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EXPLORING SPATIAL AND TEMPORAL VARIATION WITHIN RESERVOIR FOOD WEBS: PREDICTIONS FOR FISH ASSEMBLAGES

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Abstract. In the limnetic zones of small, highly productive reservoirs, young-of-year (YOY) gizzard shad (*Dorosoma cepedianum*) or threadfin shad (*D. petenense*) (henceforth, shad) often attain high densities during spring. Environmental factors facilitating early growth and survival of shad plus potential interspecific competition for zooplankton may reduce growth and survival of YOY bluegill (*Lepomis macrochirus*), another common species in reservoirs. We hypothesized that fewer YOY bluegill moving from the limnetic zone to the littoral zone in late spring probably slows or prevents the ontogenetic switch to piscivory by YOY largemouth bass (*Micropterus salmoides*), reducing their oversummer growth, overwinter survival, and hence recruitment to their second year. To determine whether shad and bluegill abundances indeed vary inversely in reservoirs, we quantified densities of YOY shad and bluegill in four reservoirs across several years (1987–1994; N = 22 reservoir-years). To assess how YOY bluegill abundance influenced the ontogenetic dietary switch to fish by largemouth bass, we conducted experiments with differing levels of realism and control (4-m^2 littoral cages, 4.5-m^2 outdoor pools, and 0.33-m^2 laboratory aquaria).

In reservoirs, peak YOY bluegill density declined weakly in the limnetic zone but strongly in the littoral zone when peak limnetic YOY *Dorosoma* spp. exceeded 10 individuals/m^3. In pools and aquaria, largemouth bass grew more rapidly at ≥ 3 than at zero bluegill per largemouth bass. Using known temperatures and largemouth bass growth in a bioenergetics model, we discovered that YOY largemouth bass in pools and aquaria ate $\leq 65\%$ of their maximum daily consumption potential (in grams of wet mass) at ≥ 6 bluegill per largemouth bass. In cages, largemouth bass consumed only 40% of their maximum and grew less at bluegill abundances similar to those in pools and aquaria, probably because dense vegetation and depletion of bluegill inhibited predatory success. In reservoirs with abundant shad, reduced littoral bluegill density likely compromises first-year growth and recruitment of largemouth bass. However, variable abiotic and biotic factors may modify YOY bluegill abundance and hence invalidate our predictions for largemouth bass recruitment success. To better predict fish community structure and develop management actions for reservoir ecosystems, multi-scale experimentation should be combined with whole-system manipulations (e.g., via adaptive management) to bound these variable interactions.

Key words: bioenergetics; Dorosoma cepedianum; Dorosoma petenense; *fish assemblages; food webs;* Lepomis macrochirus; *limnetic zone; littoral zone;* Micropterus salmoides; *ontogeny; piscivory; reservoir ecosystems; young-of-year fishes.*

INTRODUCTION

A challenging task facing ecologists and resource managers revolves around unraveling interactions underlying community structure. Because the roles of species within communities are modified by their changing ontogeny (Persson 1988, Olson et al. 1995), food web interactions are complex, rendering predictions of relative species abundances difficult. For example, organisms such as fishes increase rapidly in size during early life. Because size often dictates ontogenetic changes in foraging behavior, these organisms typically move through multiple trophic levels during their first year of life (Stein et al. 1988, Polis et al. 1989).

To predict the structure of fish communities, we must understand how processes that influence early growth and survival of young-of-year (YOY) fishes change through time and across habitats. Often ecological interactions early in ontogeny profoundly influence the development and thereby the future structure of the community (Neill 1975, Mills et al. 1987, Carpenter 1988, Crowder et al. 1988, Mills and Forney 1988, Persson and Greenberg 1990). Fishes that are piscivorous as adults generally occupy lower trophic levels during their early life (Mathias and Li 1982, Persson 1988, Olson et al. 1995). Because first-year growth often influences the survival of fish and therefore their recruitment to the adult life stage (Forney 1976, Miller et al. 1988), food web interactions during early ontogeny at one trophic level directly determine adult abun-
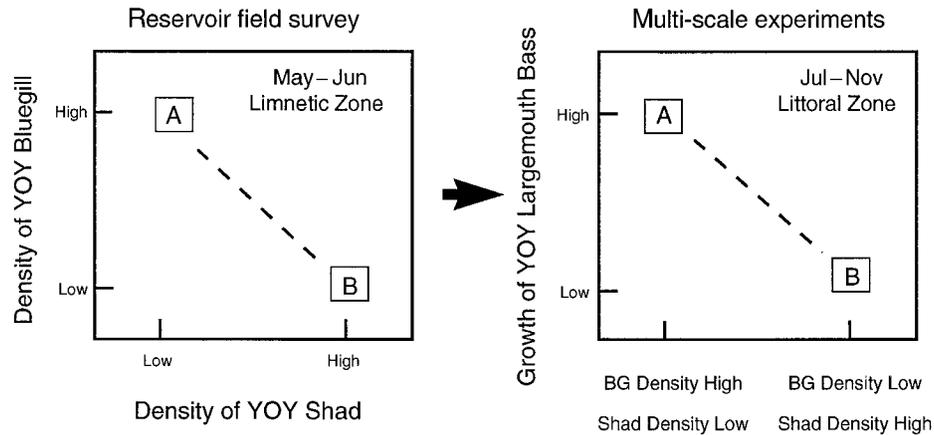
Fig. 1. Left panel: Predictions for the relative density of young-of-year (YOY) bluegill as a function of threadfin or gizzard shad density during May–June in the limnetic zone of reservoirs. Where YOY shad are rare or absent, we predict that the absence of exploitative competition plus environmental factors such as large zooplankton and low turbidity exclude shad and improve bluegill survival in the limnetic zone (symbol A). Conversely, where environmental factors foster high survival of YOY shad in the limnetic zone, we predict that YOY bluegill will grow and survive poorly (symbol B). Right panel: Predictions for the relative growth of YOY largemouth bass as a function of bluegill (BG) and shad densities during July through November in the littoral zone of reservoirs. When shad are absent, early events in the limnetic zone (left panel) result in abundant bluegill prey for YOY largemouth bass residing in the littoral zone (symbol A). When shad are abundant, their rapid growth plus low density of YOY bluegill should reduce growth of YOY largemouth bass later during the season (symbol B). For both panels, dashed lines connecting symbols depict predicted growth occurring at intermediate prey densities.

dance and therefore their potential impact as top predators (Crowder et al. 1988, Mills and Forney 1988, Mittelbach et al. 1988, Goodgame and Miranda 1993, Bergman and Greenberg 1994, Olson 1996a). Similar to food web interactions that vary through time, interactions within one habitat may be impossible to interpret without understanding interactions in other habitats (Lodge et al. 1988, Schindler et al. 1996). Both competitive and predatory interactions influence the relative profitability (e.g., maximizing growth while minimizing mortality; Gilliam 1982) of habitats to YOY fishes, often dictating their movement among them (Mittelbach 1981, Werner et al. 1983a,b, Werner and Gilliam 1984, Werner and Hall 1988, Persson and Greenberg 1990, Bergman and Greenberg 1994). Hence, to understand processes underlying fish community structure, we must explore the effects of these abiotic and biotic factors in a comprehensive fashion across appropriate temporal and spatial scales.

Stein et al. (1995) predicted that in small (<100 ha), highly productive, warm-water reservoirs in the eastern United States, conditions affecting growth and survival during the early ontogenies of three common reservoir species, largemouth bass (*Micropterus salmoides*), bluegill sunfish (*Lepomis macrochirus*), and gizzard shad (*Dorosoma cepedianum*), would dictate the relative abundances of each species by the end of their first growing season. Furthermore, they predicted that early interactions among these species should vary dramatically between systems where gizzard shad are rare and abundant. During early spring, adult gizzard shad often produce abundant offspring that reside in the limnetic zone (Johnson et al. 1988, Bremigan et al. 1991,

DeVries and Stein 1992, Dettmers and Stein 1996). When limnetic YOY gizzard shad experience high survival, rapid growth, and reach juvenile sizes (>25 mm total length [TL]), they can reduce zooplankton to low levels (DeVries et al. 1991, DeVries and Stein 1992, Dettmers and Stein 1992, 1996). After virtually eliminating zooplankton, juvenile gizzard shad switch to feeding on benthic organic detritus (Mundahl and Wissing 1988, Mundahl 1991), thereby escaping the effects of food limitation. Though preferred by piscivores over bluegill (Aggus 1973), gizzard shad grow so rapidly through their first year of life that they often exceed the gapes of a large proportion of piscivores (Noble 1981, Storck 1986, Hambright et al. 1991, Garvey and Stein, *in press*; J. E. Garvey and R. A. Wright, Aquatic Ecology Laboratory, The Ohio State University, *unpublished data*). Faced with apparently unlimited detritus and relatively few predators, gizzard shad dominate fish biomass in many reservoir communities (Stein et al. 1995).

