids and larval hydrophilid coleopterans). When significant differences ($P < 0.05$) were detected, Tukey's multiple comparison test was used to examine differences among specific treatments. Because low- and high-biomass treatment levels for the same species were expected to affect the response variables similarly, we also combined and analyzed species effects by use of ESTIMATE statements (SAS Institute 1991). To correct for nonnormal distributions, chl *a,* cladoceran, *Daphnia*, cyclopoid copepod, and chydorid densities were log transformed, densities of calanoid copepods and total zooplankton were square-root transformed, and *Bosmina* density was reciprocal transformed (Zar 1984).

Results

Phase 1: Effects of Bluegills and Gizzard Shad on Water Chemistry, Macrozooplankton, and Benthos

During phase 1 (weeks 1–6), water chemistry variables showed few treatment-specific differences. There were no treatment-related changes in either TP (treatment effect: $F_{4,15} = 0.14$, $P = 0.96$; date × treatment interaction: $F_{4,15} = 0.24$, $P = 0.91$) or SRP (treatment: $F_{4,15} = 0.58$, $P = 0.68$; interaction: $F_{4,15} = 0.45$, $P = 0.77$; Table 1). Total nitrogen increased in the HG treatment (Tukey's test: $P < 0.01$) but not in the other treatments ($P > 0.62$ for all other comparisons; date × treatment interaction: $F_{4,14} = 3.30$, $P = 0.04$; Table 1). Turbidity also had treatment-specific changes during phase 1 (date × treatment interaction: $F_{20,75} = 5.77$, $P < 0.01$; Figure 1A). Turbidity increased in the HB and LB treatments (initial and week 2 compared to weeks 3 and 6; Tukey's test: $P < 0.04$ for all comparisons) but not in the gizzard shad treatments ($P > 0.61$ for all comparisons). This change was likely attributable to sediment suspension caused by benthic feeding by bluegills but may also be partially explained by the small (non-significant) increase in chl *a* (treatment: $F_{4,15} = 1.02$, $P = 0.43$; date × treatment interaction: $F_{8,30} = 0.54$, $P = 0.82$; Figure 1B) seen in the bluegill treatments.

Changes in total macrozooplankton were evident (date × treatment interaction: $F_{12,45} = 3.10$, $P < 0.01$; Figure 2A). Higher average zooplankton values during weeks 4 and 6 were observed in the bluegill treatments than in the other treatments. Examined individually, these differences were only significant on week 4, when the LB treatment had significantly higher zooplankton abundance

TABLE 1.—Extended.

Treatment	TP (mg/L)	TN (mg/L)		
	End of phase 2	Initial	End of phase 1	End of phase 2
High bluegill	0.58 (0.04)	1.17 (0.05)	1.32 (0.14)	1.14 (0.07)
High gizzard shad	0.56 (0.21)	1.00 (0.08)	2.06 (0.32)	1.28 (0.06)
Low bluegill	0.61 (0.11)	0.92 (0.08)	1.33 (0.09)	1.02 (0.04)
Low gizzard shad	0.56 (0.12)	1.20 (0.06)	1.36 (0.10)	1.19 (0.12)
Fishless control	0.52 (0.11)	0.93 (0.15)	1.39 (0.19)	1.02 (0.07)

than the gizzard shad (Tukey's test: HG, $P < 0.01$; LG, $P = 0.02$) and NO ($P = 0.03$) treatments. When the low and high biomass treatments for each species were combined, bluegill treatments had significantly higher total macrozooplankton levels than did the gizzard shad treatments or the

FIGURE 1.—Mean ± SE **(A)** turbidity and **(B)** chlorophyll a (chl a) of 1.6-m³ tanks during a 10-week experiment examining the effect of gizzard shad and bluegills on invertebrate communities (first 6 weeks) and on largemouth bass growth and diet (final 4 weeks). Treatments (4 replicates each) were high biomass levels (71.5 g) of bluegills (HB) and gizzard shad (HG), low biomass levels (24.2 g) of bluegills (LB) and gizzard shad (LG), and a fishless control (NO). Arrows indicate the date when juvenile largemouth bass were added.

NO treatments ($P < 0.01$ for all comparisons) for both sample dates.

