

Direct and Indirect Effects of Gizzard Shad on Bluegill Growth and Population Size Structure

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Abstract.—Competition with gizzard shad *Dorosoma cepedianum* has been shown to influence survival of larval bluegills *Lepomis macrochirus* as well as growth and size structure of largemouth bass *Micropterus salmoides*, which prey on these planktivorous species. However, little is known about how the presence of gizzard shad influences bluegills beyond the larval stage. We examined bluegill–gizzard shad interactions across 10 reservoirs with and 10 without gizzard shad to determine direct and indirect effects of gizzard shad on bluegill population size structure. In the presence of gizzard shad, bluegills exhibited smaller adult (>3 years old) size structure. Benthic invertebrate densities were higher in non-gizzard shad reservoirs, which may have contributed to increased bluegill growth in these systems. In contrast, zooplankton densities were similar in reservoirs with and without gizzard shad. Turbidity was higher in reservoirs with gizzard shad, which may have reduced foraging success and growth of bluegill. Finally, higher bluegill densities occurred in reservoirs with gizzard shad, which may have resulted from decreased largemouth bass predation due to gizzard shad availability as alternative prey. These results demonstrate that the presence of gizzard shad is associated with reduced bluegill growth rates and adult size structure and that mechanisms other than direct competition for food resources may be responsible.

Gizzard shad *Dorosoma cepedianum* is a common freshwater fish species that can predominate fish biomass in many central and southern U.S. reservoirs (Johnson et al. 1988; DeVries and Stein 1992; Stein et al. 1995). Occupying an intermediate trophic level, gizzard shad can have tremendous influence on reservoir systems through middle-out community regulation (Stein et al. 1995). Foraging by gizzard shad can influence zooplankton and phytoplankton communities (Cramer and Marzolf 1970; DeVries and Stein 1992; Schaus and Vanni 2000) and the abundance and size structure of piscivores (Swingle 1946; DeVries et al. 1991; Michaletz 1998a, 1998b). Gizzard shad can affect growth and size structure of piscivores through competition with other zooplanktivorous prey-fish species (e.g., Dettmers and Stein 1992; Garvey and Stein 1998a). The links between these competitive interactions at intermediate trophic

levels and timing of piscivory, growth rates, and size structure of piscivores have received considerable attention (Kirk and Davies 1987; Guest et al. 1990; DeVries and Stein 1992; Pope and DeVries 1994; Dettmers and Stein 1996; Olson 1996; Roseman et al. 1996; Garvey and Stein 1998a; Michaletz 1998a, 1998b). However, information about eventual effects on the adult populations of the interacting zooplanktivore species is generally lacking.

Bluegills *Lepomis macrochirus* commonly compete with gizzard shad for food resources in reservoir systems. Larvae of both species prey extensively on zooplankton, and that competition influences growth and survival of larval bluegills (DeVries and Stein 1992; Welker et al. 1994; Garvey and Stein 1998b; Garvey et al. 1998) and reproductive success of adults (Kirk et al. 1986). The mechanism responsible is probably exploitative competition for zooplankton, which gizzard shad have the potential to control and significantly reduce (Cramer and Marzolf 1970; Dettmers and Stein 1992, 1996; DeVries and Stein 1992; Welker et al. 1994; Stein et al. 1995). These interactions may be mitigated by the timing of bluegill spawning. Bluegills are protracted spawners, and the timing of their spawning bouts and the subsequent emergence of larvae relative to that of gizzard shad

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can influence the degree to which competition influences larval bluegill growth (Garvey and Stein 1998b; Garvey et al. 1998).

Clearly, the potential for population-level effects from direct biotic interactions between larval bluegill and gizzard shad has been clearly established. However, if or how these interactions ultimately influence bluegill population size structure remains unknown. The few investigations to consider the effects of gizzard shad on adult bluegills have been either in small ponds (Swingle 1946) or in single lakes (Jenkins 1957; Kirk et al. 1986). Furthermore, investigations of gizzard shad competition with other sport fish species have focused primarily on effects at early life stages (Guest et al. 1990; Pope and DeVries 1994). Potential effects on adult bluegill size structure are particularly important because, in addition to serving as an important prey species for largemouth bass, bluegills are a widely targeted sport fish, their harvest in many lakes often exceeding that of all other fish species (Drake et al. 1997). Because bluegills undergo a series of ontogenetic diet shifts and may rely on zooplankton as adults and as larvae (Werner and Hall 1988), competition for zooplankton has the potential to affect bluegill population size structure through reductions in growth at both the larval and adult stages.