When present in the limnetic zone of reservoirs during spring, YOY gizzard shad and a closely related species, threadfin shad (*D. petenense*), may act as strong interactors (sensu Paine 1980), reducing zooplankton and likely compromising the growth and survival of planktivorous YOY bluegill that also initially reside in the limnetic zone (Fig. 1; Jenkins 1955, Kirk et al. 1986, DeVries et al. 1991, DeVries and Stein 1992, Garvey 1997). Indeed, in one Ohio reservoir across 4 yr, DeVries and Stein (1992) demonstrated a weak, inverse relationship between limnetic YOY gizzard shad and bluegill, suggesting exploitative competition as the causal mechanism.

TABLE 1.   Ohio reservoirs surveyed for relative abundances of YOY gizzard shad, threadfin shad, and bluegill. Data from Stonelick and Clark reservoirs during 1987–1988 derive from DeVries et al. (1991) and during 1987–1990 from Bremigan et al. (1991).

Reservoir	County	Years	Area (ha)	Depth (m) Mean	Max.	Average Secchi depth (m)
Clark Lake	Clark	1987–1993	40	1	2	0.3
Stonelick Lake	Clermont	1987–1994	69	1.5	3	0.5
Kokosing Lake	Knox	1990–1994	65	1.5	3	0.5
Hargus Lake	Pickaway	1992–1994	59	3	18	1.5

Other factors during the early lives of these fishes probably influence survival and relative abundances. YOY gizzard shad forage preferentially on small zooplankton, whereas bluegill select large zooplankton (Bremigan and Stein 1994). Small zooplankton improve the survival of YOY gizzard shad (Bremigan and Stein 1997); conversely, bluegill success should increase with large zooplankton taxa. In North American and Scandinavian lakes, factors such as system productivity, turbidity, and winter oxygen levels shape fish community structure (Tonn and Paszkowski 1986, Tonn et al. 1990, Bergman 1991, Persson et al. 1991). Similarly, many abiotic and biotic factors that vary across reservoirs, including zooplankton size, system productivity, and turbidity, potentially affect early spring larval survival and thus dictate relative abundances of limnetic gizzard shad and bluegill in reservoirs (Fig. 1; Stein et al. 1996; M. T. Bremigan, *personal communication*). To test the prediction that abundances of these two species vary inversely across systems, we quantified the densities of YOY bluegill, threadfin shad, and gizzard shad in four Ohio reservoirs across several years (Fig. 1).

Differences in relative abundances of YOY bluegill and gizzard shad might influence food web interactions later in the year. YOY bluegill migrate to the littoral zone during late spring (Fig. 1; Werner 1967, Werner and Hall 1988) and serve as primary prey for YOY largemouth bass in many systems (Fig. 1; Swingle and Smith 1940, Dillard and Novinger 1975, Storck 1986, Olson 1996a,b). Because we predict that YOY gizzard shad should be relatively invulnerable to these piscivores (Stein et al. 1995), YOY bluegill abundance should primarily influence the consumption and growth of YOY largemouth bass (Fig. 1). Field patterns reveal that the ontogenetic switch from benthivory to piscivory increases the growth of YOY largemouth bass (Timmons et al. 1980, Keast and Eadie 1985, Bettoli et al. 1992, Olson 1996a). However, because these field studies simply demonstrate positive correlations between YOY largemouth bass growth rates and abundance of prey fish in the field and diets, we can only speculate that increased abundances of bluegill will increase the energy intake and growth of YOY largemouth bass (Fig. 1). Furthermore, as density of fish prey increases, complex interactions with piscivores may produce unanticipated effects, such as declining

piscivore growth, or enhanced prey growth and abundance (Wilbur 1988, Abrams 1993). To address this, we conducted experiments across multiple scales to determine whether increased abundance of fish prey, as predicted for systems without gizzard shad, indeed translated to increased growth of YOY largemouth bass (Fig. 1). With this approach, we began to identify important temporally and spatially complex food web linkages, testing our predictions for fish community structure in reservoirs.

METHODS

Field pattern

To determine whether bluegill were scarce where threadfin shad or gizzard shad were abundant, we quantified densities of YOY threadfin shad, gizzard shad, and bluegill (the most common *Lepomis* species) in four Ohio reservoirs across several years (Table 1). These data were combined with results from DeVries et al. (1991) and Bremigan et al. (1991), where adult threadfin shad and gizzard shad were stocked into Clark and Stonelick reservoirs in 1988 (Table 1). In all reservoirs, limnetic threadfin shad, gizzard shad, and bluegill larvae (6–25 mm TL) in the limnetic zone were sampled weekly during April through June with a 0.75 m diameter, 540-μm mesh net towed at 1–1.5 m/s for 5 min twice at sites near the dam. The volume of water sampled was quantified with an attached flowmeter. Larval fish were preserved in 95% ethanol, identified to species, and counted to estimate the number of YOY fish per cubic meter. Because YOY bluegill move from limnetic to littoral zones during late spring (Werner and Hall 1988), we quantified their inshore abundances weekly or biweekly by seining (9-m bag seine, 3-mm mesh) 25–40 m transects located near the downstream, middle, and upstream of each reservoir ($N = 1$ haul at each site).

Rather than assuming that a functional relationship exists between all densities of shad and bluegill, we should quantify how variance and the associated mean of bluegill densities change with shad densities. For example, bluegill densities might only decline beyond some threshold density of shad. To test the null hypothesis that the joint distribution of peak densities of shad and bluegill arise independently, we conducted a two-dimensional Kolmogorov-Smirnov test, compar-

ing the observed joint distribution of densities to that which would be expected if densities occurred independently (Fasano and Franceschini 1987, Press et al. 1992, Garvey et al., *in press*). Each test generated a test statistic, *D,* representing the maximum point of departure between the observed and expected distributions. To determine the significance for each test, we then rerandomized the observed *X, Y* pairs 5000 times (Manly 1991), determining the proportion of randomly generated *D*s exceeding the actual test statistic. If this proportion exceeded 0.05, we concluded that the observed pattern was generated by chance.

Experimental organisms

During all experiments, all fishes were age 0. Largemouth bass and bluegill used during experiments came from St. Marys State Fish Hatchery, St. Marys, Ohio, and Hebron State Fish Hatchery, Hebron, Ohio, respectively (Table 2). At the beginning, ending, and intermediate dates of experiments, we weighed fish (to the nearest 0.1 g) and measured them (to the nearest 1 mm TL). We individually marked largemouth bass in all experiments with unique combinations of dorsal and pelvic fin clips. Unless stated otherwise, all bluegill were at lengths vulnerable to largemouth bass predation (25–45 mm TL). During experiments, wet mass (in grams) of individual YOY bluegill ranged from 3.7 to 5.7% of that of individual largemouth bass. Because largemouth bass densities and sizes of experimental arenas varied among experiments (Table 2), we report bluegill abundances as number of bluegill per largemouth bass as well as number of bluegill per square meter, referring to both as bluegill ''density.'' At the outset of all experiments, we estimated handling mortality of bluegill in separate enclosures and adjusted the number added to treatments accordingly.

