Larval Gizzard Shad Success, Juvenile Effects, and Reservoir Productivity: Toward a Framework for Multi-System Management

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Abstract. — Recruitment success of larval fishes can determine subsequent effects of older life stages on ecosystem structure and function. Because size and abundance of juvenile gizzard shad *Dorosoma cepedianum* determines, in large part, their effects on zooplankton abundance and sport-fish recruitment, we investigated recruitment of larval gizzard shad to the juvenile stage. We hypothesized that larval survival would correlate positively with availability of small (<0.40 mm) zooplankton and reservoir productivity and would dictate abundance of individuals reaching the juvenile stage. In downstream and upstream areas of four Ohio reservoirs ranging from mesotrophic to hypereutrophic, we evaluated larval gizzard shad success by comparing hatch, growth, and survival of weekly cohorts of larvae with availability of small zooplankton, and then we determined whether larval success could predict juvenile gizzard shad size and abundance. Total larval hatch abundance increased with reservoir productivity and was higher upstream than downstream. Weekly cohorts that produced abundant survivors reflected not only high hatch but also high survival in upstream areas during periods of abundant small zooplankton. Overall, larval hatch and survival predicted juvenile abundance but not juvenile size. Juvenile abundance increased with reservoir productivity, particularly in upstream areas, whereas juvenile size reflected the combined influence of juvenile abundance and reservoir productivity. Across mesotrophic to eutrophic conditions, juvenile gizzard shad size decreased with increasing abundance; but across eutrophic to hypereutrophic conditions, juvenile gizzard shad size increased despite continued increasing juvenile abundance. A conceptual framework for management, which incorporates reservoir productivity and anticipated effects of juvenile gizzard shad, should improve our success in attaining fisheries objectives across disparate systems.

Fisheries ecologists typically view larval fish as quite distinct from juvenile or adult fish. Considering larval fish, we often investigate how system characteristics (i.e., prey availability, temperature, or water level fluctuations) affect larval survival and ultimately recruitment (Sale 1990; Pepin 1991; Leggett and DeBlois 1994). Beyond the age at which recruitment is set, we often investigate the effects of fish either on other fishes (i.e., competitive or predatory interactions; Knight et al. 1984; Kitchell and Crowder 1986; Olson et al. 1995) or on food web dynamics (i.e., effects of top predators on primary production and water clarity; McQueen et al. 1989; Kitchell and Carpenter 1993). Considering both success of larval fish and effects of older fish on system dynamics, variability among systems often compromises single explanations and challenges managers striving to achieve similar objectives in disparate systems.

Further, larval success and fish effects are not independent, for the intensity of impact of older fish depends, in part, on their recruitment success. For example, interannual variability in recruitment of a top predator can produce interannual variability in food web dynamics (Carpenter 1988). Because fish recruitment not only varies interannually but among systems as well, intersystem recruitment variability should produce variable food web dynamics among

systems. Within this context, we investigated recruitment of larval (age-0, <25 mm) gizzard shad *Dorosoma cepedianum* and subsequent food web effects of juvenile (age-0, >25 mm) gizzard shad along a productivity gradient of midwestern reservoirs. All shad lengths given throughout are total length.

Juvenile Gizzard Shad Effects

During the past 50 years, both gizzard shad and threadfin shad *D. petenense* have been stocked extensively in midwestern and southeastern reservoirs in attempts to improve sportfish production, but mixed results preclude a general conclusion about how shad influence sportfishes (Noble 1981; DeVries and Stein 1990). Even less is known regarding the specific effects of juvenile gizzard shad on sportfish recruitment. For example, juvenile gizzard shad may positively affect success of age-0 largemouth bass *Micropterus salmoides* if the shad remain vulnerable to this predator throughout its first summer (Storck 1986; Adams and DeAngelis 1987; Garvey and Stein 1998). Conversely, in shallow, hypereutrophic reservoirs, rapid growth rates of juvenile gizzard shad quickly make them invulnerable to age-0 largemouth bass predators (DeVries and Stein 1992; Stein et al. 1995). In these systems, consumption of zooplankton by juvenile gizzard shad can severely depress midsummer zooplankton (Dettmers and Stein 1992; DeVries and Stein 1992), which can lead to exploitative competition with, and poor recruitment of, zooplanktivorous larvae of later spawned fishes, particularly bluegills *Lepomis macrochirus* (DeVries et al. 1991; DeVries and Stein 1992; Stein et al. 1995; Garvey et al.1998a). In turn, existence of fewer age-0 bluegills in these hypereutrophic systems translates to slower growth of their age-0 largemouth bass predators (DeVries et al. 1991; Stein et al. 1995; Garvey and Stein 1998).

Thus, both direction (i.e., positive or negative) and intensity of effects of juvenile gizzard shad on age-0 sportfish depend on juvenile gizzard shad size (which primarily dictates their vulnerability to predators) and abundance (which primarily dictates their consumptive demand for zooplankton), both of which vary across reservoirs (Noble 1981; Willis 1987; Buynak et al. 1992; Michaletz 1997). To date, we know little regarding the relationships among juvenile gizzard shad size and abundance and reservoir productivity. Yet variation in juvenile gizzard shad size and abundance among systems must be understood to generate broadscale management plans that incorporate variability in juvenile gizzard shad effects. Specifically, by identifying ecological mechanisms underlying juvenile gizzard shad size and abundance, we can determine the feasibility of manipulating gizzard shad populations to improve sportfish recruitment.

Larval Gizzard Shad Success

To identify the ecological mechanisms that determine juvenile gizzard shad size and abundance, we seek to predict the success of larval gizzard shad in reaching the juvenile stage. Larvae feed solely on zooplankton (Bodola 1966; Cramer and Marzolf 1970; DeVries et al. 1991) but typically have little effect on reservoir food webs due to their small size (3.5–25 mm; Dettmers and Stein 1992). Because experimental evidence demonstrates that larval gizzard shad foraging, growth, and survival positively correlate with availability of small (<0.40 mm) zooplankton prey (Bremigan and Stein 1994, 1997; Welker et al. 1994), we focused our field sampling on assessing the effects of zooplankton size and density on recruitment of larval gizzard shad to the juvenile stage. In previous work, through comparison of only the downstream areas of 12 reservoirs whose trophic states ranged from mesotrophic to hypereutrophic, we demonstrated that both hatch abundance and survival of larval gizzard shad were positively cor-

related with reservoir productivity (Bremigan 1997). In addition, although biomass of small crustacean zooplankton (<0.40 mm) was positively correlated with foraging success, mean larval gizzard shad survival was not correlated with mean small zooplankton biomass (both estimated as means across May and June, i.e., at course temporal and spatial scales; Bremigan 1997). The apparent ''disconnect'' between small zooplankton availability and larval survival, as indicated by this previous work, suggests that the relationship between larval survival and zooplankton availability must be evaluated at finer spatial and temporal scales. Indeed, that is the goal of this paper.

Herein, we evaluate the relationship between small crustacean zooplankton abundance and larval gizzard shad survival at finer temporal and spatial scales, and we assess juvenile gizzard shad size, abundance, and potential for effects on sport-fish recruitment across four Ohio reservoirs with conditions ranging from mesotrophic to hypereutrophic. Through separate analysis of upstream and downstream areas, we explore larval gizzard shad recruitment and subsequent juvenile effects across longitudinal productivity gradients within each reservoir as well as among eight reservoir area combinations. We address three specific questions. (1) Can small zooplankton abundance explain larval gizzard shad success when viewed at spatial and temporal scales finer than those examined in 1993 (Bremigan 1997)? To address this question, we evaluated hatch abundance, growth, and survival of weekly cohorts (using otolith analysis) of larval gizzard shad. (2) Can larval gizzard shad growth and survival predict juvenile gizzard shad size and abundance? To address this, we compared larval gizzard shad growth and survival during May and June with juvenile gizzard shad abundance and size in late June and early August. (3) Do juvenile gizzard shad effects vary with reservoir productivity? To address this,

TABLE 1. — Characteristics of four Ohio reservoirs sampled during 1994. Turnover was calculated as reservoir capacity (ha-m) divided by reservoir inflow (ha-m; Youger 1982). Depth, turbidity (nephelometric turbidity units, NTU), total phosphorus (TP), and chlorophyll were determined separately for upstream (U, within 0.6–1.2 km of the inlet stream) and downstream (D, within 0.8 km of the dam) reservoir areas.

Lake (code) and county	Area (ha)	Shoreline (km)	Turnover	Watershed (km^2)	Sampling area	Depth (m)	Turbidity (NTU)[a]	TP (μg/L)[b]	Chlorophyll (μg/L)[a]
Delaware (D)	526	56.0	16.0	987	U	2.0	54.7	151.6	31.6
Delaware					D	6.0	15.9	62.2	15.7
Knox (K)	200	19.3	7.3	81.3	U	3.0	12.7	74.6	30.1
Knox					D	7.0	6.8	55.4	15.4
Logan (L)	138	16.1	3.4	36	U	2.0	14.2	86.1	20.1
Hocking					D	5.5	6.9	58.2	17.5
Burr Oak (B)	269	32.2	2.6	85	U	2.5	22.1	59.2	8.2
Athens					D	6.5	4.39	30.5	5.4

[a] Determined as a mean of weekly samples taken from mid-May through June.
[b] Determined as a mean of samples taken every 2 weeks from May through June.

we quantified differences in juvenile gizzard shad size, to evaluate their vulnerability to age-0 predators, and differences in midsummer zooplankton assemblages, to evaluate availability to later spawned larval fishes.

Methods
Study Reservoirs

We sampled downstream and upstream areas of four reservoirs during May through early

August 1994 to evaluate to what extent (and why) larval gizzard shad hatch abundance, growth, and survival and juvenile gizzard shad size, abundance, and effects varied with reservoir productivity. Similar in size and morphometry, these reservoirs encompassed a broad range in productivity (Table 1). Downstream sampling areas were within 0.8 km of the dam and were characterized by maximum reservoir depth, whereas upstream areas were quite shallow and within 0.6–1.2 km of stream inflow. Downstream and upstream sampling areas were typically 2.8 km apart.

Our sampling protocol and data analysis reflected a perspective that incorporated gizzard shad ontogeny, first evaluating larval success and subsequently juvenile impact. During May through June, we sampled the eight reservoir areas once per week to compare growth and survival of weekly hatched cohorts of larval gizzard shad. During late June through early August, we sampled every 2 weeks to quantify size structure and relative abundance of juvenile gizzard shad and to explore the extent to which their impact on midsummer zooplankton, and their vulnerability to age-0 predators, varied.

