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COMPETITION BETWEEN PREDATOR AND PREY: RESOURCE-BASED MECHANISMS AND IMPLICATIONS FOR STAGE-STRUCTURED DYNAMICS¹

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Abstract. In predator–prey interactions between size-structured populations, small (young) predators may compete with species that ultimately become their prey. We tested experimentally whether such competition occurs between young-of-year (YOY) largemouth bass and their eventual prey, bluegill. In a divided experimental pond, target densities of YOY bass and juvenile bluegill were subjected to different densities of bass and bluegill neighbors to examine the dependence of juvenile growth on fish density and species composition. After 7 wk, clear differences in growth rates of both species existed across densities. Bass growth was reduced in the presence of both bass and bluegill neighbors, whereas bluegill growth was primarily affected intraspecifically. Bluegill had strong competitive effects on bass despite substantial resource partitioning between the two species. These effects were mediated through changes in the size-structure of important invertebrate prey in both open water and vegetation habitats. Data collected from a set of seven lakes in Michigan indicate that interspecific competition between juvenile bluegill and YOY bass is an important process in natural populations. However, once bass become piscivorous, bluegill become a significant resource for bass. As a result, bass populations are split into two functionally distinct stages that respond differently across a gradient of bluegill density. Because of the competitive stage between predator and prey, dynamics of the interaction differ from predictions based on classical predator–prey or competition theory.

Key words: competition; *Lepomis macrochirus*; Michigan; *Micropterus salmoides*; ontogenetic niche shifts; predation; species interactions; stage-structure.

INTRODUCTION

The ontogeny of predators is typically marked by a succession of niche shifts and trophic level changes involving progressively larger prey (Werner and Gilliam 1984, Stein et al. 1988, Polis et al. 1989). When predator and prey are similar in size they may occupy the same trophic level, but as the predator grows it moves up to the next trophic level. Thus, the overall interaction between predator and prey is a potential mixture of competition and predation, and prey may have both a negative and a positive effect on their predator (Persson 1988, Polis et al. 1989). If competition is strong enough, a prey species can even impose a bottleneck on its predator, and restrict recruitment to the predatory stage (Werner 1977, Neill and Peacock 1980, Persson 1988). Bottlenecks may be quite common because prey densities are usually much higher than predator densities, and survivorship of predators

through early life history stages is sensitive to changes in growth rates (Werner and Gilliam 1984, Neill 1988). As a result, population dynamics of stage-structured predator–prey systems may be very different from the dynamics of simple, nonstructured systems.

Largemouth bass (*Micropterus salmoides*) and bluegill (*Lepomis macrochirus*) are two common fish species in lakes and ponds across much of eastern North America that potentially interact through both competitive and predatory stages. Young-of-year (YOY) bass initially pass through a stage in which they feed predominantly on invertebrates in the littoral zone (Applegate and Mullen 1966, Gilliam 1982, Olson, *in press*). Late in their first year, bass generally switch to piscivory and subsequently rely heavily on small bluegill and other fishes for food (Hackney 1975, Heidinger 1975, Keast 1985, Olson, *in press*).

Bluegill also undergo a series of ontogenetic niche shifts. Following a brief larval stage in which bluegill are primarily limnetic (Werner 1967, Werner and Hall 1988), small bluegill (20–75 mm standard length) are restricted by predators (often large bass) to the protection of littoral-zone vegetation, where they feed on a variety of benthic invertebrates (Mittelbach 1981a, Werner et al. 1983a, Turner and Mittelbach 1990). In

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TABLE 1. Initial and final fish numbers in the competition experiment. All sections received 50 target bluegill and 70 target bass initially. Number of neighbor bluegill stocked initially is listed under Neighbors; number of bluegill replaced in the first week to account for initial stocking mortality is listed under Replacements (TG BG = target bluegill, NB BG = neighbor bluegill). Final numbers are the number of fish recovered at the end of the experiment. Pond sections were numbered consecutively, starting with the southernmost section and moving clockwise.

Treatment	Section	Neighbors	Replacements	Final numbers		
				Bass	TG BG	NB BG
Target	3	None	None	9	29	0
	7	None	11 TB BG	11	32	0
Bass	1	+ 150 bass	8 TG BG	33	25	0
	5	+ 150 bass	14 TG BG	23	34	0
Low Bluegill	2	+ 150 BG	10 TG BG, 11 NB BG	15	27	117
	4	+ 150 BG	5 TG BG, 8 NB BG	10	33	121
High Bluegill	6	+ 750 BG	13 TG BG, 70 NB BG	8	29	659
	8	+ 750 BG	11 TG BG, 60 NB BG	5	21	652

southern Michigan lakes this littoral stage typically lasts 2–4 yr (Mittelbach 1984). Above 75 mm, bluegill are relatively invulnerable to predators and are able to feed in the open water on more energetically profitable zooplankton (Mittelbach 1984, Werner and Hall 1988, Mittelbach and Osenberg 1993). The nature of the interaction between bluegill and bass therefore depends on the life history stage. When bass and bluegill are both in their littoral invertebrate feeding stages, the two species overlap in both habitat and resource use and are potential competitors (Osenberg et al. 1995). However, the interaction changes to predator–prey when bass become sufficiently large to prey on small bluegill.