Species-specific macrozooplankton patterns were similar to those observed for total macrozooplankton. Cyclopoid copepod density was higher in the LB treatment than in the LG treatment ($F_{3,15} = 2.96$, $P = 0.05$; Tukey's test: $P = 0.04$; Figure 2B). Calanoid copepod density in the LB treatment also increased and was higher than in the HG and NO treatments by week 6 (Tukey's test: $P < 0.01$ for both comparisons; date × treatment interaction: $F_{12,45} = 2.62$, $P = 0.01$; Figure 2C). Combining low and high fish biomass levels (to measure species-specific effects), we found that bluegill treatments had significantly higher calanoid copepod densities than did the gizzard shad treatments or NO treatment on weeks 4 and 6 ($P < 0.01$ for all) and the NO treatment on week 2 ($P = 0.03$). Chydorid abundances were higher in the HB (Tukey's test: $P = 0.02$), LB ($P = 0.04$) and NO ($P = 0.03$) treatments than in the HG treatment ($F_{4,15} = 4.65$, $P = 0.01$). The other individual zooplankton taxa exhibited varying patterns through time, and their abundances did not appear to be strongly related to the presence of fish. There was a significant date × treatment interaction effect for *Daphnia* density during phase 1 ($F_{12,45} = 2.82$, $P < 0.01$); however, densities strongly declined in all treatments (Figure 2D). The significant interaction was caused by highly variable initial densities and a large decrease in *Daphnia* density within the LB and LG treatments during week 2 and a subsequent increase in week 4 (LB) or 6 (LG) that was not observed in the other treatments (Tukey's test: $P < 0.04$). Otherwise, the pattern of *Daphnia* abundance during the experiment was similar among treatments. The *Bosmina* abundances during phase 1 were similar among treatments (treatment effect: $F_{4,15} = 0.94$, $P = 0.47$; date × treatment interaction: $F_{12,45} = 0.66$, $P = 0.78$).

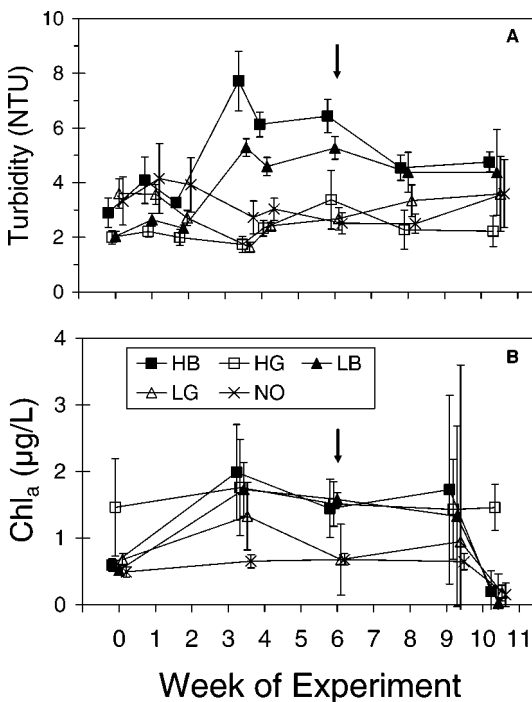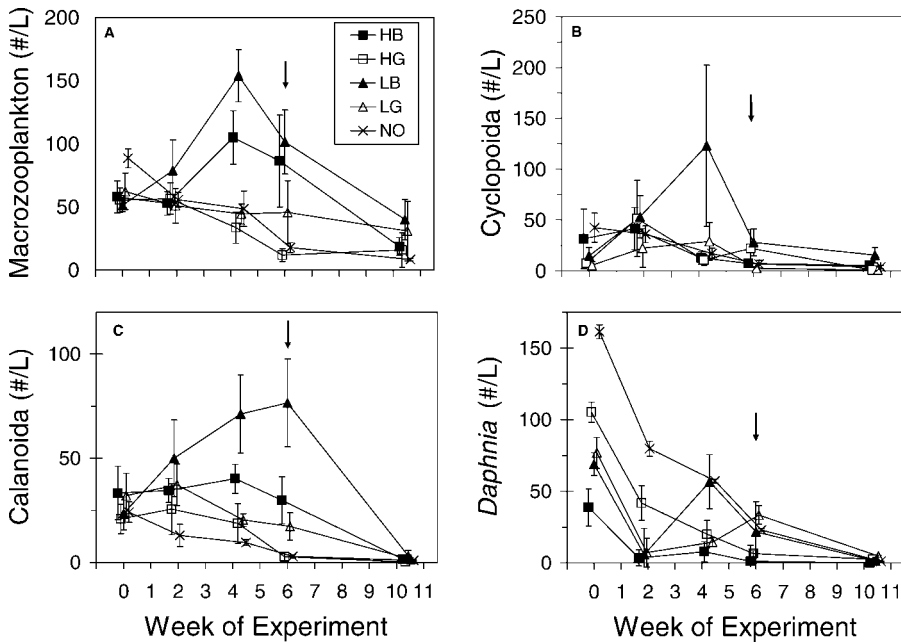FIGURE 2.—Mean ± SE (**A**) total macrozooplankton, (**B**) cyclopoid copepod, (**C**) calanoid copepod, and (**D**) *Daphnia* densities in 1.6-m³ tanks during a 10-week experiment examining the effect of gizzard shad and bluegills on invertebrate communities (first 6 weeks) and on largemouth bass growth and diet (final 4 weeks). See Figure 1 for additional details.