May–June: Recruitment Environments and Larval Gizzard Shad Success

Abiotic factors and chlorophyll. — At two replicate sites within each area, we collected an integrated water sample from the photic zone (defined to be 1.5 × Secchi depth) to quantify total phosphorus (TP), turbidity, and chlorophyll. We used 2.5-cm-diameter Tygon tubing lowered to the depth of the estimated photic zone and then retrieved in a U-shaped fashion to obtain the integrated water sample. A nephelometer in the field provided turbidity measurements; samples for laboratory determination of chlorophyll and TP (TP was measured once every two weeks) were transported to the laboratory on ice. Once per week, at the most upstream and downstream sites (i.e., one site per area) we measured temperature and dissolved oxygen profiles.

To measure chlorophyll from phytoplankton available to zooplankton, we filtered 50-mL water samples in a darkened room through 35-µm mesh (Gliwicz 1975; Porter 1977). Small phytoplankton passing through the 35-µm mesh were filtered onto Whatman GF/C glass fiber filters, rinsed with distilled water, frozen, and then extracted with 25 mL of methanol. Chlorophyll-*a* concentrations were determined fluorometrically (corrected for pheopigments; Soranno 1990).

To measure TP concentrations, we froze photic zone water samples in Nalgene bottles immediately upon return to the laboratory. Subsequently, TP was determined via persulfate digestion followed by spectroscopic analysis with the acid molybdate method.

Within downstream and upstream areas, we calculated daily means of turbidity and edible chlorophyll by averaging between the two replicate sites. Mean May through June values of TP, turbidity, and chlorophyll within each reservoir area were calculated by averaging across sample dates.

Zooplankton. — Zooplankton were sampled at the two replicate sites within each reservoir area using vertical net hauls from bottom to surface. The net was a simple cone, 98 cm long × 35 cm in diameter (54-µm mesh). Once collected, zooplankton were preserved in 70% ethanol. We assumed 100% net efficiency.

To quantify crustacean zooplankton, we identified (cladocerans to genus; adult copepods as calanoid or cyclopoid; immature copepods as nauplii), counted, and measured crustacean

zooplankton by using a digitizing tablet viewed through a dissecting microscope drawing tube (per Stahl and Stein 1994). Each zooplankton sample was placed in a dish divided into 16 equal-sized wedges; all individuals were counted from two opposite wedges of the dish. From these counts, the total number of individuals within each taxon in the entire sample was estimated. If this number was 25 or greater, then counting of complete wedges continued until at least 50 individuals of that taxon were counted and the first 22 individuals encountered were measured (total body length, excluding spines, helmets, caudal rami). If the total number of individuals of a taxon, as estimated from the first two wedges, was less than 25, then counting of that taxon stopped because it contributed so little to the entire sample, and the original estimate of abundance was retained. For these rare taxa, the individuals encountered in the first two wedges were measured, as described above. We calculated crustacean zooplankton biomass using taxon-specific length-dry weight regressions (Dumont et al. 1975; Bottrell et al. 1976; G. G. Mittelbach, Kellogg Biological Station, Michigan State University, unpublished data). To calculate crustacean zooplankton production rates (per Culver and DeMott 1978), we quantified, for each sample, percent of females in each taxon bearing eggs and the mean number of eggs per egg-bearing female.

We calculated two metrics: (1) the rate of increase in mass of existing individuals (growth in mg dry mass/L per day) and (2) the rate at which zooplankton mass was generated via births of new individuals (reproduction in mg dry mass/L per day), using temperature-dependent zooplankton development rates (DeMott 1976; Bean 1980). Summing these two estimates (growth and reproduction) yielded taxon-specific crustacean zooplankton production. By summing estimates across taxa, we calculated total crustacean zooplankton production. To estimate total biomass of small zooplankton available to small-gaped larval gizzard shad (Bremigan and Stein 1994), we summed the biomass of zooplankton attributable to individuals less than 0.40 mm and the biomass attributable to birth of individuals less than 0.40 mm. For each zooplankton parameter (density, size, biomass of small zooplankton, total biomass, and total production), we calculated daily means by averaging across replicate sites within each reservoir area.

Larval gizzard shad success. — During May through June, larval gizzard shad were collected offshore, between 0900 and 1500 hours, at two replicate sites within each reservoir area (upstream and downstream) via surface tows of a 0.75-m diameter ichthyoplankton net (500- μm mesh) towed for 5 min at 1-1.5 m/s. Larvae were preserved in 95% ethanol. A flowmeter, mounted in the mouth of the net, provided an estimate of the water volume filtered, permitting estimation of larval gizzard shad density.

Larval gizzard shad were counted in each ichthyoplankton sample to estimate their density. We measured total length (nearest 0.1 mm) of 50 larval gizzard shad randomly taken from one randomly chosen replicate per reservoir area per date. To estimate age in days (Davis et al. 1985), we removed sagittal otoliths from up to 10 larval gizzard shad in each of two size-classes (9-14.9 and 15-21 mm) for each reservoir area on each weekly sample date. Otoliths were mounted whole and cleared on glass slides using a polyester resin, then the age of the left otolith was determined by two independent readers using a transmitted-light microscope at 400 × magnification. To avoid bias, neither reader knew collection date, location, or size of larvae. If ring counts from the two readers were within three rings, the mean of the two counts was taken. If readings differed by more than three rings, the otolith was discarded. Of 319 otoliths read, 22 were discarded.

To estimate larval gizzard shad density in each reservoir area on each date, we calculated a mean density between the two replicate tows. By combining density and length data, we estimated production of 5-6-mm larval gizzard shad (an index of hatch density) in each reservoir area. To do so, we calculated the cumulative abundance (May through June) of 5-6-mm larvae because larvae, which hatch at about 3.5 mm (Carlander 1969), have recruited to our nets by 5 mm and by 8 mm, substantial larval mortality has occurred.

In generating our index of larval gizzard shad hatch for May through June, we accounted for the potential for larval growth rate differences across reservoirs to influence estimates. Because slow-growing larvae remain in a size-class longer than fast-growing ones, production of a slow-growing population of larvae will be overestimated as compared with a fast-growing one despite similar densities. Based on otolith analysis of 9–15-mm larval gizzard shad (described below), we identified minimum and maximum growth rates (0.66 and 0.94 mm/d, respectively; based on mean values for weekly hatch cohorts) for larval gizzard shad less than 15 mm. Minimum and maximum growth rates were not reservoir specific. Using these extreme growth rates, we generated two density estimates in each reservoir area, as described below, for larval gizzard shad hatch abundance. For each reservoir area, density estimates obtained in this fashion represent the range for true cumulative reservoir hatch abundance.

To generate cumulative hatch abundance estimates (May through June) from our weekly samples, we determined the number of days of growth (hereafter, time interval for 1 mm growth) represented by a 1-mm (5–6-mm) increment (for both minimum and maximum growth rates). Next, we determined how many time intervals for 1 mm growth occurred within 1 week and multiplied the density of 5–6-mm larvae on each sampling date by this number to estimate the abundance of 5–6-mm larvae produced each week. We summed these weekly hatch abundance estimates to generate minimum and maximum estimates of the cumulative hatch abundance for May through June in each reservoir. We use these estimates as an index of hatch abundance rather than as an absolute measure.

Larvae hatch 3 d after fertilization and otolith ring deposition begins about 4 d later (Davis et al. 1985) at about 5 mm (M. T. Bremigan, personal observation). Because our estimates of larval gizzard shad hatch were based on abundance of 5mm individuals, we used otolith ring count as our estimate of larval age. This age estimate reflects the number of days since larvae reached 5 mm, such that our use of ''hatch date'' refers to the date on which larvae reached 5 mm. Larval gizzard shad growth rates (mm/d) were estimated by subtracting 5 mm from the total length of each larva and dividing this number by the mean ring count.

July – August: Juvenile Gizzard Shad Effects

Zooplankton. — We continued to sample zooplankton once every 2 weeks during July through early August (see *Zooplankton* above).

Juvenile gizzard shad. — Alarval gizzard shad vulnerability to our ichthyoplankton net declined for individuals greater than 15 mm, we replaced it with a larger (1 × 2 m) neuston net (1-mm mesh), towed at the surface for 1.5-5 min at 1–1.5 m/s to collect larval and early juvenile gizzard shad once every 2 weeks during late June through July. On each date, two replicate tows were completed in each reservoir area. A flowmeter, mounted in the mouth of the net, provided an estimate of the water volume filtered, permitting estimates of gizzard shad density. Gizzard shad were preserved in 95% ethanol.

Because juvenile gizzard shad vulnerability to the neuston net declined for individuals

greater than 40 mm, we shifted in August to pulsed DC electrofishing. In each reservoir area, we conducted two shoreline and two open-water 5-min transects, attempting to collect all juvenile gizzard shad. Capture efficiency declined when gizzard shad were extremely abundant. As a result, estimates of juvenile gizzard shad abundance in situations of high abundance are quite conservative. Upon capture, gizzard shad were placed on ice and frozen for storage. When numbers collected were more than 100, we retained 100 random individuals; excess fish were counted and returned to the reservoir. In the laboratory, gizzard shad from each neuston sample and electrofishing transect were counted, and up to 50 individuals were measured (nearest 1 mm).

Abundance and size data were combined to calculate density of gizzard shad in 2-mm length-classes. Mean values across two replicate neuston tows or across four electrofishing transects within each area were calculated for each sample date. Juvenile gizzard shad greater than 40 mm avoided our neuston net by mid-July; in addition, abundance estimates were quite variable between neuston net replicate tows. Therefore, we assessed juvenile gizzard shad size in late June (via neuston net) and we assessed juvenile gizzard shad size and abundance in early August (via electrofishing). For juvenile gizzard shad size distributions in late June, we calculated gizzard shad body depth (Storck 1986) and estimated the proportion of individuals vulnerable to age-0 largemouth bass, based on typical age-0 predator sizes (R. Wright, Auburn University, personal communication) and assuming that gizzard shad with body depths smaller than predator gapes were vulnerable. For analysis of juvenile gizzard shad size in early August (when juvenile gizzard shad typically have outgrown vulnerability to age-0 largemouth bass), we compared mean sizes of juvenile gizzard shad among reservoir areas.