In this study, we examined the importance of stage-dependent interactions between largemouth bass and bluegill. The hypothesis that YOY bass and small bluegill compete was tested in an experimental pond in which densities of the two species were independently manipulated. In particular, we compared growth rate responses of both species across a range of densities to determine the strength and symmetry of the competitive interaction. To assess potential mechanisms of the interaction, we also quantified the size-structure, abundance, and composition of invertebrate prey. Finally, we used data collected from a series of small lakes to relate findings of our experiment to natural systems and to explore the implications of competitive and predatory stages for bass and bluegill dynamics. Patterns of growth and abundance were compared with predictions based on nonstructured models to determine if both competition and predation play an important role in the dynamics of bass and bluegill populations.

METHODS

Competition experiment

We used a target–neighbor design (sensu Goldberg and Werner 1983) to evaluate the competitive interaction between small bluegill and YOY bass. In this design, a constant density of “target” individuals (of

both bass and bluegill) was assigned to each experimental unit, and competitive environments (treatments) were created by adding predetermined densities of “neighbor” individuals. The experimental design had a total of four treatments (Table 1): target bass and bluegill with no additional neighbors (henceforth referred to as the Target treatment), targets plus 150 bass neighbors (Bass treatment), targets plus 150 bluegill neighbors (Low Bluegill treatment), and targets plus 750 bluegill neighbors (High Bluegill treatment). With this design (assuming no differential mortality; but see *Results*), the relative per capita effects of intra- and interspecific competition could be assessed by comparing growth in the Low Bluegill and Bass treatments (i.e., at the same neighbor density), and absolute effects of competition could be assessed by comparing each treatment with the Target treatment (see Spiller 1986 for a similar analysis). Because bluegill are, on average, 5 times (Range: 2.5–6.2) more abundant than bass in local lakes (M. Olson, *unpublished data*), population-level competitive effects could be assessed by comparing growth rates of targets in the High Bluegill and Bass treatments (which differed five-fold in neighbor density). The highest bluegill neighbor density was chosen, based on previous pond experiments, to yield competitive intensities and fish growth rates similar to those found in nearby, natural lakes.

The experiment was conducted in a circular pond (30 m diameter and 2 m deep) located at the Kellogg Biological Station (KBS), Michigan State University. The pond was ringed by a 1–1.5 m wide border of cattails (*Typha* spp.), beyond which a thick mat of *Chara* covered the pond bottom and left no bare patches. We divided the pond into eight pie-shaped sections (88 m² each) using partitions of nylon netting (3.2-mm mesh), suspended 30 cm above the water from cables anchored to shore and to a central post. Partition bottoms were attached to chain and buried into the sediment. Once deployed, the partitions were quickly colonized by periphyton and water flow between sections was minimal.

Juvenile bluegill were collected from nearby Crooked Lake, whereas YOY bass were collected from a brood pond on site. Bass ranged in size from 16 to 23 mm standard length (SL: as measured from snout to the tip of the caudal peduncle), averaged 19.3 ± 0.2 mm ($\bar{X} \pm 1$ SE), and represented a size range typical of YOY bass cohorts within local lakes. Potential bluegill competitors come from a wider size range (20–75 mm SL: Mittelbach 1981a, 1984), consisting of individuals feeding predominantly on vegetation-dwelling invertebrates. Neighbor bluegill used in the experiment encompassed much of this range (36–55 mm SL: $\bar{X} = 47.1 \pm 0.4$ mm SL), whereas target bluegill were chosen from a narrower, numerically dominant subset (31–41 mm SL; $\bar{X} = 36.5 \pm 0.2$ mm SL) to better characterize their growth response. Target bluegill were distinguished from neighbors by clipping the right pelvic fin of each target; target and neighbor bass were the same size and were not distinguished.

Initial stocking densities of bluegill and bass are summarized in Table 1. For both bluegill and bass we used a fairly large number of target individuals (50 and 70 individuals per section, respectively) because we anticipated losses due to natural mortality (with greater mortality expected for the smaller bass). Mortality due to fish predation (by bass on bluegill or vice versa) was extremely unlikely because neither species had a sufficient size advantage to consume the other (G. Mittelbach and M. Olson, *unpublished data*). Bass were added on 10 July 1992, neighbor bluegill on 11 July, and target bluegill on 12 July.