Chironomids contributed over 92% of the benthic community on all dates and were most responsible for the pattern observed for total benthos (Figure 3A, B). However, chironomid density was not affected by treatment (treatment effect: $F_{4,15} = 0.24$, $P = 0.91$; date × treatment interaction: $F_{4,15} = 0.41$, $P = 0.80$). Other species found included larval hydrophilid and dytiscid coleopterans, ephemeropterans, and planarians. However, these taxa never made up more than 8% of the samples from any date. Larval hydrophilid coleopterans, which are large-bodied predaceous invertebrates, were not as numerically abundant as chironomids were (Figure 3C) but may have been energetically important to fish. The density of larval hydrophilids varied (date × treatment interaction: $F_{4,15} = 8.66$, $P < 0.01$; Figure 3) and was consistently low in the bluegill treatments. In contrast, larval hydrophilid density increased in the LG treatment up to week 6 (Tukey's test: $P < 0.01$) and a similar pattern was observed in the HG treatment ($P = 0.09$). When we combined the low and high fish biomass levels, we found significantly higher larval hydrophilid densities in the presence of gizzard shad than in the bluegill treatments (estimate $P < 0.01$) or the NO treatment (estimate $P = 0.02$) after 6 weeks.

Phase 2: Water Chemistry, Macrozooplankton, and Benthos after Addition of Largemouth Bass

Phosphorus and chl *a* were not further affected by treatment conditions during phase 2, when largemouth bass were present in the tanks (TP: treatment, $F_{4,15} = 0.07$, $P = 0.99$; time × treatment, $F_{4,15} = 0.51$, $P = 0.73$; SRP: treatment, $F_{4,15} = 0.59$, $P = 0.67$; time × treatment, $F_{4,15} = 0.41$, $P = 0.80$; Table 1; chl *a*: treatment, $F_{4,15} = 2.22$, $P = 0.12$; time × treatment, $F_{8,30} = 0.25$, $P = 0.98$; Figure 1B). Turbidity was higher in the HB treatment than in the HG treatment ($F_{4,15} = 4.44$, $P = 0.01$), but this was due to higher week-6 values (as a result of bluegill and gizzard shad effects) being maintained for the rest of the experiment rather than to additional changes during phase 2 (time × treatment interaction: $F_{8,30} = 0.70$, $P = 0.69$; Figure 1A). Similarly, TN was slightly higher in the HG treatment than in the HB treatment ($F_{4,15} = 3.37$, $P = 0.04$) but only because of higher starting values (time × treatment interaction: $F_{4,15} = 1.33$, $P = 0.31$).