In pools and aquaria, we obtained macroinvertebrates and zooplankton from the littoral zone of Hargus Lake and West Campus Pond, a 0.3-ha fishless pond located on the campus of Ohio State University. In many of the experiments, we sampled zooplankton and benthic macroinvertebrates, sieving them through a 54-μm and 250-μm mesh net, respectively, and preserving them in 70% and 95% ethanol, respectively. At the end of the experiments, we froze largemouth bass, later quantifying their diets. In the laboratory, taxa from largemouth bass diets or zooplankton/macroinvertebrate samples were identified to family when possible, and counted (following the methods of Stahl and Stein 1994). To estimate their biomass, we quantified appropriate body dimensions (0.0001 mm) and used corresponding length-dry mass relationships (zooplankton, Culver et al. 1985, Dumont et al. 1975; macrobenthos, Smock 1980, G. G. Mittelbach, Kellogg Biological Station, *unpublished data*) for all taxa to estimate total biomass (in milligrams of dry mass) for each sample. For largemouth bass diets, we converted dry mass of dietary items to wet mass, assuming that fish were 16%

dry mass (J. Breck, Michigan Department of Natural Resources, *unpublished data*), whereas macroinvertebrates and zooplankton were 20% and 12% dry mass, respectively (Cummins and Wuycheck 1971, Hewett and Johnson 1992).

Cage experiment

To assess how littoral bluegill density influenced the growth of largemouth bass, field cages were constructed in the inshore of Hargus Lake (Tables 1, 2). For treatments containing largemouth bass plus bluegill, we used covered, 1-m deep cages (Table 2). Because cages initially contained dense vegetation dominated by water willow, *Justicia americana,* we removed vegetation from half of each cage (Table 2). For treatments with largemouth bass but no bluegill, we used 1-m² enclosures with bottoms.

Seining all cages until three consecutive hauls yielded no fish, we estimated that ambient densities of bluegill were 21 ± 11 individuals/m² (unless stated otherwise, all means and variance are means ± 1 SD). We then restocked cages at ambient or twice ambient densities of 21 bluegill/m² (17 bluegill per largemouth bass) and 43 bluegill/m² (35 bluegill per largemouth bass), respectively. We then added five largemouth bass (Table 2) to all bluegill and no-bluegill treatment enclosures. Largemouth bass mean total length (TL, in millimeters) and mass (in grams) did not differ among initial treatments within experiments (Table 2; ANOVA, $P > 0.1$). Because 50 ± 9% of bluegill in cages exceeded gape sizes of largemouth bass (>35 mm TL; Lawrence 1958), the actual treatment densities approached 10 and 20 bluegill/m² (8 and 16 bluegill per largemouth bass), respectively (Table 2). Because we could not quantify consumption of bluegill by largemouth bass, bluegill densities were restored in cages on 9 September (day 14) by arbitrarily assuming that largemouth bass consumed ~3% and 5% of their biomass (wet mass, in grams per gram per day) in the 10 and 20 bluegill/m² (8 and 16 bluegill per largemouth bass) treatments, respectively.

We sampled zooplankton and benthic macroinvertebrates within cages and in four cageless control plots (4 m² each) at the outset and end of the cage experiment. Zooplankton within each cage or cageless control were sampled with a 2 m long, 7.6 cm diameter plastic tube (DeVries and Stein 1991). Within each cage or cageless control, we quantified benthic invertebrates from two benthic samples collected with a 22.5 cm diameter core sampler (Klosiewski 1991).

During the cage experiment, vegetation compromised our ability to recover largemouth bass by seining. Thus, the number of largemouth bass recovered from cages for growth and diets was often low. Even though small holes (1–3 cm diameter) occurred in many cages, cages with holes and number of fish recovered were not related. Consequently, we believe that vegetation rather than holes contributed to our low recap-

TABLE 2. Design of cage, pool, and aquarium experiments quantifying growth of YOY largemouth bass (LMB) with different densities of YOY bluegill (BG; 25–45 mm TL). Yes (Y) or no (N) shows whether abundances of macroinvertebrates (MI) or zooplankton (ZP) were quantified. The total numbers of microcosms per experiment were 18, 12,

Experiment	Year	Date	Microcosm area (m^2)	No. reps./treatment	Vegetation (stems/m^2)	Temp. range (°C)	Treatment	
							Initial no. BG/m^2	Initial no. BG per LMB
Cage	1991	27 Aug–17 Sep	4	6	dense	25–27	0, 10, 20,‡ control	0, 8, 16,‡ control
Pool	1992	25 Aug–25 Sep	4.5	4	125	18–24	0, 10, 20§	0, 9, 18§
Pool	1993	21 Aug–20 Sep	4.5	4	125	18–24	0, 1, 3, 6§	0, 1, 3, 6§
Aquarium 1	1992	26 Aug–25 Sep	0.33	5	75	22–24	0, 30, 60‖	0, 10, 20‖
Aquarium 2	1992	1–31 Oct	0.33	4	75	22–24	0, 3, 9, 27‖	0, 1, 3, 9‖

Note: Each aquarium housed only one largemouth bass, whereas each cage and pool contained five largemouth bass.

† Data are means ± 1 SD.

‡ Bluegill densities were restored in cages on 9 September 1991.

§ Bluegill densities were maintained by stocking every 3 d.

‖ Bluegill and macroinvertebrate densities were maintained by stocking every 3 d.

ture rates and that uncaptured largemouth bass probably remained in cages after seining. We only recovered largemouth bass in 2 of 6 cages and 4 of 6 cages from the 8 and 16 bluegill per largemouth bass treatments, respectively. In those cages, we only captured 16.7 ± 32% and 43.3 ± 42.7% of the originally stocked largemouth bass from the 8 and 16 bluegill per largemouth bass treatments, respectively. Analyses on largemouth growth, diets, zooplankton, and macroinvertebrates derive from cages where we recovered largemouth bass. Because we recovered 97 ± 0.08% of largemouth bass from the no-bluegill enclosures, all six no-bluegill replicates were analyzed.

Pool experiments

To increase our ability to (1) sample largemouth bass and bluegill, (2) control vegetation density, and (3) control macroinvertebrate density, we conducted largemouth bass growth experiments in 0.5 m deep, flow-through, outdoor pools (Table 2). Due to low suspended solids and algae, visibility in pools was high during experiments. Though more artificial than cages, these experiments improved control without sacrificing spatial scale. All pools contained artificial vegetation constructed from green, 15 cm long, polypropylene rope strands (Table 2), anchored in sand that was covered with 10 cm of flocculent organic sediment from Hargus Lake. We stocked all pools with macroinvertebrates and zooplankton at the outset and 1–2 times during the middle of the 1992 and 1993 pool experiments.

In 1992, 5 largemouth bass were combined with 0, 9, or 18 bluegill per largemouth bass (Table 2). Initial mean length (TL, in millimeters) and mass (in grams) of largemouth bass did not differ among treatments within the 1992 experiment (Table 2; ANOVA, $P > 0.6$). During 1993, pools contained 5 largemouth bass and 0, 1, 3, or 6 bluegill per largemouth bass (Table 2). In this experiment, initial size of largemouth bass in the 1 bluegill per largemouth bass treatment exceeded that in the 6 bluegill per largemouth bass treatment by ~1 mm TL and 0.25 g (ANOVA on length,

$F_{3,12} = 5.06$, $P = 0.02$; ANOVA on mass, $F_{3,12} = 5.09$, $P = 0.02$; Tukey's test, $P < 0.05$). Because these differences were quite small and occurred at an intermediate bluegill density, we still included growth results from these treatments in our analyses. Until 9 September (day 15) in 1992, we added bluegill to pools every 3 days, assuming that largemouth bass consumption was 3% and 5% of their wet biomass per day in the 9 and 18 bluegill per largemouth treatments, respectively. We then used electrofishing to sample bluegill for the remainder of the 1992 experiment and the entire 1993 experiment, restoring bluegill densities in pools every 3 days according to our most recent electrofishing estimate. Survival of largemouth bass during the pool experiments was high (>97%).

At the outset and end of both experiments, zooplankton and benthic samples were taken from randomly chosen sections near the wall, middle region, and center of each pool, resulting in three samples. We collected zooplankton with a 3.5 cm diameter plastic tube sampler, combining all three samples. Benthic invertebrates were quantified within each pool with a 0.7 m long, 0.018 m^2 PVC tube and a wet/dry shop vacuum. To collect each sample, water within the PVC sampler was stirred by hand and vacuumed for 10–15 s. Unlike zooplankton, we did not combine these three resulting samples.