Results
May – June: Recruitment Environments and Larval Gizzard Shad Success

Abiotic factors and chlorophyll. — Both total P and chlorophyll ranged broadly across the eight reservoir areas, spanning mesotrophic to hypereutrophic conditions. Both total P and chlorophyll, as well as turbidity, were higher upstream than downstream within each reservoir (see Table 1). Temperature regimes were similar across reservoirs, increasing from 15°C to 29°C during May through June.

Zooplankton. — Crustacean zooplankton assemblages were primarily composed of calanoid and cyclopoid copepod nauplii and adults, *Bosmina* spp., and *Daphnia* spp. These taxa consistently accounted for more than 95% of total zooplankton biomass (hereafter, zooplankton refers to crustacean zooplankton). Percent contribution among these groups varied across reservoir areas and through time but without consistency.

We regressed mean zooplankton production against mean edible chlorophyll concentration to determine if a relationship existed. Although mean zooplankton production ranged from 7 to 48 mg dry weight/m^3 per day across reservoir areas, mean edible chlorophyll explained virtually none of this variance ($N = 8$, $P > 0.9$, $r^2 = 0$).

We characterized recruitment environments for larval gizzard shad by evaluating biomass of zooplankton less than 0.40 mm. Copepod nauplii and copepodids, preferred prey of small (<15 mm) larval gizzard shad (Dettmers and Stein 1992; Bremigan and Stein 1997), constituted the majority of small zooplankton. Biomass of small zooplankton during May through June varied among reservoir areas, tending to be highest in Delaware Reservoir, the most productive

reservoir of the study (Table 2).

To determine if the size structure of zooplankton assemblages varied among the eight reservoir areas, we compared percent of total zooplankton biomass (after arcsine square root transformation to normalize variance) accounted for by small (<0.40 mm) zooplankton via analysis of variance (ANOVA). Percent contribution of small zooplankton, which did not vary across reservoir areas ($N = 8$, $P < 0.24$, $r^2 = 0.08$), typically ranged 12-27%.

Lake	Area	Mean biomass of ZP (μg dry/L)	SE
Delaware	D	17.1 z	4.7
Delaware	U	12.1 zy	5.5
Knox	U	7.0 zy	3.7
Burr Oak	U	6.9 zy	1.0
Burr Oak	D	5.2 zy	0.7
Logan	U	4.3 zy	0.9
Knox	D	3.5 y	1.4
Logan	D	2.4 y	0.4

TABLE 2. — Mean biomass (dry weight/L) of small (<0.40 mm) zooplankton (ZP) collected once per week during May through June 1994 in downstream (D) and upstream (U) areas in four Ohio reservoirs, from most to least productive ($N = 9$ ZP samples per reservoir area). Biomass differed among reservoir areas (ANOVA; $F = 2.76$, $P < 0.015$, $r^2 = 0.23$); values with a letter in common are not significantly different. Tukey's pairwise comparisons were significant at $\alpha = 0.05$.

Larval gizzard shad hatch. — Cumulative hatch abundance during May through June varied broadly across reservoirs, was positively correlated with TP, and was higher upstream than downstream (Figure 1). Most often, the majority of larval hatch was distributed across 3-4 weeks (Figure 2); however, upstream in Logan Reservoir, more than 90% of the cumulative May through June hatch was concentrated in 1 week. We compared small zooplankton biomass, only considering weeks for which larval gizzard shad hatch exceeded 0.1 larvae/m^3, to assess the potential for differences in small zooplankton biomass across reservoir areas during the hatch to influence larval success. Differences in biomass of small zooplankton among the eight reservoir areas were more pronounced during hatch (ANOVA: $F = 5.4$, $P < 0.0005$, $r^2 = 0.57$; see Figures 2, 5A) than through May and June. Again, small zooplankton were most abundant in Delaware Reservoir, the most productive of the study.

Larval gizzard shad survival and growth. — Only 6 of 30 weekly cohorts across the eight reservoir areas produced abundant 9-14.9-mm survivors (range 8-50/m^3; Figure 3A); of these six, only three cohorts produced abundant 15-21-mm survivors (range 1-4/m^3; Figure 3B). Low cohort survivor abundance coincided with low cohort hatch density (hereafter, low hatch is <10/m^3; Figure 3). In contrast, hatch was never low for cohorts with abundant survivors (Figure 3). Yet, whereas high hatch appeared necessary for success (hereafter, high hatch is >10/m^3), it was not sufficient for production of survivors. Rather, among cohorts with high hatch density,
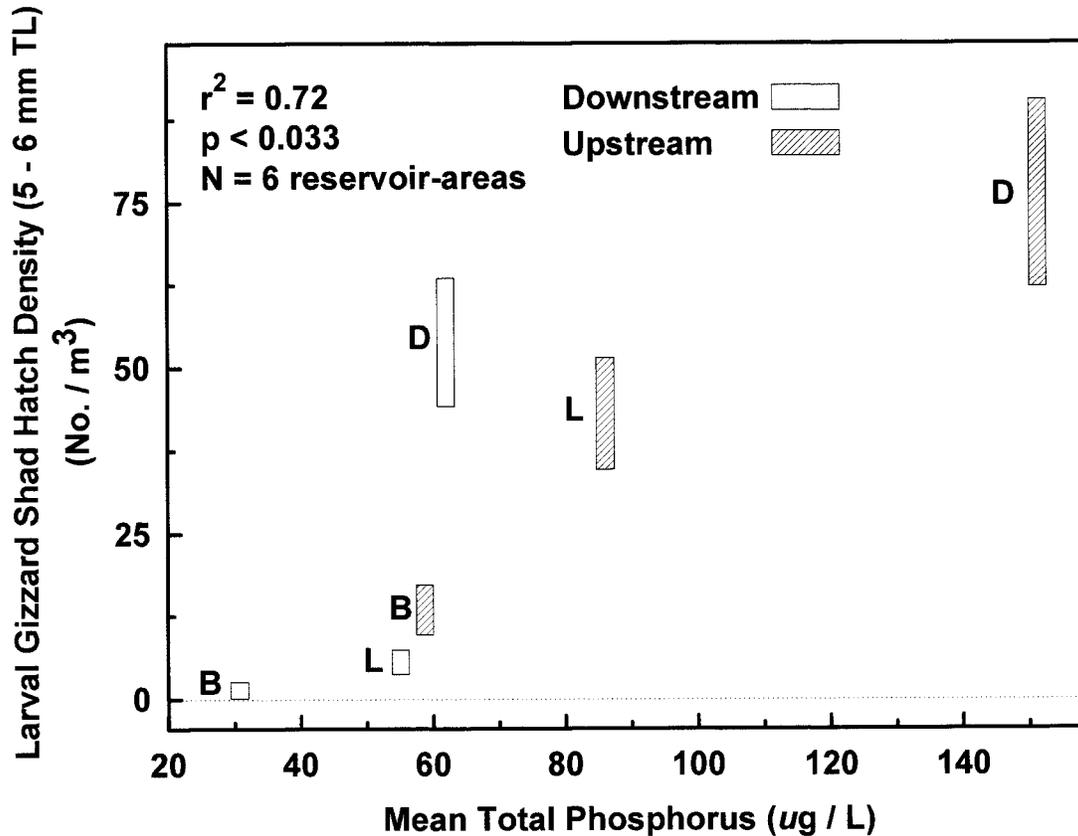
FIGURE 1. — Relationship between larval gizzard shad hatch abundance (total density of larvae 5–6 mm in total length produced during May through June) and mean total epilimnetic phosphorus concentration in the upstream and downstream areas of three Ohio reservoirs (D, Delaware; L, Logan; B, Burr Oak) in 1994. A missed sampling date during the hatching period in the fourth reservoir (Knox) precluded estimation of total hatch. For each reservoir area, total hatch abundance represents the range within which we estimate the actual value falls, accounting for potential differences in larval growth rate across reservoir areas to influence density estimates. Endpoints of each range were generated using minimum and maximum larval gizzard shad growth rates (see Methods). We used mean larval hatch abundance (calculated as the average of the values generated via minimum and maximum growth rates) in the regression analysis.

density of larval survivors varied broadly and was unrelated to cohort hatch density ($P > 0.6$, $r^2 <$ 0.1 for both 9-14.9-mm and 15-21-mm size-classes).

To evaluate conditions that distinguish between cohorts with few and with many survivors, we grouped larval cohorts into three categories: (1) low hatch and few survivors, (2) high hatch and few survivors, and (3) high hatch and many survivors. We expected cohorts with high hatch and many survivors to have experienced high biomass of small zooplankton and favorable temperatures and therefore faster growth than cohorts with high hatch and few survivors. For cohorts with low hatch, evidence of fast growth and high survival of larvae would suggest that low hatch limited survivor numbers. Overall, comparing larval hatch, growth, survival, and recruitment environments among these three categories allows us to explore the relative importance of hatch density and survival in establishing survivor abundance.

We first compared growth rate distributions (separate analyses for 9–14.9-mm and 15–21-mm survivors) among our three larval cohort categories. To do so, we calculated the

proportion of larvae in 0.1-mm/d growth rate-classes, weighting individual growth rates by cohort density. Next, for each category, we multiplied the proportion of larvae in each 0.1-mm/d growth rate-class by the total number of otoliths analyzed for that category to determine the number of observations in each growth rate-class. We then compared weighted growth rate
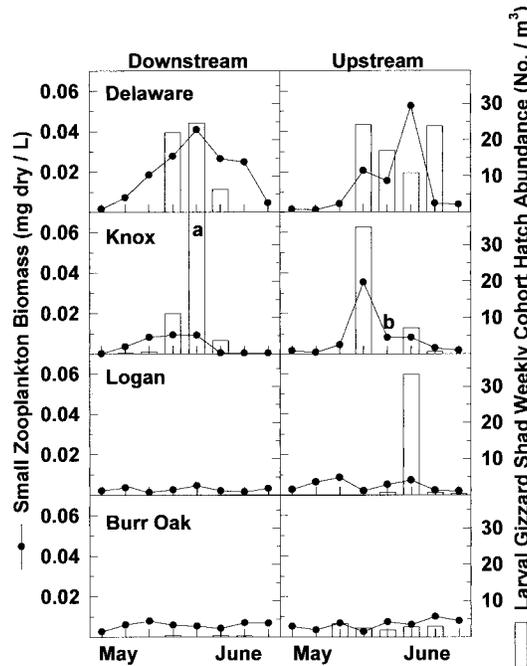

FIGURE 2. — Biomass of small (<0.40 mm) zooplank-ton (●) and abundance of weekly hatch cohorts of larval gizzard shad (histogram bars) in downstream and upstream areas of four Ohio reservoirs sampled during May through June 1994. See Methods and Figure 1 for explanation of larval gizzard shad hatch calculations.

distributions via the Kolmogorov–Smirnov test for equal distributions. Growth rates of 9-14.9-mm survivors from cohorts with low hatch did not differ from those from cohorts with high hatch and high survival (Kolmogorov-Smirnov test, $P > 0.21$; Figure 4A, C). In contrast, growth rates of survivors from cohorts with high hatch but few survivors differed from those of cohorts with low hatch and few survivors (Kolmogorov-Smirnov test, $P < 0.00003$; Figure 4A, B). Cohorts with high hatch and many survivors appeared to have a higher percentage of individuals with rapid growth rates than did cohorts with high hatch but few survivors. Comparison of growth rates from cohorts with high hatch and few survivors against survivors from cohorts with high hatch and many survivors yielded a marginally significant difference (Kolmogorov-Smirnov test, $P < 0.091$; Figure 4B, C).