In addition to the potential importance of direct interactions, the presence of gizzard shad could also influence bluegill growth and size structure through indirect pathways. For example, gizzard shad foraging and resuspension of nutrients can increase turbidity (Schaus and Vanni 2000) and may disrupt bluegill foraging (Vinyard and O'Brien 1976; Miner and Stein 1993). In addition, as an alternative prey for largemouth bass *Micropterus salmoides* (the dominant piscivore in many aquatic systems), the presence of gizzard shad could decrease predation rates on bluegills. Therefore, the presence of gizzard shad could influence bluegill population size structure through direct competition, indirect interactions, or both.

The goal of our investigation was to determine the influence of gizzard shad on bluegill growth and size structure across reservoirs with a range of gizzard shad densities. We quantified sex-specific growth rates, size-specific densities, and size structure of bluegills in reservoirs with and without gizzard shad. To examine potential mechanisms associated with gizzard shad effects on bluegill population size structure, we also quantified the most likely biotic (zooplankton, benthic

TABLE 1.—Surface area, latitude, and mean gizzard shad catch per unit effort (CPUE) for the 20 Illinois study reservoirs in which effects of gizzard shad on bluegills were examined. Age-0 gizzard shad were sampled in fall during 2 years.

Reservoir	Area (ha)	Latitude	CPUE (fish/h \pm SE)
Bloomington	250	39°69'98"	172 \pm 211
Dolan	29	38°03'31"	124 \pm 11
Forbes	226	38°42'50"	70 \pm 23
Homer	33	40°03'45"	39 \pm 30
Lake of the Woods	11	40°12'01"	228 \pm 243
Mingo	72	40°12'27"	30 \pm 6
Pana	85	39°21'55"	219 ^a
Paris	68	39°37'53"	99 \pm 81
Pierce	61	42°20'43"	77 \pm 63
Woods	11	39°31'39"	112 \pm 68
Apple Canyon	200	42°29'00"	0
Glendale	33	37°28'00"	0
Kakusha	23	41°33'38"	0
Lincoln Trail	57	39°20'20"	0
Murphysboro	58	37°46'25"	0
Red Hills	17	38°43'39"	0
Ridge	6	39°27'08"	0
Round	95	42°21'42"	0
Sterling	29	42°28'26"	0
Walnut Point	22	39°40'21"	0

^a Pana Lake was only sampled for gizzard shad in 1 year; therefore, no estimate of variation is available.

invertebrate, and bluegill abundance) and abiotic (turbidity) pathways.

Methods

To examine the effects of gizzard shad on bluegill growth and population size structure, we sampled bluegill populations in 10 reservoirs with and 10 without gizzard shad. In lakes with gizzard shad, electrofishing (AC) catch per unit effort (CPUE; fish/h) of age-0 gizzard shad in the fall ranged from 30 to 228 individuals over 2 years (Table 1). With the exception of gizzard shad, fish communities were similar and dominated by bluegills and largemouth bass. Other zooplanktivorous and piscivorous fish species were either absent or present at very low densities. Study sites were shallow (<15 m) impoundments located throughout Illinois having surface areas of 5–250 ha (Table 1). Watersheds of the study reservoirs were similar: generally in state parks, lakes predominantly (>75%) surrounded by forests, and source streams predominantly within forested riparian zones. The exception was Lake Kakusha, which had an entirely agricultural (nonforested) watershed.