Because few replicates were available for analysis in the cage experiment, insufficient statistical power prevented detailed analysis of largemouth bass diet composition. For pool experiments, we used multivariate analysis of variance (MANOVA) of mean total wet mass (in milligrams per gram) and relative proportions (in milligrams of wet mass) of different items (pooled into categories of fish, macroinvertebrates, or zooplankton) within largemouth bass stomachs to test the null hypothesis that bluegill density did not affect diet composition. All proportional data were arcsine square-root transformed before analyses to homogenize variances.

16, 15, and 16 for cage (Hargus Lake, Table 1), 1992 pool, 1993 pool, aquarium 1, and aquarium 2 experiments, respectively.

Variables quantified				
Initial LMB TL (mm)†	Initial LMB wet mass (g)†	LMB diet data?	MI data?	ZP data?
91.4 ± 1.8	11.42 ± 1.03	Y	Y	Y
63.7 ± 0.9	2.68 ± 0.15	Y	Y	Y
62.0 ± 0.8	3.36 ± 0.17	Y	Y	N
65.9 ± 2.3	3.39 ± 0.53	N	Y	N
83.4 ± 1.2	6.39 ± 0.18	N	Y	N

Aquarium experiments

Via two laboratory experiments in 1992, we determined how varying densities of macroinvertebrates and bluegill affected largemouth bass growth (Table 2). In addition to vegetation consisting of 75% milfoil (*Myriophyllum* spp.) and 25% water willow (Table 2), the bottoms of 0.33-m deep aquaria were covered with sediment from Hargus Lake. Water clarity was high in aquaria during experiments. In both experiments, macroinvertebrates were added every 3 days to each aquarium in equal portions. A subsample of macroinvertebrates was preserved in 95% ethanol during each addition to estimate the biomass added. Aquaria in experiment 2 received about four times more macroinvertebrate biomass every 3 days (on average 42.4 mg dry mass per addition) than those in experiment 1 (on average, 8–15 mg dry mass per addition). In experiment 1, we completely removed all sediment and fish every 6 days to quantify remaining bluegill densities and ensure that all macroinvertebrates were removed before the next addition. For experiment 2, we did not destructively sample aquaria. Rather, we collected bluegill and largemouth bass with a net. Because macroinvertebrates were rapidly consumed during both experiments, we did not quantify their final density and biomass.

Each aquarium contained one largemouth bass; diets of these largemouth bass were not sampled. Initial mean length (TL, in millimeters) and mass (in grams) of largemouth bass did not differ among treatments within the 1992 experiment (Table 2; ANOVA, $P > 0.2$). During experiment 1, bluegill were stocked and restored every 3 days at 0, 10, or 20 bluegill per largemouth bass (Table 2). During experiment 2, we stocked bluegill every 3 days at 0, 1, 3, or 9 bluegill per largemouth bass (Table 2). We restored bluegill densities every 3 days using estimates based on number of bluegill collected during destructive sampling in experiment 1 and visual counts in aquaria in experiment 2. Similar to pools, largemouth bass survival exceeded 97% in aquarium experiments.

General analyses

We analyzed growth and diet data from largemouth bass similarly for all experiments. Instantaneous growth (ΔG based on grams of wet mass; Ricker 1975) of each largemouth bass was calculated. Because each replicate cage and pool contained five largemouth bass, length, mass, or ΔG for each largemouth bass were averaged across all individuals. Conversely, each replicate aquarium contained a single largemouth bass; hence, these growth responses were treated individually. For each experiment, we used a one-way analysis of variance (ANOVA) to assess bluegill treatment effects on largemouth bass growth (SAS Institute 1985). For each ANOVA, all post hoc multiple comparisons were conducted with a Tukey's multiple comparisons test.

Because sizes of largemouth bass and temperatures differed across experiments, we used bioenergetics modeling, which incorporated size and temperature effects, to compare their responses to differing bluegill densities. To grow, largemouth bass consume some proportion, *p*, of their maximum potential consumption for a given temperature and body mass through time (for parameters and methods see Rice and Cochran 1984, Hewett and Johnson 1992, Trebitz 1991, Wright 1993). By directly calculating the *p* values of largemouth bass with bioenergetics, we could compare their predicted consumption across experiments. For each largemouth bass, beginning and ending wet masses were used in bioenergetics simulations to predict its *p* value during each experiment. All largemouth bass were assumed to be 4.6 kJ/g (wet mass, Hewett and Johnson 1992) whereas bluegill and benthic invertebrates, which generally comprised >95% biomass of largemouth bass diets, were assumed to be 4.2 kJ/g (Cummins and Wuycheck 1971, Hewett and Johnson 1992).

RESULTS

Neither gizzard shad nor threadfin shad occurred in Clark and Stonelick reservoirs during 1987 (DeVries et al. 1991, Bremigan et al. 1991). After adults were stocked in spring 1988, shad spawned and produced larvae (YOY individuals 6–25 mm TL; Fig. 2; DeVries et al. 1991, Bremigan et al. 1991). During that year, YOY threadfin shad dominated YOY shad biomass in both reservoirs (Bremigan et al. 1991, DeVries et al. 1991). The following spring (1989), gizzard shad represented the majority of YOY shad biomass and within 1 yr, became the sole *Dorosoma* present (Bremigan et al. 1991). Adult gizzard shad apparently were introduced into Hargus Lake in 1993. Though YOY gizzard shad appeared in the limnetic zone in 1993 and 1994 (Fig. 2), we never encountered them while seining (this study) or during intensive electrofishing (Garvey 1997) in the littoral zone, probably because few survived to older, juvenile stages. In Kokosing Lake, species composition of fishes was stable during 1991–1994. Combining larval and juvenile abundance data from DeVries et al. (1991) and Bremigan et al. (1991) with our data from Clark, Stonelick, Kokosing, and Hargus reservoirs across years, peak limnetic bluegill and shad
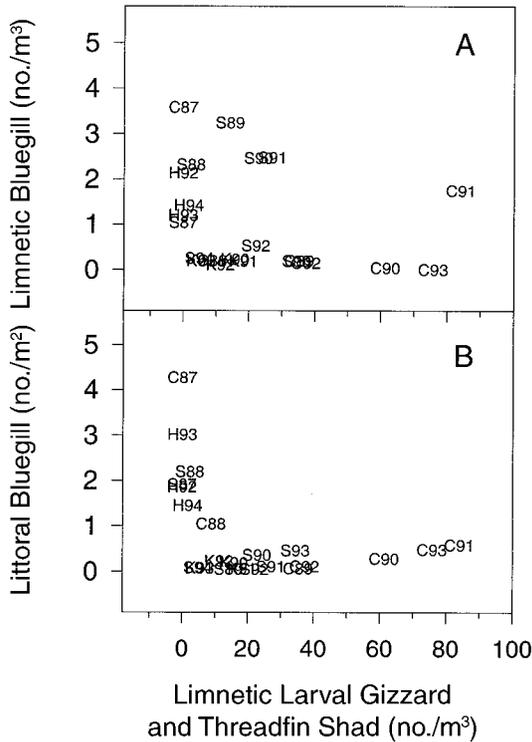
FIG. 2. Relationship between peak densities of limnetic YOY threadfin and gizzard shad and YOY bluegill from the limnetic (A) and littoral (B) zones of Hargus, Kokosing, Stonelick, and Clark reservoirs, Ohio. Shad and bluegill larvae in the limnetic zone were sampled with net tows, whereas littoral bluegill were sampled by seining. The coefficient of variation for mean density estimates averaged ~40%. Symbols are the first letter of each reservoir name, followed by year sampled. The years sampled for each reservoir were Hargus, 1992–1994; Kokosing, 1991–1994; Stonelick, 1987–1994; and Clark, 1987–1993. Because littoral sunfish densities were estimated by seining, they are relative, not absolute, catch-per-unit-effort estimates. Overlapping symbols on panel (A) represent ~0–20 shad/m³ vs. 0–0.25 bluegill/m³ for S92 and K91–K94. On panel (B), symbols for K91–K94 and S91, S92, and S94 overlap at 0–20 shad/m³ and 0–0.25 bluegill/m²; symbols for H92 and S87 overlap at 0 shad/m³ and 2 bluegill/m²; and symbols for C89 and C92 overlap at 40 shad/m³ and 0.5 bluegill/m².
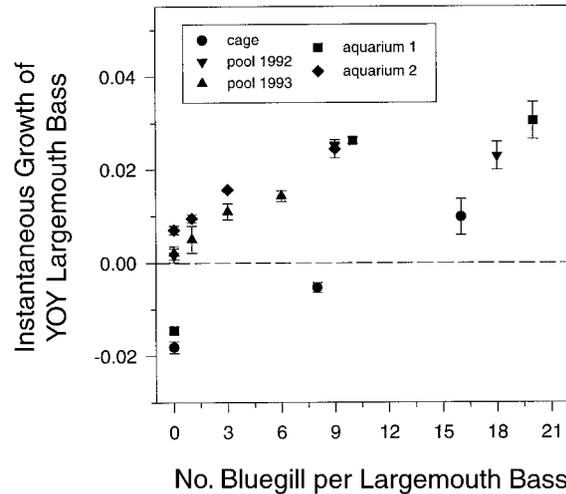
FIG. 3. Mean (± 1 SE) instantaneous growth (ΔG, wet mass) of YOY largemouth bass as a function of YOY bluegill density in cages in Hargus Lake ($N = 2$–6 cages per treatment with 1–5 largemouth bass per cage, depending on treatment, see *Results*), pools ($N = 4$ pools per treatment with 5 largemouth bass per pool), and aquaria ($N = 5$ per treatment in 1992, $N = 4$ per treatment in 1993, with 1 largemouth bass per aquarium) during summer. See Table 2 for initial conditions; see Table 3 for ANOVA statistics.