Considering 15-21-mm larval gizzard shad survivors, growth rates did not differ between survivors from cohorts with low hatch and survivors from cohorts with high hatch and many survivors (Kolmogorov-Smirnov test: $P > 0.9$; Figure 4D, F). Growth rates among cohorts with high hatch and few survivors differed from both those among cohorts with low hatch (Kolmogorov-Smirnov test: $P < 0.017$) and those among cohorts with high hatch and high survival (Kolmogorov-Smirnov test: $P < 0.025$; Figure 4D, E, F).

To determine if available small zooplankton biomass or temperature experienced by larval cohorts differed among the three categories, we compared both of these variables, via ANOVA, during the week that each cohort hatched. Because only three cohorts produced abundant 15-21-mm survivors, and because these three cohorts also produced abundant 9-14.9-mm survivors, we consider only the 9-14.9-mm survivors. Given the differences in growth rates among the three categories, we expected cohorts with high hatch and few survivors to experience lower levels of small zooplankton biomass and cooler temperatures at hatch.

Temperature at hatch ranged from 16°C to 29°C but did not vary consistently among the three categories (ANOVA, $P > 0.5$). In contrast, available biomass of small zooplankton varied among the three categories (ANOVA, $F = 8.45$, $P < 0.0014$, $r^2 = 0.39$; Table 3), being lower among cohorts with low hatch (Tukey's pairwise comparison, $\alpha = 0.05$). Contrary to our expectations, cohorts with high hatch, regardless of survivor abundance, experienced high biomass of small zooplankton. However, abundant survivors were derived primarily from cohorts that hatched during high abundance of small zooplankton in *upstream* areas (Figure 5A, B). Even though several downstream cohorts hatched when small zooplankton biomass was high (particularly in Delaware Reservoir), they produced few survivors. This pattern was especially apparent among 15-21-mm survivors. All three cohorts with abundant survivors hatched up-stream during high abundance of small zooplankton (Figure 5A, B).

July–Early August: Juvenile Gizzard Shad Effects

Overall, larval gizzard shad hatch abundance, growth, and survival increased with reservoir productivity and was higher in upstream than downstream areas. Therefore, if larval success establishes patterns of juvenile gizzard shad size and abundance, then these characteristics of juvenile gizzard shad populations should increase with reservoir productivity, particularly in upstream reservoir areas. To evaluate if larval success could predict size and abundance of juvenile gizzard shad populations, we compared juvenile gizzard shad abundance in early August and juvenile gizzard shad size in late June and early August across the eight reservoir areas.
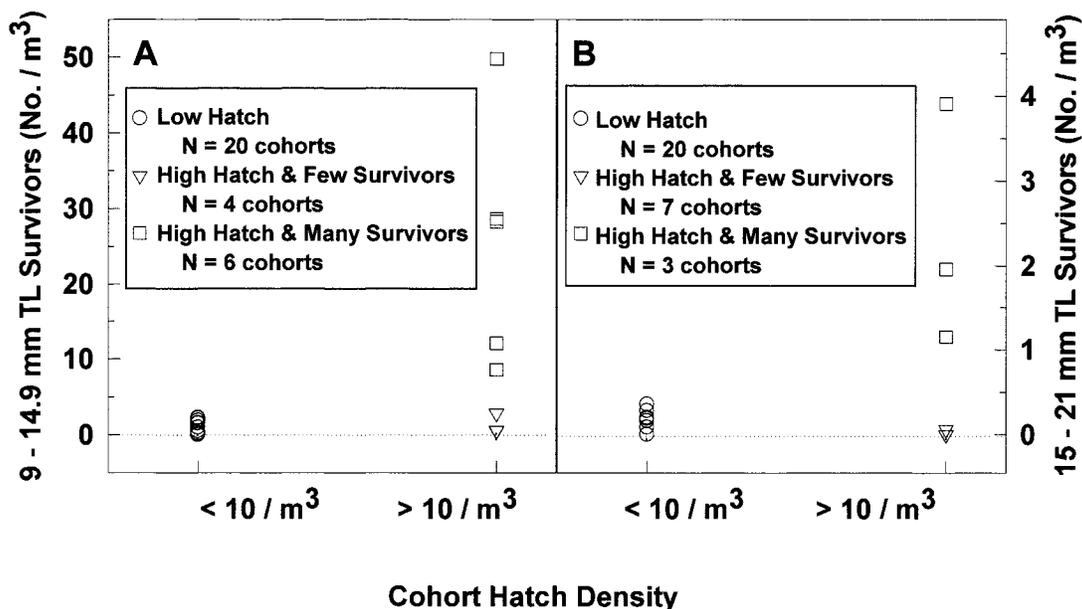
FIGURE 3. — Survivor abundance for 30 weekly hatch cohorts of larval gizzard shad surviving to **(A)** 9–14.9 mm in total length, TL, and **(B)** 15–21 mm TL from weekly cohorts with low (<10/m³) and high (>10/m³) hatch abundance in four Ohio reservoirs sampled during May through June 1994.See Methods and Figure 1 for explanation of larval gizzard shad hatch calculations.

Juvenile gizzard shad abundance. — Juvenile gizzard shad abundance differed across the eight reservoir areas in early August (ANOVA: $F = 6.51$, $P < 0.0031$, $r^2 = 0.71$; Figure 5C). No juvenile gizzard shad were caught in the downstream areas of Burr Oak and Logan reservoirs, both with relatively low larval hatch abundance and survival. The number of juvenile gizzard shad captured during four 5-min electrofishing transects in the downstream areas in each of Knox and Delaware reservoirs also was quite low (typically < 10 fish/ transect). Juvenile gizzard shad abundance was much higher in the upstream areas of these two reservoirs, where larval gizzard shad hatch and survival had been relatively high as well. In particular, juvenile gizzard shad were most abundant upstream in Delaware Reservoir, with about 200 juvenile gizzard shad captured per 5-min electrofishing transect (Figure 5C).

Juvenile gizzard shad size .— In both late June and early August, we compared age-0 gizzard shad size between downstream and upstream areas within reservoirs, as well as among reservoirs. In late June, most individuals captured by the neuston net were still larvae (Figure 6). Juveniles (individuals > 25 mm) were abundant upstream in Knox and Delaware reservoirs, where larval hatch abundance and survival had been relatively high. No juvenile gizzard shad were captured downstream in Logan or Burr Oak reservoirs, where larval hatch abundance and survival had been low. We compared paired size distributions using the Kolmogorov-Smirnov test for equal distributions, first considering differences in gizzard shad size between upstream and downstream reservoir areas. In late June, gizzard shad in Delaware and Knox reservoirs were larger upstream than downstream (Kolmogorov-Smirnov tests, $P < 0.0001$). Sizes did not differ between areas in Logan Reservoir (Kolmogorov-Smirnov, $P > 0.69$), whereas low sample size downstream in Burr Oak Reservoir ($N = 3$ gizzard shad captured) prevented comparison with upstream sizes. Among reservoirs, we ordered reservoirs according to mean gizzard shad size (separate analyses for downstream and upstream areas) and compared adjacent pairs (Table 4). Downstream, age-0 gizzard shad were largest in Knox Reservoir, followed by Delaware and Logan reservoirs. Each pairwise comparison yielded a significant difference between distributions (Table 4), although the difference between Knox and Delaware reservoirs was only marginally significant. Upstream, age-0 gizzard shad sizes were ordered as Delaware > Knox > Burr Oak > Logan. Again, all pairwise comparisons yielded significantly different distributions (Table 4).

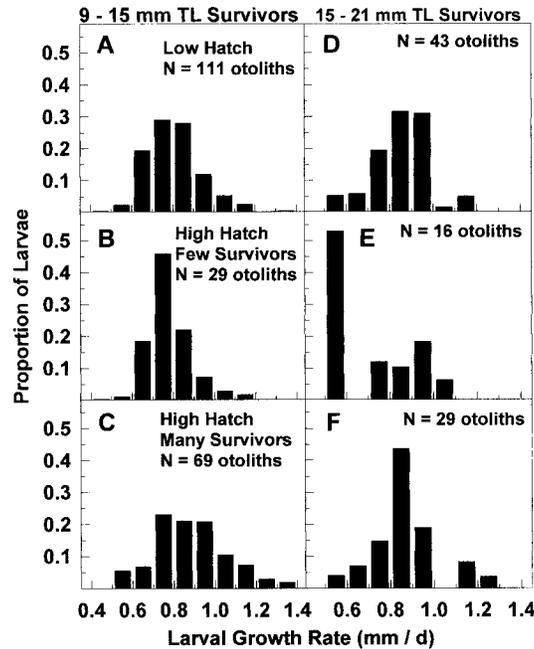FIGURE 4. — Growth rate distributions for **(A–C)** 9– 14.9-mm-TL (total length) and **(D–F)** 15–21-mm-TL survivors from 30 weekly hatch cohorts grouped into three categories based on hatch and survivor abundance (see Figure 3): (A, D) cohorts with low hatch ($<10/m^3$) abundance; (B, E) cohorts with high hatch ($>10/m^3$) but few survivors; and (C, F) cohorts with high hatch ($>10/ m^3$) and many survivors. To account for multiple statistical comparison, we divided the overall significance level (0.05) by the number of comparisons (3) to yield 0.017 as the cut-off for significance. Growth rate distributions were compared in pairs via the Kolmogorov-Smirnov test for equal distributions. See Results for statistical results.