Bluegills were collected for aging and determination of size structure throughout spring and early summer months of 1996 and 1997 by boat

AC electrofishing during the day. Collected bluegills (mean total $N = 240$ per lake) were placed on ice and returned to the laboratory for length (total length, mm) and weight (g) measurement, determining sex, and removal of otoliths. Annual fall electrofishing surveys also were conducted in each population during 1996–1999 to determine whether bluegill population characteristics remained stable; bluegill abundance and size structure remained consistent throughout this period (D. D. Aday unpublished data). To age fish we chose otoliths because they are more precise and less influenced by population-specific variation than scales (Hoxmeier et al. 2001). Otoliths were submerged in ethanol and examined on a black background with a dissecting scope (12 \times magnification) and reflected light in whole view.

We used a variety of metrics to determine bluegill growth and size structure. Length at age was used to compare growth rates between reservoirs with and without gizzard shad. Because this metric is sex-specific for fish older than 3 years, male and female bluegill were analyzed separately. Relative density and CPUE were used to determine differences in the size structure of populations. To assess length-specific differences we calculated a modified relative stock density (MRSD) and CPUE of bluegill at 180 mm. The MRSD was determined by dividing the number of 180-mm bluegills by the number of 80-mm bluegills (Anderson and Gutreuter 1983). Although 200 mm is the preferred size for bluegills, as classified by Gabelhouse (1984), we chose 180 mm because many of our lakes did not contain 200-mm individuals.

Densities and species composition of prey available to bluegills were determined by collecting zooplankton and benthic invertebrate samples for 1 year in each study lake. Zooplankton was collected once per month, May through September, at four offshore sites by vertical tows of a 0.5-m-diameter, 64- μ m-mesh zooplankton net. Samples were collected from the thermocline (or from the lake bottom when the lake was not stratified) to the surface, preserved in a 4% Lugols solution, and returned to the laboratory for processing. During processing, subsamples were counted until reaching either 200 organisms from the major taxonomic groups or until 10% of the total sample was counted (Dettmers and Stein 1992; Welker et al. 1994). Densities of total zooplankton, copepods, cladocerans, and rotifers were compared between reservoirs with and without gizzard shad.

Benthic macroinvertebrates were collected in June and August at six littoral sites in each lake

with a modified stovepipe sampler (Merritt and Cummins 1996; 20-cm diameter). Samples were washed through a 250- μ m sieve bucket and preserved in ethanol and rose bengal. In the laboratory, macroinvertebrates were sorted and identified to order or family. Densities for total macroinvertebrates and the most abundant macroinvertebrate taxa (from all reservoirs combined) were quantified to determine any taxon-specific differences among reservoirs.

Water quality was measured once per month, May–September, at one fixed site (generally the deepest point of each lake) in each impoundment. Turbidity was measured with a Secchi disk, and temperature and dissolved oxygen were measured at 1-m intervals from the surface to the bottom with a YSI model-55 meter. Water samples were collected for total phosphorus and chlorophyll-*a* determinations with an integrated water sampler lowered to twice the Secchi depth (to sample the entire photic zone). Chlorophyll *a* was measured in a fluorometer with a nonacidification technique (Welshmeyer 1994). Total phosphorus was analyzed according to Wetzel and Likens (1991) and quantified with a spectrophotometer.

Analysis of variance (ANOVA) was used to compare bluegill growth and population size structure in reservoirs with and without gizzard shad. In addition, summer means for water quality measurements and benthic invertebrate densities (June and August) were analyzed with ANOVA. Repeated-measures ANOVA was used to examine monthly values for differences in zooplankton densities between treatments. When necessary, data were log-transformed to normalize the variance. Differences in treatment means were considered significant at $\alpha = 0.05$.