Total macrozooplankton abundance declined during phase 2 in both the LB and HB treatments (date × treatment interaction: $F_{4,15} = 5.51$, $P = 0.03$; Tukey's test: $P < 0.01$ for both) but not in
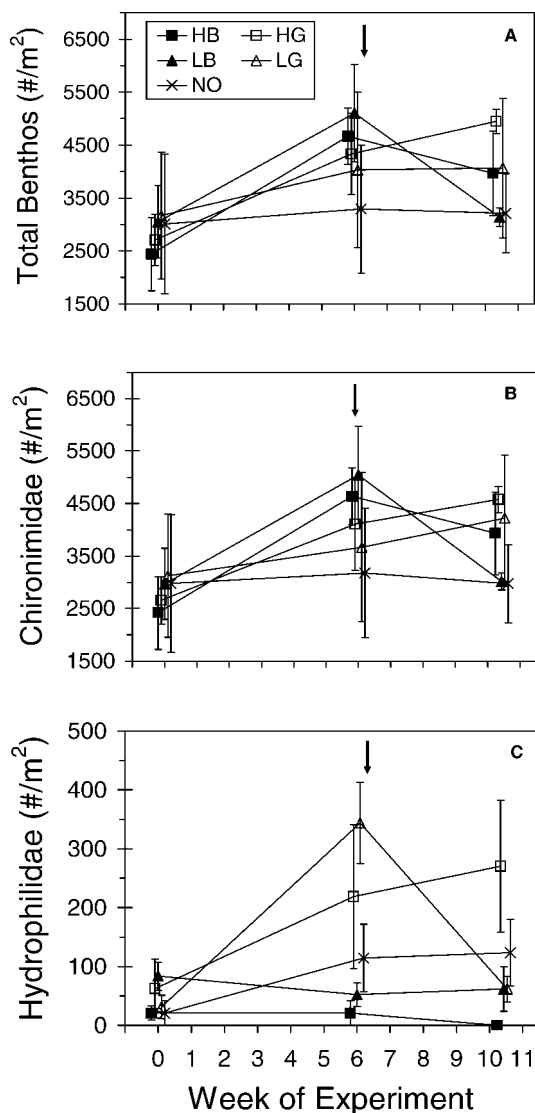
FIGURE 3.—Mean ± SE **(A)** total benthic invertebrate, **(B)** chironomid, and **(C)** hydrophilid densities of 1.6-m³ tanks during a 10-week experiment examining the effect of gizzard shad and bluegills on invertebrate communities (first 6 weeks) and on largemouth bass growth and diet (final 4 weeks). See Figure 1 for additional details.

the other treatments. *Bosmina* abundance also varied (date × time interaction: $F_{4,15} = 3.08$, $P = 0.05$) because of a significant decline in abundance in the HB treatment (Tukey's test: $P = 0.05$) that did not occur in other treatments. There were no treatment-specific changes in the abundances of *Daphnia* (treatment: $F_{4,15} = 2.26$, $P = 0.11$; date × treatment interaction: $F_{4,15} = 1.67$, $P = 0.21$), cyclopoid copepods (treatment: $F_{4,15} = 3.63$, $P =$ 0.03; interaction: $F_{4,15} = 0.54$, $P = 0.71$), calanoid copepods (treatment: $F_{4,15} = 6.45$, $P < 0.01$; interaction: $F_{4,15} = 0.88$, $P = 0.50$), or chydorids (treatment: $F_{3,23} = 3.23$, $P = 0.04$; interaction: $F_{4,15} = 0.16$, $P = 0.96$) when largemouth bass were present.

Changes in total benthic invertebrate density (treatment: $F_{4,15} = 0.90$, $P = 0.49$; date × treatment interaction: $F_{4,15} = 0.86$, $P = 0.51$) and chironomid density (treatment: $F_{4,15} = 0.97$, $P = 0.45$; interaction: $F_{4,15} = 0.74$, $P = 0.58$; Figure 3) were similar among treatments when largemouth bass were present. However, larval hydrophilid density in the LG treatment decreased to the point that it was no longer significantly different from those in the other treatments (Tukey's test: $P > 0.12$ for all week-10 comparisons). Larval hydrophilid density in the HG treatment increased such that it was significantly higher than that in the HB treatment (Tukey's test: $P < 0.01$). Other treatments did not show any changes in larval hydrophilid density when largemouth bass were present.

Largemouth Bass Growth and Diet

Largemouth bass weight change differed among treatments ($F_{4,15} = 11.27$, $P < 0.01$; Figure 4A). Largemouth bass lost weight at both bluegill biomass levels, and weight changes differed significantly (Tukey's test: $P < 0.04$) from those of other treatments. Weight gain was similar in the HG, LG, and NO treatments (Tukey's test: $P > 0.52$; Figure 4A). Similarly, largemouth bass stomach fullness differed among treatments ($F_{4,15} = 4.80$, $P = 0.01$; Figure 4B). Stomach fullness was lowest in the two bluegill treatments; stomach fullness in the HB treatment was significantly lower than the stomach fullness measured in the HG (Tukey's test: $P = 0.01$) and NO ($P = 0.05$) treatments and marginally lower than that of the LG treatment ($P = 0.06$).