Overall, size distributions were skewed toward larger individuals in late June in reservoirs with relatively high larval hatch abundance and survival.

Age-0 gizzard shad length distributions among reservoir areas during late June differed dramatically in the context of their vulnerability to age-0 largemouth bass predators (Figure 6). Upstream in Delaware and Knox reservoirs, more than 50% of age-0 gizzard shad were invulnerable even to relatively large age-0 largemouth bass in late June. In contrast, the majority of age-0 gizzard shad in Logan and Burr Oak reservoirs during late June were vulnerable to age-0 largemouth bass.

By early August, age-0 gizzard shad typically have grown beyond vulnerability to age-0 large-mouth bass across Ohio reservoirs (Garvey and Stein 1998). Therefore, we compared the
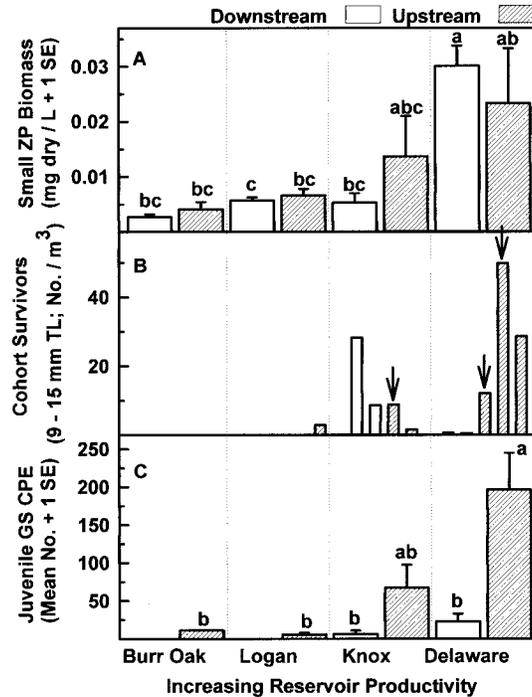
FIGURE 5 .— **(A)** Mean biomass of small (<0.40 mm) zooplankton (ZP) available during the period of larval gizzard shad hatching in upstream and downstream areas of four Ohio reservoirs sampled during May through June 1994 (ANOVA: $F = 5.4$, $P < 0.0005$, $r^2 = 0.57$). Tukey's pairwise comparisons were significant at $\alpha = 0.05$; means with a letter in common are not significantly different. **(B)** Abundance of larval gizzard shad survivors 9–14.9 mm in total length, TL, produced from 10 weekly hatch cohorts with hatch density greater than 10/ m^3. Cohorts with low hatch density (<10/m^3) are not shown because none produced abundant survivors. Arrows indicate weekly hatch cohorts that produced 15– 21-mm-TL survivors at 1/m^3 or higher. **(C)** Mean number of juvenile gizzard shad (GS) captured during four 5-min electrofishing transects in upstream and downstream areas of the reservoirs (ANOVA: $F = 6.51$, $P < 0.0031$, $r^2 = 0.71$). Tukey's pairwise comparisons were significant at $\alpha = 0.05$; means with a letter in common are not significantly different.

mean size of juvenile gizzard shad captured in the eight reservoir areas during early August electrofishing. By early August, differences in juvenile gizzard shad size were even more apparent (ANOVA: $F = 101.08$, $P < 0.0001$, $r^2 = 0.97$; Table 5) than in late June. However, among-reservoir patterns had changed, indicating that differences in juvenile gizzard shad growth during midsummer prevent correlation between larval success and early August juvenile gizzard shad size (Table 5). Juvenile gizzard shad were largest in Burr Oak and Logan reservoirs, in which small gizzard shad size

TABLE 3 .— Mean biomass (mg dry weight/L) of small (<0.40 mm) zooplankton (ZP) available upon hatch to weekly cohorts (*N*) of larval gizzard shad collected in four Ohio reservoirs during May through June 1994. Shad cohorts were grouped into three categories based on their hatch abundance and production of survivors 9–15 mm in total length. Small zooplankton biomass varied among the three categories (ANOVA; $F = 8.45$, $P < 0.0014$, $r^2 = 0.39$); values with a letter in common are not significantly different. Tukey's pairwise comparisons were significant at $\alpha = 0.05$.

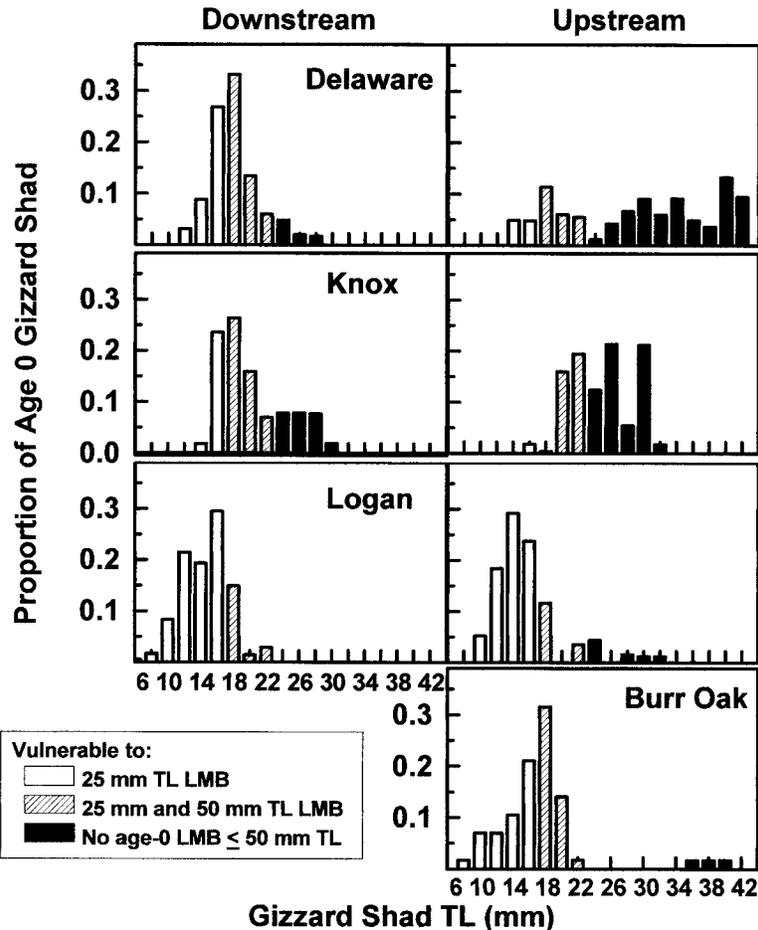| Category		N	Mean biomass of ZP (mg/L)	SE
Hatch	Survivors			
Low	Few	20	0.0067 z	0.0016
High	Few	4	0.0279 y	0.0074
	Many	6	0.0193 y	0.0070

FIGURE 6. — Size distribution in 2-mm length-classes of age-0 gizzard shad collected in upstream and downstream areas of four Ohio reservoirs sampled during late June 1994. Length-classes are distinguished according to vulnerability to relatively small (25 mm in total length, TL) and relatively large (50 mm TL) age-0 largemouth bass (LMB) in late June.

in late June had accompanied low larval gizzard shad hatch abundance and survival. In contrast, juvenile gizzard shad were smallest in Knox Reservoir, where larval hatch abundance and survival had been relatively high and size had been large upstream in late June. Thus, juvenile gizzard shad in Knox Reservoir demonstrated density-dependent growth in midsummer. However, density dependent reduction in juvenile gizzard shad growth, relative to Knox Reservoir, was not apparent in Delaware Reservoir despite even greater abundance of juvenile gizzard shad. Rather, mean size of juvenile gizzard shad in Delaware Reservoir was twice that in

Knox Reservoir. Overall, gizzard shad remained vulnerable to age-0 largemouth bass throughout

TABLE 4.—Mean total length (TL) and SE of age-0 gizzard shad captured in four Ohio reservoirs sampled during late June 1994. Upstream and downstream areas were analyzed separately. Reservoir areas are ordered according to decreasing mean gizzard shad size. Based on this order, adjacent pairs of size distributions were compared using the Kolmogorov–Smirnov test for equal distributions. To account for multiple comparisons being made, we divided our overall significance level (0.05) by the number of comparisons (5) to yield 0.01 as the cut-off for significance. Size distributions are shown in Figure 6. Low sample size downstream in Burr Oak precluded comparison with other reservoirs.

Sampling area and lake	Mean TL (mm)	SE	P
Downstream			
Knox	19.6	0.39	
Delaware	17.6	0.32	0.016
Logan	14.1	0.29	0.0001
Upstream			
Delaware	27.9	0.91	
Knox	22.9	0.40	0.0001
Burr Oak	16.9	0.78	0.0001
Logan	15.2	0.42	0.0034

June and July in Knox Reservoir, despite initial rapid growth upstream. In Delaware Reservoir, most juvenile gizzard shad remained invulnerable through June and July. In Burr Oak and Logan reservoirs, slow growth among larval gizzard shad in June was followed by rapid growth among juveniles, reducing vulnerability to age-0 largemouth bass as the season progressed.

Zooplankton. — We sought to determine the extent to which zooplankton density varied across reservoirs during early summer (May through June) when larval gizzard shad are recruiting, and again during midsummer (July through early August) when consumption by juvenile gizzard shad may deplete zooplankton needed by later spawned larval fishes, particularly bluegills. We expected zooplankton density to increase with productivity during May through June, reflecting positive effects of higher chlorophyll levels at high TP. However, by midsummer, we expected zooplankton densities to fall to low levels in more productive systems (reflecting intense consumption by juvenile gizzard shad) and to persist at relatively high densities in low productivity reservoirs with few juvenile gizzard shad.