Results

Bluegill Growth and Population Size Structure

The presence of gizzard shad was significantly related to bluegill growth and size structure. Both male and female bluegills were smaller in reservoirs containing gizzard shad than in those without gizzard shad. For females, significant differences in length were found at age 3 (ANOVA: $df = 1, 19$, $F = 4.64$, $P = 0.05$) and age 4 ($F = 8.02$, $P = 0.01$); for males, differences were significant at age 4 ($F = 6.35$, $P = 0.02$; Figure 1). Differences in length between males and females were not significant in bluegills less than age 3 ($P > 0.10$). Correlation analysis indicated no relationship between gizzard shad density and male bluegill size

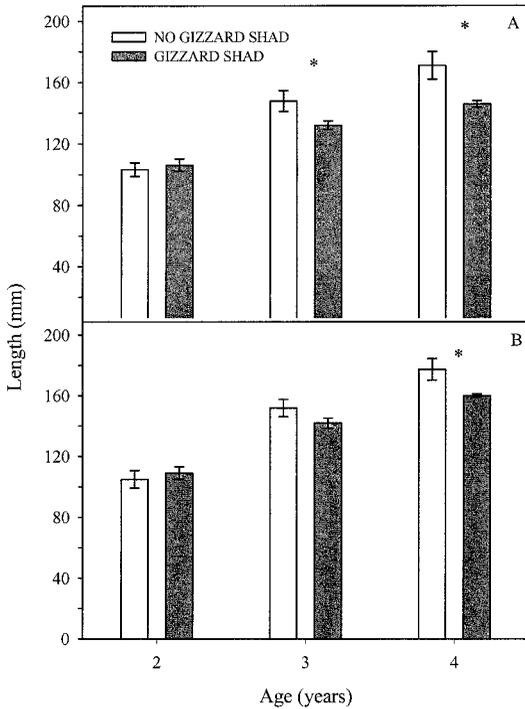


FIGURE 1.—Mean ($\pm 1SE$) total length at age for female (A) and male (B) bluegills in 10 Illinois reservoirs with gizzard shad and 10 without gizzard shad. Asterisks indicate significant differences (analysis of variance, $\alpha = 0.05$).

at age 3 ($r = 0.30$, $P = 0.40$) or age 4 ($r = 0.17$, $P = 0.64$) or female size at age 3 ($r = 0.32$, $P = 0.39$) or age 4 ($r = 0.57$, $P = 0.08$).

Bluegill density also differed in lakes with versus without gizzard shad. Absolute and relative numbers of large bluegills were higher in lakes without gizzard shad; MRSD of 180-mm bluegills was approximately 11 times higher, and CPUE of bluegills greater than 180 mm was approximately 6 times higher in lakes without gizzard shad than in those with them (Table 2). Conversely, overall bluegill density was higher in reservoirs with gizzard shad than in those without gizzard shad because of the higher number of bluegills less than 150 mm in the gizzard shad reservoirs (Table 2).

Abiotic Variables and Prey Populations

Individual water quality parameters were variable in lakes with versus without gizzard shad. Secchi depth was significantly deeper ($F = 7.29$, $P = 0.02$; Figure 2) in reservoirs without gizzard shad; turbidity was increased over twofold in lakes with gizzard shad. Temperature did not differ ($F = 1.13$, $P = 0.30$) between lakes with (24.5°C ,

TABLE 2.—Mean ($\pm SE$) bluegill catch per unit effort (CPUE; fish/h) for three size-groups (total for all sizes, ≤ 150 mm, and ≥ 180 mm) and modified relative stock densities (MRSD) of 180-mm bluegills in 10 Illinois reservoirs with and 10 without gizzard shad. P -values are for one-way analyses of variance.

Metric	Lake type		P -value
	Gizzard shad	Non-gizzard shad	
CPUE, total	316 \pm 58.6	173 \pm 27.4	0.04
CPUE, ≤ 150 mm	263.5 \pm 58.4	133.6 \pm 26.7	0.05
CPUE, ≥ 180 mm	3.40 \pm 1.66	19.4 \pm 8.21	0.016
MRSD, 180 mm	1.52 \pm 0.65	16.5 \pm 5.09	0.001

$SE = \pm 0.37$) and without ($25.2^{\circ}\text{C} \pm 0.58$) gizzard shad. In addition, neither total phosphorus ($F = 3.38$, $P = 0.08$) nor chlorophyll a ($F = 2.31$, $P = 0.15$) differed between lake type. However, Lake