Largemouth bass diets differed among the gizzard shad, bluegill, and NO treatments. Largemouth bass ate primarily chironomids, larval hydrophilids, and other terrestrial insects (percent by number) at both biomass levels of gizzard shad (Table 2). In contrast, largemouth bass consumed a higher percentage of zooplankton (specifically Bosminidae, Chydoridae, and cyclopoid copepods) in the LB treatment than in either of the gizzard shad treatments (Table 2). Largemouth bass in the HB treatment consumed very little food (Table 2); of the four replicates, only one fish had food (a single chironomid larva) in its stomach.
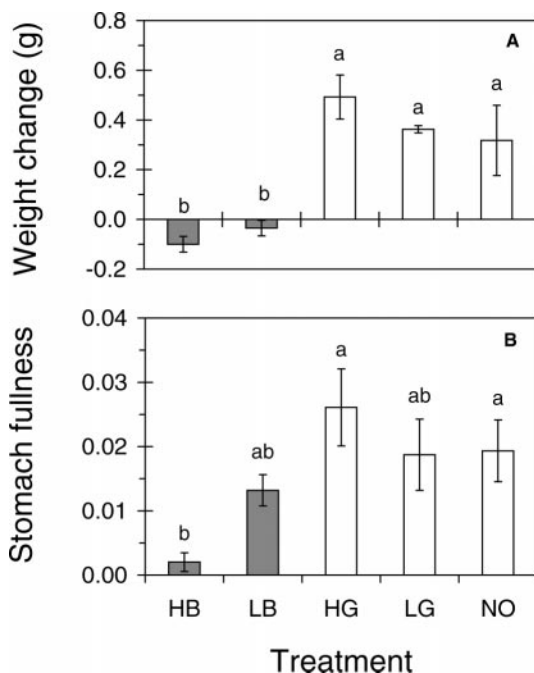
FIGURE 4.—Mean ± SE **(A)** weight change and **(B)** stomach fullness of largemouth bass during the final 4 weeks of a 10-week experiment examining the effect of bluegills and gizzard shad on invertebrate prey communities and largemouth bass growth. Stomach fullness was calculated as the difference in stomach wet weight before and after diet items were removed, divided by the wet weight of the fish with stomach intact. Different letters indicate significant differences in Tukey's multiple-comparison test. See Figure 1 for additional details.

Largemouth bass diets in the control tanks differed from those of the HG, LG, and LB treatments. These largemouth bass consumed mostly chironomids and larval hydrophilids but included chydorids and cyclopoid copepods in their diets as well. They did not, however, eat *Bosmina* as did the largemouth bass in the LB treatment.

Discussion

By controlling the natural variation inherent in whole-lake systems, we were able to examine the effects of bluegills and gizzard shad on water quality and prey community structure and offer insight into the ways in which variable foraging behaviors can influence juvenile largemouth bass growth. Mesocosms with bluegills exhibited higher turbidity than other treatments as well as taxon-specific differences in zooplankton and macrobenthos, and largemouth bass in bluegill treatments lost weight. Largemouth bass experienced better growth in the

gizzard shad and NO treatments than in tanks with bluegills. Because lakes are often dominated by either bluegills or gizzard shad, our results suggest that species-specific foraging patterns and competitive interactions (in addition to the physical and chemical differences that might predispose these systems to support bluegills versus gizzard shad) can have a substantial influence on the growth of juvenile largemouth bass (sensu Garvey and Stein 1998a). This is particularly important in light of the influence of juvenile growth rate and timing of piscivory on largemouth bass size structure (e.g., Olson 1996).

We found some species-specific effects on water quality, zooplankton, and macrobenthos densities that partially supported our first hypothesis. In general, bluegills generated higher turbidity, higher copepod and chydorid densities, and lower larval hydrophilid densities than did gizzard shad. The increased turbidity observed in the bluegill treatments is presumably the result of their benthic feeding tactics; we observed bluegills feeding directly on the bottom substrate. Previous studies have also found that summer bluegill diets were dominated by macrobenthos (Seaburg and Moyle 1964; Olson et al. 2003). Other experiments with enclosures containing bluegills have generated similar results (Hambright et al. 1986; Nowlin and Drenner 2000). In contrast to our study, previous investigations have found that gizzard shad can also increase turbidity (e.g., Schaus and Vanni 2000; Aday et al. 2003). Regardless, higher turbidity in the bluegill treatments may have influenced the foraging ability of largemouth bass and contributed to the observed weight loss.