Consistent with these predictions, crustacean zooplankton reached the highest densities (> 150/ L) during May through June upstream and downstream in Delaware Reservoir, the most productive of those in our study (Figure 7). Crustacean zooplankton densities in the other three reservoirs remained less than 100 zooplankton/L. By midsummer, zooplankton densities in

TABLE 5 .— Mean total length (TL) and SE of juvenile gizzard shad (GS) captured during four 5-min electrofishing transects in upstream (U, near the inlet stream) and downstream (D, near the dam) areas of four Ohio reservoirs sampled during early August 1994. Reservoir areas were ordered from maximum to minimum mean shad TL. No juvenile gizzard shad were captured downstream in Logan or Burr Oak reservoirs. Juvenile gizzard shad length varied among reservoir areas (ANOVA: $F = 101.08$, $P < 0.0001$, $r^2 = 0.97$); values with a letter in common are not significantly different. Tukey's pairwise comparisons were significant at $\alpha = 0.05$.

Lake	Area	Mean juvenile GS TL (mm)	SE
Logan	U	127.0 z	0.74
Burr Oak	U	113.0 y	4.8
Delaware	U	91.0 x	2.0
Delaware	D	87.6 x	6.9
Knox	U	44.1 w	2.42
Knox	D	35.9 w	0.06

Delaware Reservoir had fallen to quite low levels and remained less than 10/L throughout midsummer. Patterns of zooplankton peak and subsequent decline were far less marked in other reservoirs. Upstream in Knox Reservoir, a peak in mid-May (~75/L) slowly declined, resulting in less than 10 zooplankton/L from mid-June through early August. In both areas of Logan Reservoir and downstream in Burr Oak, zooplankton densities fluctuated but remained below 50/L during early and midsummer. Upstream in Burr Oak Reservoir, zooplankton densities persisted at more moderate densities, ranging from about 40 to 100/L throughout midsummer (Figure 7).

To explore if differences in zooplankton reproductive rates could explain zooplankton dynamics, particularly the strong midsummer declines in Delaware Reservoir, we calculated zooplankton production : biomass (hereafter P:B) ratios. For each sample date in each reservoir area, we first divided taxon production by biomass. We calculated a mean value across zooplankton taxa, weighted by taxon biomass. In late May, zooplankton P:B was not higher in Delaware Reservoir, where zooplankton densities were highest. If zooplankton declined due to a decline in reproductive success (as would be expected if zooplankton became resource limited), then we would expect a decline in zooplankton P:B ratios, mirroring the decline in zooplankton density. However, zooplankton P:B ratios did not decline as midsummer zooplankton density declined in Delaware Reservoir (Figure 7). Rather, zooplankton P:B ratios appeared to increase. In
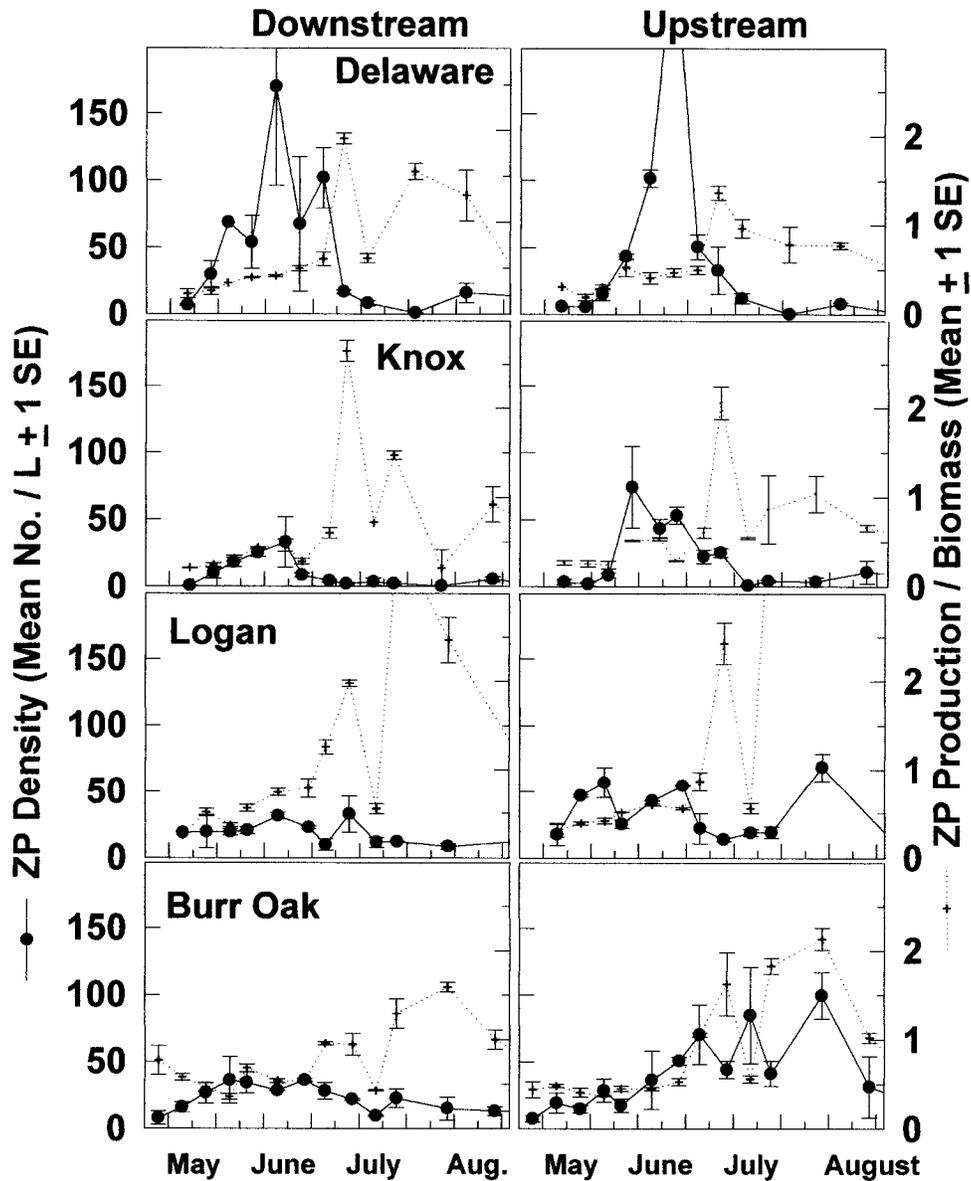
FIGURE 7 .— Mean crustacean zooplankton (ZP) density (●) and ZP production: biomass estimates (+) in upstream and downstream areas of four Ohio reservoirs sampled during May through early August 1994.

general, zooplankton P:B ratios spanned similar ranges (0–2) across reservoir areas, increasing gradually through summer. Strong peaks in P:B ratios, as in midsummer in Logan Reservoir, were due primarily to peaks in *Daphnia* spp. abundance and reproduction.

Overall, declining zooplankton reproductive rates could not explain the midsummer decline in zooplankton abundance in Delaware Reservoir. Given that juvenile gizzard shad abundance (and hence consumption) exhibited a broad range of values across reservoir areas, with their greatest abundance in Delaware Reservoir, we conclude that juvenile gizzard shad consumption likely caused the midsummer zooplankton decline in this reservoir.

Discussion

      Larval gizzard shad success (hatch abundance, growth, and survival) as well as juvenile gizzard shad size, abundance, and food web effects ranged broadly across reservoirs but varied somewhat predictably with reservoir productivity. In our view, a conceptual framework for management, which incorporates reservoir productivity and anticipated juvenile gizzard shad effects, should improve our success in attaining fisheries objectives across disparate systems. Towards this end, we discuss our findings in the context of our three initial questions.

(1) Can small crustacean zooplankton abundance explain larval gizzard shad success?

      Small crustacean zooplankton contributed to patterns of larval gizzard shad survival, but alone it did not dictate recruitment. Rather, abundant juvenile gizzard shad were produced only when high larval hatch abundance combined with high larval survival. These two processes (hatch and survival) reflect different time scales. Hatch abundance likely reflects both long-term (i.e., adult abundance and fecundity) and short-term (i.e., hatch success) processes, whereas larval survival primarily reflects short-term processes (i.e., starvation). We first consider hatch and then survival.

      Our index of larval gizzard shad hatch abundance and reservoir productivity were positively correlated—largely driven, we believe, by increasing densities of adult gizzard shad and abundance of spawning habitat (as per Storck et al. 1978) in upstream areas with increasing reservoir productivity. Reproductive potential of gizzard shad should increase with system productivity because adult gizzard shad become increasingly more abundant with increasing system productivity (Bachman et al. 1996; DiCenzo et al. 1996), especially from eutrophic to hypereutrophic systems (Bachman et al. 1996). Although density-dependent adult growth and condition may temper increasing egg production (Kampa 1984; Willis 1987), reduced adult growth with increasing density only has been documented across mesotrophic to eutrophic conditions (DiCenzo et al. 1996). In hypereutrophic Ohio reservoirs, adult gizzard shad do not appear to decline in size relative to eutrophic reservoirs (M. Bremigan, unpublished data). Therefore, high adult gizzard shad biomass in hypereutrophic reservoirs likely supports much higher reproductive potential, and hence hatch, than in mesotrophic and eutrophic reservoirs.

      Both temperature and water level fluctuations can influence timing of spawning as well as abundance of larvae (Michaletz 1997). However, these abiotic factors could not explain our patterns even though recruitment varied markedly. Temperature regimes were similar across reservoirs. Because water level fluctuations reflect spring precipitation patterns, interannual differences in hatch abundance due to water level fluctuations would likely exceed intersystem differences. Our data indicate against water level fluctuations as the forcing function for spawning success in Ohio reservoirs because intersystem differences in larval gizzard shad hatch abundance are consistent across years and more extensive than interannual differences within systems (Bremigan 1997; Bremigan and Stein, unpublished data). Perhaps the relative importance of water level fluctuations (and hence interannual variability in gizzard shad recruitment) varies with system size. Michaletz (1997) worked in larger reservoirs (> 1,000 ha) that varied less broadly in productivity (mesotrophic to slightly eutrophic) than did our smaller reservoirs (<550 ha), which ranged from mesotrophic to hypereutrophic. Thus, for midwestern reservoirs less than 550 ha, we believe reservoir productivity coupled with adult gizzard shad abundance underlies intersystem patterns of larval gizzard shad hatch abundance, whereas temperature and water level fluctuations likely contribute to its interannual variability.