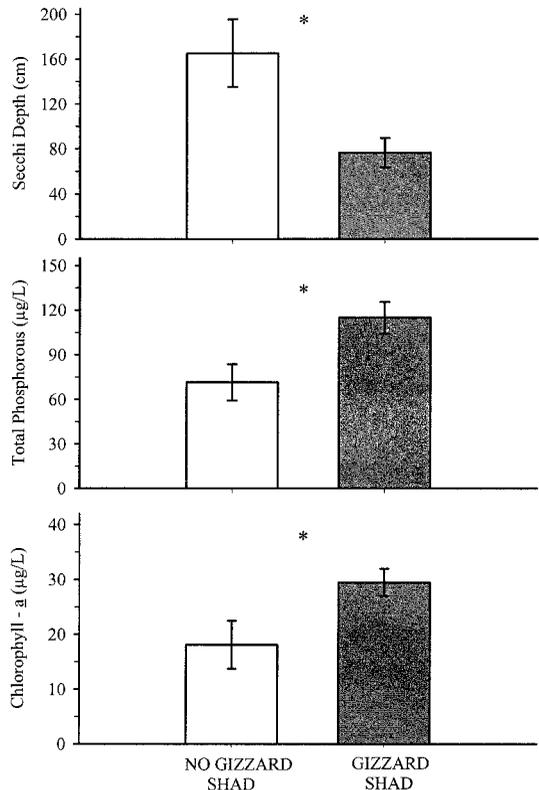


FIGURE 2.—May–September monthly means ($\pm 1SE$) for Secchi depth (cm), total phosphorus ($\mu\text{g/L}$), and chlorophyll a ($\mu\text{g/L}$) in 10 Illinois reservoirs with gizzard shad and 9 without gizzard shad (1 non-gizzard shad reservoir, Lake Kakusha, was deleted for comparisons of total phosphorus and chlorophyll a , as explained in the text). Asterisks indicate significant differences (analysis of variance, $\alpha = 0.05$).

TABLE 3.—Mean (\pm SE) prey densities for zooplankton (number/L) and benthic invertebrate (number/m²) taxa in 10 Illinois reservoirs with and 10 without gizzard shad. Zooplankton were collected monthly from May to September, and benthic invertebrates were collected twice during summer (June and August). Mean values for zooplankton were calculated by averaging across months within lakes and then across lakes. *P*-values are from repeated-measures analysis of variance (ANOVA) for zooplankton and from one-way ANOVA for benthic macroinvertebrates.

Taxon	Gizzard shad		<i>P</i> -value
	Present	Absent	
Zooplankton			
Total zooplankton	458 \pm 37.2	961 \pm 507	0.34
Copepods	21.6 \pm 3.23	23.4 \pm 4.99	0.77
Cladocerans	24.9 \pm 4.10	44.8 \pm 26.3	0.46
Rotifers	308 \pm 36.6	809 \pm 492	0.32
Benthic Invertebrates			
Total benthic invertebrates	2,605 \pm 716.6	6,179 \pm 1,654	0.05
Ceratapogonids	177.5 \pm 55.41	559.9 \pm 197.0	0.12
Gastropods	31.40 \pm 17.90	403.0 \pm 280.3	0.01
Amphipods	109.6 \pm 44.40	813.0 \pm 334.7	0.001
Chironomids	1,294 \pm 299.7	2,258 \pm 806.0	0.53

Kakusha, a statistical outlier, had unusually high values for both total phosphorus and chlorophyll *a*, differing from the mean by at least 5 SDs, which was probably due to the comparatively high proportion of agriculture on this watershed. When Lake Kakusha was removed from the analysis, reservoirs with gizzard shad had significantly higher levels of total phosphorus (ANOVA: *df* = 1,18, *F* = 7.22, *P* = 0.02) and chlorophyll-*a* (*F* = 5.34, *P* = 0.03; Figure 2) than those without gizzard shad.