Macrozooplankton densities increased in the bluegill treatments prior to the addition of largemouth bass. This result was driven by copepods, which increased in the presence of bluegills but not in the gizzard shad treatments or the NO treatment. Bluegills are often insectivorous, and when they do eat zooplankton they use cladocerans much more heavily than they use copepods (Seaburg and Moyle 1964; Olson et al. 2003). It may be that foraging by gizzard shad caused the reduction of copepods in these treatments, as previous investigations have indicated that gizzard shad will consume copepods (Roseman et al. 1996; cyclopoid copepods: Drenner et al. 1982). *Daphnia* abundance decreased in all treatments, which suggests that these were consumed early in the experiment by all fish, that their production was insufficient to sustain substantial populations, or that the decline was simply due to a natural population cycle.

TABLE 2.—Mean (SE) percent diet composition by weight and number and percentage of empty stomachs for juvenile largemouth bass (50–80 mm TL) after 4 weeks in four replicate tanks with high biomass (71.5 g) of bluegills (HB) or gizzard shad (HG), low biomass (24.2 g) of bluegills (LB) or gizzard shad (LG), or a fishless control (NO). Bluegills and gizzard shad were present for 6 weeks before largemouth bass were introduced. Other aquatic invertebrates included Hemiptera, Hydracarina, and Ostracoda. Terrestrial invertebrates included arachnids, Chironomidae, Formicidae, and hydrophilid coleopterans.

Taxa	Percent by weight					Percent by number				
	HB	LB	HG	LG	NO	HB	LB	HG	LG	NO
Zooplankton										
Bosminidae		19 (19)					21 (21)			
Daphnia		<1 (0)						5 (5)		
Calanoid copepods							<1 (0)			
Chydoridae		19 (15)	<1 (0)		10 (10)		31 (16)	1 (1)		15 (15)
Cyclopoid copepods		18 (9)	<1 (0)		12 (10)		12 (9)	1 (1)		8 (6)
Aquatic invertebrates										
Chironomids	100	36 (29)	29 (23)	35 (31)	32 (32)	100	6 (5)	53 (14)	56 (12)	47 (15)
Hydrophilid coleopterans		a	68 (23)	62 (31)	33 (33)		8 (8)	14 (9)	20 (5)	13 (6)
Lepidoptera					12 (12)					<1 (0)
Other aquatic invertebrates		7 (0)	1 (0)	1 (0)	1 (0)		3 (2)	3 (2)	2 (2)	1 (1)
Terrestrial invertebrates		a	2 (1)	1 (1)	a		19 (16)	24 (15)	22 (11)	16 (6)
Percent empty stomachs	75									

a Organisms were found in the diets but were too digested to measure lengths for conversion to weight.

Larval and age-0 gizzard shad have been shown to have a strong influence on zooplankton (e.g., Drenner et al. 1982; DeVries and Stein 1992; Dettmers and Stein 1996), yet we did not observe that outcome in our experiment with larger, older fish. The gizzard shad densities in our tanks ranged from 97 to 286 kg/ha, which is similar to or slightly above estimates of gizzard shad biomass in Ohio reservoirs (Johnson et al. 1988). DeVries and Stein (1992) saw strong effects of age-0 gizzard shad on zooplankton in enclosures (2 m³) at gizzard shad densities of 7.15 kg/ha. As such, the lack of effect of gizzard shad on zooplankton in our experiment does not appear to be due to low fish density. Instead, we believe this reflects ontogenetic diet differences between larger, age-1 gizzard shad and the young-of-year fish examined in many previous investigations; it seems likely that the gizzard shad in our tanks were consuming fewer zooplankton, having switched primarily to detritivory or foraging on algae and periphyton (Drenner et al. 1986; Muth and Busch 1989; J. Neviackas, personal observation).