densities appeared to be negatively related (Fig. 2A; two-dimensional Kolmogorov-Smirnov test, $D = 0.14$, $P = 0.02$). Similarly, peak bluegill (<30 mm TL) densities declined inshore as peak densities of threadfin and gizzard shad (<25 mm TL) increased offshore (Fig. 2B; two-dimensional Kolmogorov-Smirnov test, $D = 0.18$, $P = 0.002$) among reservoirs and years. Thus, when threadfin and gizzard shad produced >10 larvae/m³, YOY bluegill densities were low and relatively invariant.

Within any experiment, largemouth bass grew faster with increasing bluegill density, although the magnitude of this increase declined at high bluegill densities (Table 3; Fig. 3). Generally, largemouth bass grew faster at 3 than at zero bluegill per largemouth bass (Table 3; Fig. 3; Tukey's test, $P < 0.05$). Largemouth bass in pools and aquaria grew faster at ≥8 than at zero bluegill

TABLE 3. Results of one-way ANOVAs and post hoc Tukey's multiple comparisons for differences in instantaneous growth (ΔG, wet mass) of YOY largemouth bass (LMB) in response to different densities of bluegill (BG) (treatment effect: no. BG per LMB) in cages, pools, and aquaria. Treatments not sharing an underline differ with regard to LMB growth, with growth ordered left to right and from low to high (Tukey's multiple comparisons, $P < 0.05$). See Table 2 for initial conditions.

Experiment	df (model, error)	MS	F	P	No. BG per LMB
Cage (Hargus Lake)	2, 9	9.0×10^{-4}	36.73	0.0001	0 8 16
Pool (1992)	2, 9	6.7×10^{-4}	41.65	0.0001	0 9 18
Pool (1993)	3, 12	1.2×10^{-4}	8.33	0.003	0 1 3 6
Aquarium 1	2, 12	3.1×10^{-3}	130.32	0.0001	0 10 20
Aquarium 2	3, 12	2.4×10^{-4}	57.13	0.0001	0 1 3 9
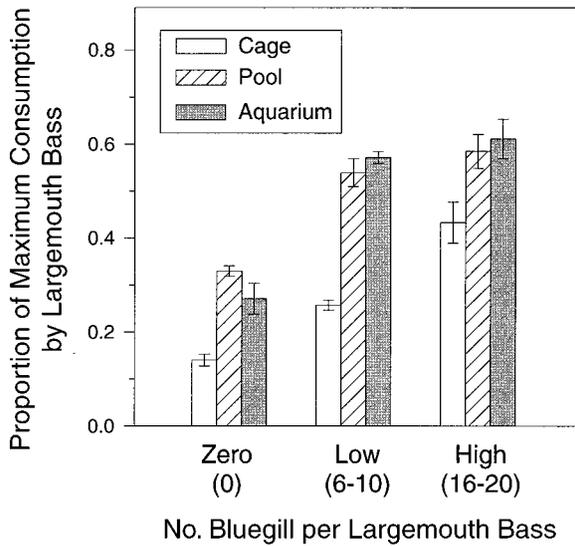
FIG. 4. Mean (± 1 SE) predicted proportion of maximum consumption by largemouth bass as a function of zero (0 bluegill per largemouth bass, $N_{cage} = 6$, $N_{pool} = 8$, $N_{aquarium} = 9$), low (6–10 bluegill per largemouth bass, $N_{cage} = 2$, $N_{pool} = 8$, $N_{aquarium} = 9$), and high (16–20 bluegill per largemouth bass, $N_{cage} = 4$, $N_{pool} = 8$, $N_{aquarium} = 9$) categories of bluegill density. See Table 2 for initial conditions.

per largemouth bass (Table 3; Fig. 3; Tukey's test, $P < 0.05$). Largemouth bass growth only differed between treatments with ≥ 8 bluegill per largemouth bass in the 1991 cages (Fig. 3; Table 3; Tukey's test, $P < 0.05$).

Size differences and temperatures prevented us from directly comparing largemouth bass growth across experiments. With bioenergetics modeling, we could compare the average proportion of maximum consumption (p values) of largemouth bass across experiments, pooling bluegill availability in experiments into categories of zero (0), low (6–10), and high (16–20) numbers of bluegill per largemouth bass. To compare responses across experiments statistically, responses

from the 1 and 3 bluegill per largemouth bass treatments in the 1993 pool and aquarium 2 experiments were dropped because these treatments were not included in other experiments. Predicted p values of largemouth bass increased with increasing bluegill density (Fig. 4; two-way ANOVA, bluegill effect, $F_{2,46} = 40.76$, $P = 0.0001$); however, p values did not differ between low and high bluegill availability, regardless of experiment (Fig. 4; Tukey's test, $P > 0.05$). The p values of largemouth bass with bluegill were higher than without bluegill (Fig. 4; Tukey's test, $P < 0.05$). Largemouth bass in pools and aquaria consistently consumed equivalent proportions of their maximum consumption (Fig. 4; Tukey's test, $P > 0.05$) and had higher p values than individuals in field cages (Fig. 4; two-way ANOVA, scale effect, $F_{2,46}$, $P = 0.0001$; Tukey's test, $P < 0.05$), regardless of bluegill density (Fig. 4; two-way ANOVA, scale $\times$ treatment effect, $F_{4,46}$, $P = 0.06$).