Zooplankton availability was similar among populations; densities of all groups of zooplankton, including cladocerans, copepods, and rotifers, were similar between both reservoir types (repeated-measures ANOVA: *df* = 1,18, *P* > 0.32; Table 3). In this analysis, time did not have a significant effect (*P* = 0.09), and there was no significant (*P* = 0.56) time-treatment interaction. This suggests that patterns of change in zooplankton densities through time were consistent in populations with and without gizzard shad. High variation in rotifer densities resulted in high mean densities and high variation for total zooplankton in nongizzard shad lakes (Table 3). Removal of rotifers resulted in similar mean crustacean zooplankton densities (*F* = 0.52, *P* = 0.48) in lakes with (69.4 zooplankton/L, SE = \pm 30.7) and without (46.9 zooplankton/L \pm 5.0) gizzard shad.

Total benthic macroinvertebrate density was higher in lakes without gizzard shad than those with them (*F* = 4.39, *P* = 0.05; Table 3). The most common groups of benthos were chironomids, gastropods, amphipods and ceratopogonids. Both gastropods (*F* = 8.10, *P* = 0.01) and amphipods (*F* = 15.12, *P* = 0.001; Table 3) were more abundant

in lakes without gizzard shad. Although higher mean densities of chironomids and ceratopogonids were also found in nongizzard shad lakes, the differences were not significant (Table 3).

Discussion

We found that the presence of gizzard shad was associated with reduced bluegill growth and decreased maximum size of adult bluegills. Our results extend those of previous investigations on competition between larval gizzard shad and bluegills (Dettmers and Stein 1992; DeVries and Stein 1992; Welker et al. 1994; Garvey and Stein 1998b) by demonstrating that negative consequences for bluegills living with gizzard shad may extend well beyond the larval stage. The potential for smaller adult bluegills in the presence of gizzard shad was suggested by Swingle (1946), who found that gizzard shad rapidly accumulated in small ponds and reduced the size of bluegills. Although lacking replication, Jenkins (1957) found that bluegills grew faster and were larger in a lake without gizzard shad than in a comparable lake with gizzard shad. Removal of gizzard shad from a lake in Alabama resulted in a short-term increase in harvestable-size bluegills (Kirk et al. 1986). Combined, these results demonstrate that gizzard shad can directly or indirectly reduce adult bluegill size structure.

We did not find a correlation between gizzard shad density and size at age of adult bluegills. However, given the difficulty in sampling juvenile and adult gizzard shad (Van Den Avyle et al. 1995; Michaletz 1996), this finding could be spurious.

High variability in gizzard shad reproduction and recruitment is common (Johnson et al. 1988; Table 1). The ANOVA approach we used provided a conservative assessment of the effects of gizzard shad abundance on bluegill population size structure. Combining across 10 gizzard shad lakes enabled us to reveal a strong gizzard shad effect on bluegill growth rates and maximum size. Additional research that uses alternative techniques (e.g., hydroacoustics) to more accurately estimate gizzard shad abundance may identify the existence of a density threshold above which the effects of gizzard shad become important.

Studies of interactions between gizzard shad and other species with planktivorous larvae have yielded varying outcomes. The presence of gizzard shad and threadfin shad *D. petenense* decreased numbers of age-0 white crappies *Pomoxis annularis* but increased their mean size (Guest et al. 1990). This was confirmed by Pope and DeVries (1994), who demonstrated that age-0 white crappies were larger in ponds containing gizzard shad than those without. Roseman et al. (1996) found no indication of gizzard shad competition having adverse effects on yellow perch *Perca flavescens*. Because older fish were not examined in these studies, additional work will be required to predict the effects of gizzard shad on adult size structure of these species.

Turbidity, which may have influenced bluegill growth and size structure, is the mechanism that we believe could be the most important in our study populations. Gizzard shad can increase phytoplankton, nutrient levels, and suspended solids (Schaus and Vanni 2000). We found that reservoirs with gizzard shad exhibited significantly higher turbidity. Numerous investigations have demonstrated reduced feeding rates of visual predators in turbid systems. Turbidity reduced the visual acuity of European flounders *Platichthys flesus* and caused an increase in time required to capture prey (Moore and Moore 1976). For bluegills, turbidity has reduced reactive distance (Vinyard and O'Brien 1976) and consumption of a range of sizes of the copepod *Daphnia pulex* (Gardner 1981). In addition, turbidity coupled with low light intensity has been shown to reduce bluegill consumption of crustacean zooplankton (Miner and Stein 1993). In a survey of Minnesota lakes, turbidity was negatively correlated with bluegill size at a variety of ages (Tomcko and Pierce 2001). Reduced foraging rates resulting from increased turbidity could have lowered growth rates of adult bluegills in our gizzard shad reservoirs.