Previous experiments (Welker et al. 1994; Bremigan and Stein 1997) and field comparisons (Miranda et al. 1994; Michaletz 1997) have demonstrated that zooplankton abundance contributes to larval gizzard shad success, although the relative importance of zooplankton in dictating recruitment patterns has not been well established. In 1994, small zooplankton abundance appeared necessary for larval gizzard shad survival. All successful cohorts experienced abundant small crustacean zooplankton upon hatch in upstream areas; yet, several downstream cohorts hatched during abundant small crustacean zooplankton but produced few survivors. These differences may derive from our sampling method for zooplankton during which an integrated sample was collected from the entire water column. For example, if zooplankton are not distributed evenly across the water column, then encounter rates for larval gizzard shad (which typically are concentrated in surface waters; Storck et al. 1978; Willis 1987) could differ between downstream and upstream areas, even when integrated water column zooplankton densities are similar between areas. To illustrate, we quantified zooplankton density at 1-m depths in both areas of Delaware Reservoir, the hypereutrophic reservoir, during mid-June when zooplankton was abundant (biomass of small zooplankton > 0.04 mg dry weight/L in both areas). Small zooplankton were more concentrated in the top 1 m upstream than downstream. In particular, 59% of the total water column abundance of copepod nauplii (pre-ferred prey of small larval gizzard shad; Dettmers and Stein 1992; Bremigan and Stein 1997) was in the top 1 m upstream, whereas only 21% of the total water column abundance of copepod nauplii was in the top 1 m downstream.

Because survivors from low-hatch cohorts grew at rates similar to those from high-hatch cohorts with many survivors, we conclude that hatch abundance limited survivor abundance for low-hatch cohorts. Low-hatch cohorts generally experienced relatively low small-zooplankton abundance at hatch, although overall these cohorts experienced the widest range of recruitment environments because they occurred in all eight reservoir areas. Therefore, we predict that those individuals with rapid growth derived from low-hatch cohorts that experienced relatively high zooplankton abundance at hatch. However, due to relatively small sample sizes for individual cohorts, we cannot compare growth rates among individual low-hatch cohorts to determine if their growth rates varied predictably with small zooplankton abundance at hatch.

Overall, considering both 9–14.9-mm and 15–21-mm survivors, cohorts with high hatch and few survivors grew more slowly than other cohorts, indicating that larval gizzard shad growth improves survival. Further, because cohorts that produced the majority of larval survivors (i.e., those with high hatch upstream and many survivors) had the greatest proportion of individuals with the highest growth rates, we conclude that high hatch upstream coincident with abundant small zoo-plankton promotes the occurrence of the extraordinary individuals that likely dictate gizzard shad recruitment (as per Crowder et al. 1992).

(2) Can larval gizzard shad success predict juvenile gizzard shad size and abundance?

Comparison of larval and juvenile gizzard shad survival in two Missouri reservoirs revealed that larval events primarily determine year-class strength (Michaletz 1997). In our study, increasing hatch abundance and survival of larval gizzard shad with increasing reservoir productivity produced increasing juvenile gizzard shad abundance through summer. Larval gizzard shad growth patterns predicted juvenile gizzard shad size in late June, but they could not predict juvenile size in early August. In late June, a greater proportion of age-0 gizzard shad had reached the juvenile stage in upstream areas of the more productive reservoirs where cohorts

with high growth rates had been most abundant. However, as summer progressed, increasing juvenile gizzard shad abundance coincided with declining juvenile gizzard shad size across mesotrophic to eutrophic conditions. Similarly, across 10 Alabama reservoirs, size at age of adult gizzard shad (age-0 gizzard shad were not evaluated) declined and abundance increased as productivity increased from mesotrophy to eutrophy (DiCenzo et al. 1996). By contrast, in hypereutrophic Delaware Reservoir, juvenile gizzard shad grew relatively rapidly despite supporting the highest juvenile gizzard shad abundance in our study, revealing that in high-productivity reservoirs, high density of juvenile gizzard shad may not result in density-dependent reductions in growth or produce smaller juvenile size. Hence, recommendations that gizzard shad abundance be enhanced to slow juvenile gizzard shad growth rates and increase their vulnerability to predators (Buynak et al. 1992) should be interpreted with caution (especially in highly productive reservoirs).

How do juvenile gizzard shad continue to grow rapidly, despite high abundance under hypereutrophy? Given that zooplankton densities were extremely low in Delaware Reservoir during midsummer, juvenile gizzard shad likely consumed detritus (Mundahl 1991; Yako et al. 1996). Conceivably, differences in detrital quality among reservoirs influence juvenile gizzard shad growth rates. In particular, the large agricultural watershed surrounding Delaware Reservoir may provide nutrient-rich detritus (as per Nürnberg 1988) at a rapid rate relative to less productive reservoirs, thus supporting faster juvenile gizzard shad growth.

(3) Do juvenile gizzard shad effects vary with reservoir productivity?

Due to differences in size of juvenile gizzard shad, their vulnerability to age-0 predators varied among reservoirs. For example, in Knox Reservoir, where juvenile gizzard shad were abundant but grew slowly, age-0 largemouth bass consumed juvenile gizzard shad and enjoyed rapid growth and high recruitment. Conversely, in Delaware Reservoir, with abundant, fast growing juvenile gizzard shad, age-0 largemouth bass captured few gizzard shad and suffered poor growth and recruitment (Garvey et al. 1998b). Future research should evaluate whether these patterns of juvenile gizzard shad size are consistent across years.

Broad differences in juvenile gizzard shad abundance across reservoirs also translate into different consumptive demands for zooplankton. As juvenile gizzard shad abundance increases with reservoir productivity during summer, zooplankton persistence should be increasingly challenged. Contrasting zooplankton dynamics in Delaware Reservoir (high juvenile gizzard shad abundance) and upstream in Burr Oak Reservoir (low juvenile gizzard shad abundance) support the hypothesis that midsummer zooplankton abundance across reservoirs declines with increasing juvenile gizzard shad abundance. Despite zooplankton densities greater than 150/L in Delaware Reservoir in mid-June, zooplankton densities rapidly declined and remained less than 10/L through midsummer. Conversely, upstream in Burr Oak Reservoir, zooplankton never exceeded 100/L but persisted at more than 50/L through midsummer. Zooplankton rarely exceeded 50/L in Knox and Logan reservoirs. In these two reservoirs, zooplankton assemblages exhibited neither a peak followed by midsummer decline (as evidenced in Delaware Reservoir) nor midsummer persistence (as evidenced in Burr Oak Reservoir). Conceivably, zooplanktivory by adult gizzard shad or other zooplanktivores, or poor food quality, maintained zooplankton at relatively low levels through early summer.

We had expected zooplankton production: bio-mass ratios to increase with reservoir productivity, demonstrating increasing resistance to predation. However, zooplankton P:B ratios

did not vary with productivity. Further, given that P:B ratios did not decline concomitantly with zooplankton decline in Delaware Reservoir, resource limitation likely did not occur; rather, consumption by abundant juvenile gizzard shad likely depleted zooplankton. If so, then reservoirs with high densities of small zooplankton in early summer that support high larval gizzard shad success may be quite vulnerable to negative effects (such as reduced bluegill recruitment; DeVries et al. 1991; Stein et al. 1995, 1996).

Based on field enclosure experiments, Dettmers and Stein (1996) predicted that midsummer reservoir zooplankton will persist (maintain > 100/L) only in situations of relatively low age-0 gizzard shad abundance ($<10/m^3$) and relatively high zooplankton production (>220 mg dry weight/m^3 per day). As predicted, zooplankton did not persist in Delaware Reservoir, where age-0 gizzard shad were extremely abundant. As discussed above, consistently low zooplankton densities in Logan and Knox reservoirs reveal that factors in addition to age-0 gizzard shad consumption (particularly in early summer) contributed to low zooplankton densities (<50/L). Upstream in Burr Oak Reservoir, contrary to the predictions of Dettmers and Stein (1996), zooplankton persisted at levels approaching 100/L despite daily zooplankton production of less than 220 mg dry weight/m^3. Thus, when age-0 gizzard shad are few, this predictive model may underestimate the ability of reservoir zooplankton populations to persist at 100/L.

Multi-System Management

Although patterns of increasing gizzard shad abundance with reservoir productivity have been established (Bachman et al. 1996; DiCenzo et al. 1996), our study is unique in exploring the mechanisms underlying that pattern. This mechanistic insight will help managers to anticipate how gizzard shad populations will respond to management actions, ranging from predator stocking to watershed manipulations. Therefore, although we lack replication across the productivity gradient in this study, the mechanisms that we have identified can help to explain a pattern that has been established across many systems. Because juvenile gizzard shad abundance and size vary somewhat predictably with reservoir productivity, we suggest a multisystem management framework, which incorporates reservoir productivity to guide both short-term and long-term management decisions.

In the short term, by anticipating specific effects of juvenile gizzard shad, managers can evaluate their probability of success in reaching management goals. For example, consider recruitment of resident largemouth bass or success of stocked saugeyes (sauger *Stizostedion canadense* × walleye *S. vitreum*) as management goals in Ohio reservoirs. If juvenile gizzard shad vulnerability to these age-0 predators varies predictably with reservoir productivity (as our study indicates), we expect age-0 predator success (particularly growth and overwinter survival, if size-dependent) to vary with productivity as well. Specifically, in relatively low-productivity reservoirs with few juvenile gizzard shad, we expect moderate success of age-0 largemouth bass due to initial slow growth of gizzard shad coupled with anticipated higher abundance of alternative forage (Garvey et al. 1998a). Yet, given relatively low total abundance of forage fish in these reservoirs, we recommend caution in stocking additional predators, such as saugeyes. We expect high recruitment success of age-0 predators in eutrophic reservoirs when juvenile gizzard shad are abundant but slow growing. Conversely, in hypereutrophic reservoirs, we expect recruitment of age-0 predators to be compromised owing to the combined effects of large, invulnerable gizzard shad and low abundance of age-0 bluegills (Garvey et al. 1998a).

In the long term, reduction of juvenile gizzard shad abundance and size in hypereutrophic

reservoirs should improve sportfish production (Stein et al. 1996). To achieve this goal, we recommend coupling high predator abundance (which could be achieved by intensive stocking of hybrid striped bass *Morone saxatilis × M. chrysops),* to reduce gizzard shad abundance, with watershed management that lowers nutrient input, to reduce gizzard shad growth rates, as suggested by Stein et al. (1996). Through watershed management coupled with biotic manipulations, we seek to reduce the suitability of hypereutrophic reservoirs to gizzard shad recruitment, improving their recruitment environments for resident sport fishes.