If densities of zooplankton and macroinvertebrates positively covaried with bluegill density, then non-bluegill prey could have contributed to observed patterns of growth by largemouth bass. Benthic invertebrates and zooplankton varied, and their density differed among cages, pools, and aquaria (Table 4). In cages and 1992 pools, initial zooplankton density and mass combined across taxa were unrelated to bluegill density (Table 4; one-way ANOVA, $P > 0.05$). During both cage and 1992 pool experiments, changes in zooplankton density and mass were extremely variable and unrelated to bluegill density (Table 4; one-way ANOVA, $P > 0.05$). Overall initial biomass (dry mass, in milligrams per square meter) and change in biomass of macroinvertebrates were variable and unrelated to treatment in combined pool experiments (Table 4; one-way ANOVA, $P > 0.05$). Unlike other experiments, we only quantified density and biomass of macroinvertebrates added to aquaria. Macroinvertebrate biomass during both aquarium experiments was dominated, from most to least abundant, by *Chaoborus, Li-*

TABLE 4. Initial biomass and numerical density, change in biomass or density (last day minus first day), and taxonomic composition (three most abundant taxa per category, ordered from most [1] to least [3] abundant) of benthic invertebrates and zooplankton in cages and pools. Data are means, with 1 SD in parentheses. Because macroinvertebrate and zooplankton biomass and density were unrelated to bluegill density, these responses were pooled across bluegill densities. Density of benthic macroinvertebrates was not quantified in aquarium experiments. See Table 2 for initial conditions.

| Experiment (treatment, no. BG per LMB) | Benthos | | | Zooplankton | | | | |
	Initial biomass (mg/m²)	Change in biomass (mg/m²)	Taxa	Initial biomass (mg/L)	Change in biomass (mg/L)	Initial density (no./L)	Change in density (no./L)	Taxa
Cage, Hargus (8, 16, control)	2158.8 (1704.9)	−320.8 (2484.6)	(1) *Hexagenia,* (2) Chironomidae, (3) Tabanidae	0.24 (0.041)	0.11 (0.34)	182.6 (51.2)	−48.2 (109.1)	(1) *Chydorus,* (2) cyclopoids, (3) *Bosmina*
Pool, 1992 (0, 9, 18)	370.8 (460.5)	2810.5 (4580.9)	(1) Libellulidae, (2) Notonectidae, (3) *Lymnaea*	0.16 (0.27)	−0.090 (0.33)	26.9 (11.1)	−4.1 (44.6)	(1) *Daphnia,* (2) calanoids, (3) *Bosmina*
Pool, 1993 (0, 1, 3, 6)	1716.4 (1207.5)	445.6 (3233.6)	(1) Oligochaeta, (2) Hirudinae, (3) Physidae	...	...	...	...	...

TABLE 5. Mean total biomass (non-fish prey plus bluegill, mean $\pm$ 1 SE) and the three most abundant benthic invertebrate and zooplankton taxa (excluding bluegill) in stomachs of largemouth bass collected on the last day of cage and pool experiments as a function of initial bluegill density. Benthic macroinvertebrates and zooplankton in diets are ordered from most (1) to least (3) abundant (measured as wet mass in milligrams per gram). Diets were not collected for largemouth bass in aquarium experiments. See Fig. 5 for relative proportions of bluegill, macroinvertebrates, and zooplankton in diets as a function of treatment.

Experiment (year)	Bluegill density			Largemouth bass diets	
	No./m^2	No. BG per LMB	Total biomass (mg/g)	Benthos	Zooplankton
Cage, Hargus (1991)	0	0	0.057 ± 0.033	(1) *Orconectes,*	(1) *Bosmina,*
	10	8	3.00 ± 3.00	(2) Chironomidae,	(2) calanoids,
	20	16	28.63 ± 14.43	(3) Caenidae	(3) *Diaphanosoma*
Pool (1992)	0	0	8.40 ± 4.27	(1) Libelluidae,	(1) *Daphnia,*
	10	9	23.41 ± 9.75	(2) *Chaoborus,*	(2) cyclopoids,
	20	18	18.59 ± 3.47	(3) Corixidae	(3) *Diaphanosoma*
Pool (1993)	0	0	2.92 ± 0.42	(1) Chironomidae,	(1) cyclopoids,
	1	1	0.84 ± 0.43	(2) Coenagrionidae,	(2) *Diaphanosoma,*
	3	3	3.49 ± 1.49	(3) Isopoda	(3) *Ceriodaphnia*
	6	6	28.38 ± 19.57		

bellulidae, and *Coenagrionidae.* During each aquarium experiment, the initial density and biomass of macroinvertebrates did not differ among treatments. Interestingly, at low bluegill densities, largemouth bass receiving a high macroinvertebrate ration in aquarium

FIG. 5. Mean (± 1 SE) proportion of wet mass (in milligrams) of bluegill, macroinvertebrates, and zooplankton in diets of largemouth bass as a function of bluegill density in 1992 and 1993 pool experiments. With the exception of mean proportions for 18 bluegill per largemouth bass arising from $N = 3$ pools (data for the fourth replicate were lost), all means are for diets of YOY largemouth bass from $N = 4$ pools at 5 largemouth bass/pool. See Table 2 for initial conditions.

experiment 2 grew more rapidly than largemouth bass receiving a low macroinvertebrate ration in experiment 1 (Fig. 3).

We quantified total biomass and composition of diets to determine whether these diets were related to bluegill density and predicted consumption (p values that translate to growth). At the end of experiments, largemouth bass diets differed both within and among experiments (Table 5). In cages and pools, the proportion of largemouth bass with empty stomachs was unrelated to bluegill density (one-way ANOVA; cage, $F_{2,11} = 3.14$; pool 1992, $F_{2,9} = 0.95$; pool 1993, $F_{3,12} = 1.02$; all tests, $P > 0.05$). Using linear regression, we tested the null hypothesis that biomass in largemouth bass stomachs at the end of the experiments was unrelated to bluegill densities or average consumption. Wet mass (in milligrams per gram) in stomachs of largemouth bass increased slightly with increasing bluegill density in cages (Table 5; cage, $N = 10$ cages, $r = 0.70$, $P = 0.02$) but not in combined pools (Table 5; $N = 27$ pools, $r = 0.35$, $P = 0.07$). Similarly, diet mass increased with predicted proportion of maximum consumption by largemouth bass in cages ($N = 9$ cages, $r = 0.87$, $P = 0.002$) but not in combined pool experiments ($N = 27$ pools, $r = 0.35$, $P = 0.07$). Only at the cage scale did increasing bluegill densities weakly increase mass in stomachs of largemouth bass.

Because mass in diets varied tremendously among largemouth bass (see regression results), increasing bluegill density did not affect the wet mass of fish, macroinvertebrates, or zooplankton in largemouth bass diets (MANOVA, overall treatment effect, Wilks' lambda, $F = 1.56$, $P = 0.1$). Conversely, increasing bluegill densities influenced the relative proportions of fish, macroinvertebrates, and zooplankton in diets from combined pool experiments (Fig. 5; MANOVA, overall treatment effect, Wilks' lambda, $F = 5.69$, $P = 0.0001$). Within diets, separate univariate ANOVAs

FIG. 6. Relationship between mean proportion of maximum consumption by largemouth bass from bioenergetics simulations and mean proportion (by wet mass, in milligrams) of bluegill in diets of largemouth bass from experiments. Numbers represent responses in pools with 0, 3, 6, 9, and 18 bluegill per largemouth bass. For 0 and 1 bluegill per largemouth bass, largemouth bass diets consistently contained no bluegill. For 3 bluegill per largemouth bass, two symbols overlap with other symbols at 0.38–0.40 proportion of maximum consumption by largemouth bass. Symbols for 6 and 9 bluegill per largemouth bass overlap at ~0.65 proportion of maximum consumption.

demonstrated that with increasing bluegill densities, the proportion (wet mass, in milligrams) of fish increased (Fig. 5; ANOVA, $F_{5,21} = 23.71$, $P = 0.0001$), that of macroinvertebrates declined (Fig. 5; ANOVA, $F_{5,21} = 9.46$, $P = 0.0001$), and that of zooplankton did not change (Fig. 5; ANOVA, $F_{5,21} = 2.15$, $P = 0.1$). With linear regression, we discovered that the proportion of fish in diets of largemouth bass from pool experiments was positively related to the predicted proportion of maximum consumption (Fig. 6; arcsine square-root transformed data, $N = 27$, $r = 0.79$, $P = 0.0001$). Though relative mass contained in stomachs varied both within experiments and between scales, bluegill clearly increased in largemouth bass diets with their increasing abundance, thus contributing to higher average consumption and growth.

DISCUSSION

Food web interactions

Combining the results from our reservoir survey with those from growth experiments, we modified the conceptual framework for reservoir food webs originally outlined by Stein et al. (1995). By considering how linkages within reservoir food webs vary through space and time, we formed predictions for fish community structure, thereby developing management strategies for enhancing sport-fish production in reservoirs.