The small size structure of bluegills in reservoirs

with gizzard shad could also result from the higher bluegill densities in these systems (relative to systems without gizzard shad). Combining all size classes, we found higher bluegill densities in reservoirs with gizzard shad than in reservoirs without them. Because densities of the largest bluegills were higher in reservoirs without gizzard shad, differences in total bluegill density resulted from the presence of more small- and intermediate-size bluegills in reservoirs with gizzard shad. In a two-lake comparison, Jenkins (1957) also noted that bluegills were smaller (at all ages) and more densely populated in a lake with gizzard shad (approximately 7,400/ha) than in a lake without them (approximately 3,500/ha.). Density-dependent slow growth resulting from high densities has been implicated in previous studies examining small adult size in bluegills (Swingle and Smith 1941; Ligler 1971; Murnyak et al. 1985; Otis et al. 1998).

Despite differences in total bluegill densities between lakes with and without gizzard shad, we found no concomitant difference in density of zooplankton, a primary prey item for bluegills throughout their ontogeny (Mittelbach 1981). The lack of a gizzard shad effect on zooplankton density differs with previous findings that gizzard shad can reduce zooplankton populations (Dettmers and Stein 1992; DeVries and Stein 1992). One explanation for this discrepancy is that zooplankton productivity could actually have been higher in lakes with gizzard shad, but zooplankton was being removed via planktivory. Estimates of zooplankton productivity would be required to address this potential explanation. However, a second explanation for the lack of gizzard shad effect on zooplankton is that gizzard shad densities were much lower in our systems than in the previous investigations. Dettmers and Stein (1996) suggest that larval gizzard shad densities must be below 10/m³ for zooplankton populations to remain abundant despite gizzard shad predation; the mean larval gizzard shad density in our reservoirs was only 4.7/m³ (range = 1.73–9.50/m³; Aday, unpublished data). We believe that gizzard shad densities and resulting predation rates were probably low enough to account for the lack of differences in zooplankton populations between lakes with and without gizzard shad.

We did find reduced abundance of benthic invertebrates in the gizzard shad reservoirs. This could be a consequence of higher densities of smaller bluegills; investigations have demonstrated that *Lepomis* spp. can reduce the densities of benthic invertebrates (Gilinsky 1984; Johnson et

al. 1996). Reduced benthic invertebrate densities due to direct consumption by gizzard shad seems unlikely. Although macroinvertebrates have been found in the diets of gizzard shad (Jude 1973), they feed primarily on organic detritus, zooplankton, and phytoplankton (Yako et al. 1996; Schaus and Vanni 2000). It is more likely that reductions in benthic invertebrate density associated with gizzard shad would be through indirect pathways. For example, the increased turbidity in systems with gizzard shad could have reduced macrophyte densities (Scheffer et al. 1993), which might make benthic invertebrates more vulnerable to fish predation (Gilinsky 1984). Future investigations that quantify macrophyte abundance and bluegill diets will be necessary to resolve these questions. Whether reduced benthic invertebrate densities in the gizzard shad populations are due to higher bluegill densities or indirect gizzard shad effects, they may have contributed to the differences we observed in bluegill growth and size structure.