References

Adams, S. M., and D. L. DeAngelis. 1987. Indirect effects of early bass–shad interactions on predator population structure and food web dynamics. Pages 103–117 *in* W. C. Kerfoot and A. Sih, editors. Predation: direct and indirect impacts on aquatic communities. University Press of New England, Hanover, New Hampshire.

Bachman, R. W., B. L. Jones, D. D. Fox, M. Hoyer, L. A. Bull, and D. E. Canfield, Jr. 1996. Relations between trophic state indicators and fish in Florida (U.S.A.) lakes. Canadian Journal of Fisheries and Aquatic Sciences 53:842–855.

Bean, D. L. 1980. Crustacean zooplankton production in Lake Erie, 1970. Master's thesis. Ohio State University, Columbus.

Bodola, A. 1966. Life history of the gizzard shad, *Dorosoma cepedianum* (LeSueur) in western Lake Erie. U.S. Fish and Wildlife Service Fishery Bulletin 65: 391–425.

Bottrell, H. H., and eight coauthors. 1976. A review of some problems in zooplankton production studies. Norwegian Journal of Zoology 24:419–456.

Bremigan, M. T. 1997. Zooplankton dynamics and gizzard shad recruitment in Ohio reservoirs: exploring the generality of food web theory. Doctoral dissertation. The Ohio State University, Columbus.

Bremigan, M. T., and R. A. Stein. 1994. Gape-dependent larval foraging and zooplankton size: implications for fish recruitment across systems. Canadian Journal of Fisheries and Aquatic Sciences 51:913–922.

Bremigan, M. T., and R. A. Stein. 1997. Experimental assessment of the influence of zooplankton size and density on gizzard shad recruitment. Transactions of the American Fisheries Society 126:622–637.

Buynak, G. L., R. S. Hale, and B. Mitchell. 1992. Differential growth of young-of-year gizzard shad in several Kentucky reservoirs. North American Journal of Fisheries Management 12:656–662.

Carlander, K. D. 1969. Handbook of freshwater fishery biology, volume 1. Iowa State University Press, Ames.

Carpenter, S. R. 1988. Transmission of variance through lake food webs. Pages 119–138 *in* S. R. Carpenter, editor. Complex interactions in lake communities. Springer-Verlag, New York.

Cramer, J. D., and G. R. Marzolf. 1970. Selective predation on zooplankton by gizzard shad. Transactions of the American Fisheries Society 99:320– 332.

Crowder, L. B., J. A. Rice, T. J. Miller, and E. A. Marschall. 1992. Empirical and theoretical approaches to size-based interactions and recruitment variability in fishes. Pages 237–255 *in* D. L. DeAngelis and L. J. Gross, editors. Individual-based models and approaches in ecology. Chapman and Hall, New York.

Culver, D. A., and W. R. DeMott. 1978. Production of zooplankton at nearshore stations in Lakes Ontario and Erie. Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen 20: 252–256.

Davis, R. D., T. W. Storck, and S. J. Miller. 1985. Daily growth increments in the otoliths of young-of-the-year gizzard shad. Transactions of the American Fisheries Society 114:304–306.

DeMott, W. R. 1976. Zooplankton productivity at Locust Point, an inshore area in western Lake Erie. Master's thesis. Ohio State University, Columbus.

Dettmers, J. M., and R. A. Stein. 1992. Food consumption by larval gizzard shad: zooplankton effects and its implications for reservoir communities. Transactions of the American Fisheries Society 121: 494–507.

Dettmers, J. M., and R. A. Stein. 1996. Quantifying linkages among gizzard shad, zooplankton, and phytoplankton in reservoirs. Transactions of the American Fisheries Society 125:27–41.

DeVries, D. R., and R. A. Stein. 1990. Manipulating shad to enhance sport fisheries in North America: an assessment. North American Journal of Fisheries Management 10:209–223.

DeVries, D. R., and R. A. Stein. 1992. Complex interactions between fish and zooplankton: quantifying the role of an open-water planktivore. Canadian Journal of Fisheries and Aquatic Sciences 49:1216– 1227.

DeVries, D. R., R. A. Stein, J. G. Miner, and G. G. Mittelbach. 1991. Stocking threadfin shad: consequences for young-of-year fishes. Transactions of the American Fisheries Society 120:368–381.

DiCenzo, V. J., M. J. Maceina, and M. R. Stimpert. 1996. Relations between reservoir trophic state and gizzard shad population characteristics in Alabama reservoirs. North American Journal of Fisheries Management 16:888–895.

Dumont, H. J., I. Van de Velde, and S. Dumont. 1975. The dry weight estimate of biomass in a selection of Cladocera, Copepoda, and Rotifera from the plankton, periphyton and benthos of continental waters. Oecologia 19:75–97.

Garvey, J. E., N. A. Dingledine, N. S. Donovan, and R. A. Stein. 1998a. Exploring spatial and temporal variation within reservoir food webs: predictions for fish assemblages. Ecological Applications 8:104– 120.

Garvey, J. E., and R. A. Stein. 1998. Linking bluegill and gizzard shad prey assemblages to growth of age-0 largemouth bass in reservoirs. Transactions of the American Fisheries Society 127:70–83.

Garvey, J. E., R. A. Wright, R. A. Stein, K. H. Ferry, and S. M. Micucci. 1998b. Assessing the influence of size on overwinter survival of largemouth bass in Ohio on-stream impoundments. Ohio Division of Wildlife, Final Report F-69-P, Columbus.

Gliwicz, Z. M. 1975. Effect of zooplankton grazing on photosynthetic activity and composition of phytoplankton. Internationale Vereinigung für theoretische und angewandte Limnologie Verhandlungen 19: 1490–1497.

Kampa, J. M. 1984. Density-dependent regulation of gizzard shad populations in experimental ponds. Master's thesis. University of Missouri, Columbia.

Kitchell, J. F., and S. R. Carpenter. 1993. Cascading trophic interactions. Pages 1–14 in S. R. Carpenter and J. F. Kitchell, editors. The trophic cascade in lakes. Cambridge University Press, New York.

Kitchell, J. F., and L. B. Crowder. 1986. Predator–prey interactions in Lake Michigan: model predictions and recent dynamics. Environmental Biology of Fishes 16:205–211.

Knight, R. L., F. J. Margraf, and R. F. Carline. 1984. Piscivory by walleyes and yellow perch in western Lake Erie. Transactions of the American Fisheries Society 113:677–693.

Leggett, W. C, and E. DeBlois. 1994. Recruitment in marine fishes: is it regulated by starvation and predation in the egg and larval stages? Netherlands Journal of Sea Research 32:119–134.

McQueen, D. J., M. R. S. Johannes, J. R. Post, T. J. Stewart, and D. R. S. Lean. 1989. Bottom-up and top-down impacts on freshwater pelagic community structure. Ecological Monographs 59:289–309.

Michaletz, P. H. 1997. Factors affecting abundance, growth, and survival of age-0 gizzard shad. Transactions of the American Fisheries Society 126:84-100.

Miranda, S., G. Jons, and H. Gu. 1994. Factors limiting recruitment of age-0 gizzard shad in Bay Springs Reservoir. Mississippi Department of Wildlife, Fisheries and Parks, Federal Aid in Sport Fish Restoration, Project F98, Final Report, Jackson.

Mundahl, N. D. 1991. Sediment processing by gizzard shad, *Dorosoma cepedianum* (LeSueur), in Acton Lake, Ohio, USA. Journal of Fish Biology 38:565-572.

Noble, R. L. 1981. Management of forage fishes in impoundments of the southern United States. Transactions of the American Fisheries Society 110:738-750.

Nürnberg, G K. 1988. Prediction of phosphorus release rates from total and reductant-soluble phosphorus in anoxic lake sediments. Canadian Journal of Fisheries and Aquatic Sciences 45:453–462.

Olson, M. H., G G Mittelbach, and C. W. Osenberg. 1995. Competition between predator and prey: resource-based mechanisms and implications for stage-structured dynamics. Ecology 76:1758–1771.

Pepin, P . 1991. Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. Canadian Journal of Fisheries and Aquatic Sciences 48:503–518.

Porter, K. G 1977. The plant–animal interface in freshwater systems. American Scientist 65:159–170.

Sale, P. F 1990. Recruitment of marine species: is the bandwagon rolling in the right direction? Trends in Ecology and Evolution 5:25–27.

Soranno, P. A. 1990. Methods of the cascading trophic interactions project. University of Wisconsin, Madison.

Stahl, T. P., and R. A. Stein. 1994. Influence of larval gizzard shad (*Dorosoma cepedianum*) density on piscivory and growth of young-of-year saugeye (*Stizostedion vitreum* X *S. canadense*). Canadian Journal of Fisheries and Aquatic Sciences 51:1993– 2002.

Stein, R. A., M. T. Bremigan, and J. M. Dettmers. 1996. Understanding reservoir systems with experimental tests of ecological theory: a prescription for management. Pages 12–22 *in* L. E. Miranda and D. R. DeVries, editors. Multidimensional approaches to reservoir fisheries management. American Fisheries Society, Symposium 16, Bethesda, Maryland.

Stein, R. A., D. R. DeVries, and J. M. Dettmers. 1995. Food-web regulation by a planktivore: exploring the generality of the trophic cascade hypothesis. Canadian Journal of Fisheries and Aquatic Sciences 52:2518– 2526.

Storck, T. W. 1986. Importance of gizzard shad in the diet of largemouth bass in Lake Shelbyville, Illinois. Transactions of the American Fisheries Society 115: 21–27.

Storck, T. W., D. W. Dufford, and K. T. Clement. 1978. The distribution of limnetic fish larvae in a flood control reservoir in central Illinois. Transactions of the American Fisheries Society 107:419–424.

Welker, M. T., C. L. Pierce, and D. H. Wahl. 1994. Growth and survival of larval fishes: roles of competition and zooplankton abundance. Transactions of the American Fisheries Society 123:703–718.

Willis, D. W. 1987. Reproduction and recruitment of gizzard shad in Kansas reservoirs. North American Journal of Fisheries Management 7:71–80.

Yako, L. A., J. M. Dettmers, and R. A. Stein. 1996. Feeding preferences of omnivorous gizzard shad as influenced by fish size and zooplankton density. Transactions of the American Fisheries Society 125: 753–759.

Youger, J. 1982. Ohio's lakes. Ohio Environmental Protection Agency, Division of Wastewater Pollution Control, Section of Surveillance and Standards, Report 305(b), Columbus.