The total density of macrobenthos was similar among treatments, indicating no influence of bluegill or gizzard shad feeding behavior. Although previous investigations have indicated variable influences (ranging from none to significant) of fish predation on benthos (see discussion in Pierce and Hinrichs 1997), several studies have reached conclusions comparable to ours (e.g., Thorp and Bergey 1981; Hanson and Leggett 1986; Pierce and Hinrichs 1997). Despite the lack of effect on total benthos density, important species-specific differences in benthos assemblages were observed. For example, larval hydrophilids increased in all treatments except those containing bluegills. Resetarits (2001) found that the hydrophilid *Tropisternus lateralis* avoided colonization and oviposition in the presence of predatory bluegills and pumpkinseeds *Lepomis gibbosus*. Gilinsky (1984) concluded that bluegills may (seasonally) concentrate on specific preferred prey items, resulting in complex responses of benthic species to vertebrate predators. Indeed, fish often preferentially forage on predacious invertebrates, which may reduce pressure on the remaining prey taxa (Gilinsky 1984; Diehl 1992, 1995). Thus, predatory effects of fish on predacious invertebrates can have significant influence on the benthos assemblage. The lack of larval hydrophilids in the bluegill mesocosms may have resulted in increased densities of other benthic food items (as described in Gilinsky 1984), which may have both confounded our ability to find differences in total density among treatments and substantially influenced growth of juvenile largemouth bass.

The growth of juvenile largemouth bass was

strongly affected by species-specific interactions, supporting our second hypothesis. Largemouth bass growth varied among treatments, presumably based on the degree of competition with bluegills and gizzard shad and variation in preferred prey resources. Juvenile largemouth bass were able to grow at both gizzard shad densities as well as in the control tanks. However, largemouth bass lost weight and their stomachs were less full when bluegills were present. The most likely explanation for these patterns is that juvenile largemouth bass competed with bluegills for a shared food resource and consumed specific prey items in the gizzard shad and NO treatments that were unavailable in the HB and LB treatments due to consumption by bluegills. Larval hydrophilids were clearly an important food item for largemouth bass in the non-bluegill treatments. By weight, this taxon represented over 25% of largemouth bass diets, yet it was not found in diets of largemouth bass in the HB treatment and only occurred in low frequency in the LB treatment. Terrestrial inputs also were important to largemouth bass in the treatments without bluegills (although, numerically, terrestrial taxa were important in the LB treatment). As such, it seems likely that the most profitable food items were unavailable to largemouth bass in the HB treatment because of consumption by bluegills, forcing the largemouth bass to feed on suboptimal zooplankton. Similarly, Olson et al. (1995) found that bluegills had the strongest influence on largemouth bass in a pond experiment via reduction of the most profitable invertebrates, and concluded that competition can drive growth rates of juvenile largemouth bass.

Another possible explanation for our results is that the variation in largemouth bass growth was due to differences in turbidity. Several investigations have demonstrated that increases in turbidity can reduce the foraging efficiency of sight feeders (Gardner 1981; Gregory and Northcote 1993; Miner and Stein 1993), even at turbidities as low as 10 NTU (Rowe and Dean 1998). We observed similar turbidity values (8 NTU); therefore, this mechanism may at least partially account for slow growth. However, higher turbidities are common in reservoir systems and do not appear to affect largemouth bass growth. Largemouth bass exhibited decreased stomach fullness and increased consumption of zooplankton when housed with bluegills; largemouth bass at the sizes used in our experiment typically consume macroinvertebrates (Phillips et al. 1995; Olson 1996). Additionally, increased turbidity has been shown to decrease consumption of insects by fish, but moderate turbidity levels can increase consumption of zooplankton by improving contrast between prey and background for some species (Boehlert and Morgan 1985; Rowe and Dean 1998).

Previous investigations have demonstrated community-level consequences of interactions between young-of-year bluegills, gizzard shad, and largemouth bass (e.g., Olson et al. 1995; Olson 1996; Garvey and Stein 1998a). We extend the implications of those studies by examining community-level effects of older, larger bluegills and gizzard shad, and our results create a more complex picture of interactions among these common species. Whereas previous investigations have clearly illustrated the potential negative influence of young-of-year gizzard shad on bluegills (Welker et al. 1994; Garvey and Stein 1998b; Aday et al. 2003) and young-of-year largemouth bass (indirectly, through reduction of appropriate-sized bluegill prey; Garvey and Stein 1998a), our results obtained with older, larger fish suggest that these negative effects might be restricted to age-0 individuals or may not occur at all (Jackson and Noble 2000a, 2000b). As such, an understanding of relative size-specific densities of bluegills and gizzard shad should provide resource managers with insight into the degree of competitive interactions among these species, thereby allowing predictions of effects on growth of juvenile largemouth bass. We believe these data are a necessary component in the development of robust initiatives for maximizing largemouth bass growth and size structure.

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