Higher bluegill densities in gizzard shad reservoirs may be attributable to differences in predation rates by largemouth bass, which could be lower when gizzard shad are available as alternative prey. Several piscivores select gizzard shad over *Lepomis* prey, including esocids (Wahl and Stein 1988) and walleyes *Stizostedion vitreum* (Einfalt and Wahl 1997). Largemouth bass were abundant in all of the study reservoirs and also prefer soft bodied gizzard shad over spiny-rayed bluegills (Lewis and Helms 1964; Miranda and Muncy 1991). Lewis et al. (1974) found that, in a lake with a variety of prey fish, gizzard shad was the principal food item selected by largemouth bass. Similarly, in three Illinois reservoirs in which largemouth bass diets have been quantified, bass always consumed more gizzard shad than bluegills (R. J. H. Hoxmeier, unpublished data). In a laboratory feeding experiment, fingerling bluegills were consumed less than any of the nine different prey items offered, including gizzard shad (Lewis and Helms 1964). Largemouth bass preference for gizzard shad over bluegills is related to differences in morphology and anti-predator behavior (Wahl and Stein 1988; Einfalt and Wahl 1997). For example, bass experience higher digestion rates and can obtain a larger ration when consuming gizzard shad rather than bluegills (i.e., at equal body depth, gizzard shad are heavier and provide 30–40% more biomass than bluegills; Miranda and Muncy 1991). Higher bluegill densities in reservoirs with gizzard shad may be attributable, in part, to differential predation by largemouth bass and may

have contributed to lower bluegill growth rates in these reservoirs.

Previous investigations have clearly indicated that competition between bluegills and gizzard shad can influence bluegill growth and survival at the larval stage (e.g., Garvey and Stein 1998b). Our study indicates that the influence of gizzard shad on bluegills may extend well beyond the larval stage, ultimately influencing growth rates of adult bluegills and overall bluegill population size structure. Direct competitive interactions at the larval stage may contribute to reduced population size structure. However, our results suggest that the indirect effects of gizzard shad, perhaps through increased turbidity, reduced benthic invertebrate densities, and by serving as alternative prey for largemouth bass, may have a greater influence on bluegill size structure than does direct competition, particularly for adults. These relationships may be most important in systems with either low densities of gizzard shad or high zooplankton productivity, such that zooplankton levels are not suppressed by gizzard shad foraging.

There has been considerable debate about the value of stocking shad in reservoir systems as prey for piscivores, and fishery managers have recognized the potential negative effects of gizzard shad on sport fish populations (see review in DeVries and Stein 1990). Numerous investigations have demonstrated that shad may compete with young-of-year sport fish for food resources (Dettmers and Stein 1992, 1996; DeVries and Stein 1992; Welker et al. 1994; Garvey and Stein 1998b). Additionally, they may grow too rapidly and become too large to serve as useful prey for the predators they were intended to benefit (Noble 1981; DeVries et al. 1991; Stein et al. 1995). Our results provide further evidence that gizzard shad should not be stocked as forage fish for piscivores. Bluegills are an important sport fish species, and the presence of gizzard shad has the potential to result in poor bluegill growth rates and small adult size structure.

Although previous investigations have considered bluegill-gizzard shad interactions, this study is unique in that we examined potential mechanisms associated with adult bluegill growth and size structure at a large spatial scale that covered multiple populations. As such, our investigation provides a framework for understanding the complex interactions between adult bluegills and gizzard shad and a foundation for future investigations. For example, angler exploitation rates can influence growth and maturation rates of bluegills (Coble 1988; Drake et al. 1997). Additional studies

are needed that focus on the ways in which variation in exploitation rates might interact with fish community composition to ultimately influence bluegill population size structure. In addition, closer examination of the gizzard shad–macrophyte–macroinvertebrate link should provide further insight into the ways in which the presence of gizzard shad might indirectly influence adult bluegill growth.

Mechanisms other than the presence of gizzard shad may be responsible for the small size structures of adult bluegills. Size and age at maturity are important in determining adult bluegill growth rates and maximum size, and the social structure of the adult bluegill population plays an important role in determining these life history traits (Jennings et al. 1997). How the presence of gizzard shad influences timing of maturation has not been assessed, but the potential exists for gizzard shad to influence size and age at maturity by influencing growth rates of individual fish. In addition, a variety of factors may influence gizzard shad survival and recruitment (e.g., Bremigan and Stein 1999); understanding these factors and their influence on bluegill growth should help managers predict the likelihood of developing and maintaining a bluegill population with a large adult size structure.

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