Limnetic events during spring.—Across reservoirs and years, peak bluegill densities were high but variable in both the limnetic and littoral zones when threadfin or gizzard shad densities were low. When shad densities increased in the limnetic zone, the negative relationship between peak YOY shad and bluegill density in the limnetic zone was weak and variable. Conversely, in the littoral zone, peak YOY bluegill density declined strongly and varied little with increasing YOY shad density. Potentially, low survival in the limnetic zone reduced the number of YOY bluegill migrating from this habitat to the littoral zone at high shad densities. Several studies have suggested that the growth and abundance of sympatric centrarchids decline with increasing shad density (Jenkins 1955, Kirk et al. 1986, DeVries et al. 1991, DeVries and Stein 1992), implicating competition as a potential causal mechanism.

In our study reservoirs, competition for shared zooplankton prey probably contributed to the negative relationship between YOY shad and bluegill. Though limnetic YOY gizzard shad and bluegill were negatively related in Kokosing Lake during 1987–1988, potentially due to interspecific competition (DeVries and Stein 1992), this relationship was only marginally significant ($P = 0.07$; see Fig. 10 in DeVries and Stein 1992) and derived from a single system. Across several reservoirs and years, we documented a similar negative relationship, suggesting that this pattern may be generalizable across systems. Dettmers and Stein (1996) documented that zooplankton was reduced at >10 YOY gizzard shad/m³ in enclosure experiments and hypothesized that this critical YOY shad density impedes sport-fish recruitment. Interestingly, in our reservoirs, peak littoral YOY bluegill density also declined strongly at ~10 YOY shad/m³, suggesting that this strong field pattern arose during the 1–3 wk between limnetic competition and movement to the littoral zone, when bluegill larvae suffered high mortality, thus compromising their recruitment to the littoral zone.

Though our field pattern and previous work suggest that shad can negatively affect growth and perhaps survival of YOY fishes (Guest et al. 1990, Bremigan et al. 1991, DeVries et al. 1991, DeVries and Stein 1992, Garvey 1997), other studies have demonstrated that planktivorous fishes may be unaffected by abundant shad (see DeVries and Stein 1990 for review; Pope and DeVries 1994, Welker et al. 1994). For example, growth and survival of planktivorous YOY white crappie (*Pomoxis annularis*) were unaffected by YOY shad in Alabama ponds, likely because YOY shad did not appear sufficiently early to reduce zooplankton and compromise white crappie foraging success (Pope and DeVries 1994). Hatching times, driven by temperature, influence relative limnetic appearance of YOY fishes (Carlander 1969, 1977) and, as such, temperature may strongly influence the potential for competitive interactions between YOY shad and bluegill (DeVries et al. 1991, Garvey 1997).

Although YOY shad may act as strong interactors affecting bluegill through competitive interactions, environmental characteristics of reservoirs may have facilitated the relative success of YOY shad and bluegill during early spring. In Scandinavian lakes, turbidity resulting from algal production has been hypothesized to influence the relative abundances of fishes (Bergman 1991, Persson et al. 1991). Ruffe (*Gymnocephalus cernuus*) are more successful foragers in these poorly lit, eutrophic lakes than species such as European perch (*Perca fluviatilis*), and thus are more abundant in these systems (Bergman 1991, Persson et al. 1991). Similarly, the small zooplankton, high turbidity (due to suspended solids), and high productivity characteristic of many reservoirs may favor successful foraging and survival of larval shad relative to bluegill (Stein et al. 1996, Bremigan and Stein 1997). Though both larval shad and bluegill were present during early spring in Hargus Lake, shad never reached juvenile stages, whereas bluegill survival was extremely high. Relative to the other three reservoirs, water clarity was highest in Hargus Lake (Table 1). Potentially, variable turbidity plus other related factors such as productivity influenced relative early survival of bluegill and shad across our study reservoirs (Stein et al. 1996, Bremigan 1997).

Competitive interactions and environmental factors influencing early larval survival are equally valid hypothetical mechanisms dictating the relative success of YOY shad and bluegill during early spring. These mechanisms are not mutually exclusive, and appear to produce communities with predictably low bluegill densities when shad are abundant. Clearly, if these patterns are widespread across reservoirs, they may allow predictions for later interactions that occur in the littoral zone.

Littoral events during summer through fall.—Ontogenetic shifts in littoral fishes can be modified by early events in the limnetic zone and are further affected by the relative size structure of predators and their prey (Werner et al. 1983*a*, *b*, Olson 1996*a*, *b*). Because YOY bluegill were abundant relative to other small fishes in systems without shad, YOY largemouth bass likely consume bluegill prey. Conversely we predict that YOY largemouth bass should remain benthivorous in systems with abundant shad (DeVries et al. 1991, Stein et al. 1995), because YOY shad quickly outgrow their sizes of vulnerability to most predators (Noble 1981) and other fish prey are relatively rare (Ploskey and Jenkins 1982, Johnson et al. 1988, this study). At sizes used in experiments, YOY largemouth bass in lakes and reservoirs have typically already switched from feeding on zooplankton to benthic invertebrates (Clady 1974, Wicker and Johnson 1987, Olson 1996*a*) and will quickly become piscivorous when appropriately sized prey fish become available in littoral areas (Summerfelt 1975, Shelton et al. 1979, Timmons et al. 1980, Keast and Eadie 1985, Wicker and Johnson 1987, Olson 1996*a*, *b*). Indeed, YOY

largemouth bass ate fewer benthic invertebrates and progressively more fish as YOY bluegill availability increased in experiments, as would be expected in shad-free systems. When bluegill were very abundant (18 bluegill per largemouth bass in pools), YOY largemouth bass diets contained >90% bluegill, suggesting that these YOY largemouth bass fed almost exclusively on fish. Though YOY largemouth bass and bluegill can potentially compete for common benthic prey, resulting in reduced largemouth bass growth with abundant bluegill (Gilliam 1982, Olson et al. 1995), this did not occur in our experiments. Largemouth bass were sufficiently large to exploit abundant bluegill, and therefore their growth was not limited by the availability of benthic invertebrates.

YOY largemouth bass should only be expected to become piscivorous if this foraging tactic increases their net energetic gain (Gilliam 1982, Werner and Gilliam 1984). Indeed, bioenergetics modeling revealed that the average proportion of maximum consumption by YOY largemouth bass increased as bluegill became more available, with this relationship only beginning to decelerate at ~6–10 bluegill per largemouth bass across all experiments. However, biomass in diets of YOY largemouth bass collected on the final day of experiments only increased with increasing bluegill density in cages. This is not surprising: because piscivores consume large rations of biomass infrequently (Breck 1993), we would not expect consumption estimates derived from diets collected on one sampling date to necessarily reflect the average daily consumption of piscivorous YOY largemouth bass. By increasing their net energetic intake by consuming bluegill, YOY largemouth bass grew rapidly. Hence, in systems where shad are rare, YOY largemouth bass should grow rapidly and reach large sizes by fall. Because overwinter survival is likely linked to fall size in YOY largemouth bass (Adams et al. 1982, Miranda and Hubbard 1994*a*, *b*, Ludsin and DeVries 1997), becoming piscivorous should improve their recruitment success by increasing their probability of surviving to reproduction. Based on our field and experimental results, limnetic events during early spring can influence littoral prey fish availability. We hypothesize that these events, separated in time and space, ultimately drive interactions between littoral YOY largemouth bass and their bluegill prey.

In many aquatic ecosystems, spatial and temporal food web linkages influence ecosystem function (e.g., nutrient dynamics; Wetzel 1979) as well as structure (e.g., species composition; Lodge et al. 1988). In reservoir ecosystems, we assert that, by understanding how limnetic-littoral linkages vary through time, we can begin to predict population dynamics of resident fishes. Interestingly, though shad may mediate limnetic-littoral food web linkages, these species also may link benthic and limnetic food webs (Vanni 1996). By feeding on organic, benthic sediments and transporting

nutrients via excretion to the limnetic zone, gizzard shad may operate as nutrient "pumps" influencing production and species composition of phytoplankton (Vanni 1996, Schaus et al., *in press*). Many species such as vertically migrating invertebrates (as suggested by Lodge et al. 1988), benthic filter-feeding planktivores (MacIssac et al. 1992), or mobile fishes (Lamarra 1975, Brabrand et al. 1990) may serve a similar function as shad by linking food webs within ecosystems. To begin to predict structure and function of ecosystems, we must first identify how species influence linkages within food webs. We then must determine how these linkages change with size-structured, ontogenetic shifts in feeding and perhaps migratory behavior of the strong interactors involved (Osenberg et al. 1994). With this approach, we can begin to unravel complex interactions influencing structure of communities within aquatic ecosystems.

Predictions for reservoir fish communities

Through field surveys and experiments, we are beginning to understand how early events in the limnetic zone may mediate summer and fall interactions in the littoral zone. Though the negative relationship between YOY shad and bluegill density appears robust, littoral interactions may vary among systems, modifying current predictions of YOY largemouth bass growth, survival, and ultimately recruitment to adulthood.

Shad-dominated systems.—In shad-dominated systems, YOY largemouth bass often may not switch to piscivory, and hence grow slowly. This prediction may be modified by density-dependent effects of YOY largemouth bass on prey fish. During the switch to piscivory, predation by abundant YOY largemouth bass may quickly reduce the few bluegill migrating inshore (i.e., declining numbers of bluegill per largemouth bass in experiments), intensifying the predicted negative effect of shad on YOY largemouth bass growth. Within 24 h of being stocked into 0.4-ha ponds, piscivorous YOY saugeye (*Stizostedion vitreum* × *S. canadense*; ~5 saugeye/m²) nearly eliminated fish prey (Stahl and Stein 1994), demonstrating that YOY piscivores can strongly affect their prey resources in a short time. Because YOY bluegill were only replaced once during cage experiments (after 14 d) rather than every 3 d as in pools and aquaria, bluegill densities likely declined to lower levels in cages before restocking than in pools or aquaria. Thus, prey depletion could have contributed to lower consumption and growth of YOY largemouth bass in cages relative to other experiments.

Conversely, if the density of YOY largemouth bass is low in shad-dominated systems, these piscivores might not reduce existing low bluegill densities-a scenario analogous to a treatment where the ratio of bluegill available to largemouth bass is high. Thus, if search time is unrelated to bluegill density, and largemouth bass density is low relative to YOY bluegill density, then YOY largemouth bass may grow moderately in

shad-dominated systems, thereby escaping the negative, indirect effects of shad. In addition, YOY shad may occasionally grow slowly during early spring, allowing a proportion of YOY largemouth bass to switch to shad and grow rapidly (Storck 1986, Adams and DeAngelis 1987). In a survey of five Ohio reservoirs across 3 yr, YOY shad grew slowly and contributed to rapid growth of YOY largemouth bass during only 1 yr in three reservoirs (i.e., 3/15 potential reservoir-years; R. A. Wright and J. E. Garvey, *unpublished data*), suggesting that these interactions are rare. Though we predict chronically slow growth and poor recruitment of YOY largemouth bass in shad-dominated systems, complex, variable factors may allow YOY largemouth to grow moderately and recruit during some years (Garvey and Stein, *in press*). Through these mechanisms, long-lived, iteroparous adult largemouth bass may occasionally produce successful cohorts that survive to reproductive age, allowing populations to persist in shad-dominated systems (i.e., the "storage effect," Warner and Chesson 1985).

Shad-free systems.—In systems where shad are rare or absent, YOY bluegill availability and sizes in the littoral can vary dramatically due to the influence of variable temperature, predation risk, and food availability on their growth and survival (Werner and Hall 1988, Olson 1996*a*). During years when YOY bluegill were scarce or grew sufficiently rapidly to exceed largemouth bass gapes, the switch to piscivory in YOY largemouth bass is delayed or prevented, resulting in slow growth in Michigan lakes (Olson 1996*a*). Patterns of density-dependent YOY largemouth bass growth during low-bluegill-density years should be similar to those predicted for shad-dominated systems. Even when YOY bluegill are extremely abundant, as they consistently were in Hargus Lake, factors such as handling constraints (Hoyle and Keast 1987), high structural heterogeneity (Savino and Stein 1982, Werner and Hall 1988, Gotceitas and Colgan 1989), bluegill antipredatory behavior (Savino and Stein 1982, 1989), and high turbidity (Gregory 1993, Miner and Stein 1996) can reduce the vulnerability of bluegill to YOY largemouth bass during the switch to piscivory (Garvey and Stein, *in press*). Indeed, across experiments, YOY largemouth bass only consumed 65% of their potential at >6 bluegill per largemouth bass, perhaps due to these limiting factors. In addition, though bluegill were abundant in some cages, vegetation was quite dense relative to that in other experiments, possibly leading to higher search times by YOY largemouth bass for YOY bluegill. Thus, in cages, abundant prey refuge together with prey depletion probably caused largemouth bass to consume fewer bluegill and grow slowly. Clearly, patterns of YOY largemouth bass growth in systems without shad are complex and potentially difficult to predict, as demonstrated by our loss of resolution when testing hypotheses in field cages, where a high level of realism made it difficult to interpret factors influencing large-

mouth bass growth. Regardless of this variability, both our field pattern and our experiments suggest that YOY largemouth bass residing in these low-shad systems have a greater probability of exploiting YOY bluegill, growing rapidly, and surviving to reproduction than those in shad-dominated systems.

Management recommendations for reservoirs.— Events that occur during early spring in the limnetic zone are potentially linked with ontogenetic changes and perhaps with the recruitment of littoral largemouth bass, an important sport fish in reservoir ecosystems. By using our conceptual understanding of spatial and temporal food-web linkages to dictate management strategies for fishes, we have adopted a ''problem-solving'' approach (Parrish et al. 1995), attempting to solve the management problem of poor sport-fish recruitment with basic ecological principles. In systems such as Kokosing Lake where YOY shad are abundant and YOY bluegill rare, our results suggest that first-year growth and potential recruitment to harvestable sizes of largemouth bass may be moderate at best, relative to systems without shad. Because expected largemouth bass recruitment in shad-dominated systems is marginal, resource managers might focus on limnetic rather than littoral fish communities (Stein et al. 1996). For example, stocked pelagic hybrid piscivores such as saugeye (Stahl and Stein 1994, Donovan 1996) or hybrid striped bass (*Morone saxitilis* × *M. chrysops,* Dettmers et al. 1996) grow rapidly and can consume fast-growing shad (Stein et al. 1996). In these systems, littoral fish communities may produce few sport fish, but managers can compensate for this outcome by creating a successful alternative limnetic fishery, operating within the constraints of the ecosystem (Stein et al. 1996). Conversely, in systems where shad are rare, such as Hargus Lake, YOY bluegill should often be abundant, contributing to the piscivorous switch, rapid growth, and moderate to high recruitment to older life stages by YOY largemouth bass. Because the switch to piscivory by YOY largemouth bass depends on abiotic and biotic factors such as spring temperature, largemouth bass density, growth rates of littoral YOY bluegill, and structural complexity of the littoral zone, littoral fish communities can be managed by studying the extensive literature available in this arena (e.g., Swingle and Smith 1940, Dillard and Novinger 1975, Timmons et al. 1980, Werner et al. 1983*a, b*, Modde and Scalet 1985, Hambright et al. 1986, Turner and Mittelbach 1990, Olson et al. 1995, Olson 1996*a, b*) and developing a predictive framework for these systems.

Conclusions and future directions

In this study, we modify our conceptual model of reservoir food web dynamics and develop testable hypotheses by combining patterns from field surveys with experiments. Our work generally supports the prediction by Stein et al. (1995) that early events in the lim-

netic zone potentially influence littoral zone interactions later during the year. However, these interactions may vary in strength across reservoirs and years (Garvey and Stein, *in press*). Though YOY bluegill density declines with increasing shad density, we require more information about mechanisms influencing this variable negative relationship across years and systems. As has been demonstrated in the field, our experiments suggest that YOY largemouth bass increase their energetic intake and grow rapidly with increasing fish prey. Still, many factors such as temperature, prey growth rates, and structural heterogeneity affect YOY largemouth bass growth and potentially influence recruitment to adulthood or harvestable sizes in reservoir ecosystems. Clearly, more work, conducted across appropriate scales and through carefully designed, whole-reservoir management manipulations (i.e., adaptive management; Walters and Holling 1990, Lee 1993), is required to bound these variable interactions. Based on our current understanding of reservoir food webs derived from field patterns and experiments, we are developing testable predictions for fish community structure and, in our view, offering sound management recommendations for reservoirs.

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