Initial mortality due to handling stress was evaluated by snorkeling through each section and walking around the pond edge each day for the 1st wk. Initial mortality was estimated at 18% for target bluegills and 8.3% for neighbors. Very few dead bass were observed (<1% of stocked density), but due to their small size, we probably found only a small fraction of the bass that had died. Target and neighbor bluegills that died and were recovered within the 1st wk were replaced with similar-sized fish collected from Crooked Lake on 17 and 20 July; no bass were replaced.

Mean sizes of bass and target bluegill were estimated two times during the course of the experiment. On 29 July (Day 17), each section was sampled with two seine hauls; all fish collected were identified, measured, and released. On 26 August (Day 45), each section was seined three times, and all fish collected were measured, weighed (to the nearest 0.01 g), and preserved in 10% neutral formalin for later diet analysis. Remaining fish were recovered over the next 2 d as the pond was drained, and final lengths and masses of all targets were recorded. Initial and intermediate masses were estimated by length–mass regressions based on final sizes. The regression for bass mass (M in grams) was $M = 0.000020(\text{SL}^{3.018})$, $r^2 = 0.99$, and for target bluegill was $M = 0.0000098(\text{SL}^{3.311})$, $r^2 = 0.96$.

Of the fish collected on 26 August, all bass and target

bluegill and 20 randomly selected neighbor bluegill were analyzed for stomach contents. Prey were identified to the lowest taxonomic level possible (typically to family or genus), enumerated, and measured (up to 20 haphazardly chosen individuals per prey category). All lengths were converted to dry masses using length–mass regressions (G. Mittelbach, *unpublished data*). Prey mass was used to characterize diets and to calculate diet overlaps.

To explore the effects of fish on their resources and determine how resource availability affected fish growth, we sampled invertebrates in the open water and vegetation habitats throughout the experiment. Zooplankton were sampled on four dates: 9 July (before fish were added), 19 July, 4 August, and 24 August (just before the experiment was terminated). On each date, three samples were collected from each section beginning $\frac{1}{2}$ h after sunset. Zooplankton were collected at a depth of 1.0 m using a 19-L Schindler-Patalas trap with an 80- μm mesh net, and were immediately preserved in cold 4% sucrose formalin. For each sample, zooplankton were identified to genus or species, counted in toto, and measured (up to 50 haphazardly chosen individuals). We used average densities and mean sizes of the three samples per pond section to yield one observation per replicate.

Vegetation-dwelling invertebrates were sampled from each section on three dates: 9 July (2 samples were taken per section before stocking fish), 27 July (3 samples per section) and 24–25 August (3 samples per section on each day). Samples were collected from the *Chara* vegetation by a diver using a modified Gerk-ing sampler (Mittelbach 1981b). Invertebrates were separated from vegetation by washing samples onto a 0.5-mm mesh sieve. All invertebrates retained on the sieve were then removed manually and preserved in 10% neutral formalin. Invertebrates were identified (typically to family or genus level), counted, and measured (up to 50 haphazardly chosen individuals per taxon). All samples from a given section on a given sampling date were pooled to estimate treatment effects.

To gain a more mechanistic understanding of how changes in density and size distribution of zooplankton and vegetation-dwelling invertebrates affected resource quality, we used a foraging model developed for bluegill to calculate predicted foraging rates (joules per second) in the open water and vegetation habitats (Mittelbach 1981a). Resources were summarized by dividing the size–density distribution of all cladocerans for the open-water and soft-bodied invertebrates in the vegetation into discrete size classes (10 size classes for zooplankton and six size classes for vegetation prey). The model then used size-specific encounter rates, handling times, and energetic contents to calculate the maximal foraging return for a bluegill of a given size. This model has been used numerous times in the past and has been successful in predicting growth rates in

natural and experimental populations of bluegill (Werner et al. 1983b, Mittelbach and Osenberg 1993, 1994). Detailed data needed to construct a similar foraging model for bass are not available; however, it is likely that small bass perceive habitats qualitatively in the same manner as bluegill, although exact values may differ.

Among-lake patterns

To examine the response of bass and bluegill to natural density variation among lakes, we estimated densities and growth rates of small and large bass and bluegill in a set of seven lakes within 30 km of KBS. These lakes are typical of small, hardwater lakes in the region and are similar in size (5–26 ha) and depth (10–16 m, except for Three Lakes III which is only 4 m deep; see Osenberg et al. 1988 for a description of the lakes). The fish communities in these lakes are dominated by fishes of the family Centrarchidae, particularly bluegill and bass, which are the two most abundant species in terms of biomass.

Bass were separated into two size classes to reflect differences in diet. Small bass were defined as the young-of-year cohort, and represented sizes in which bass fed predominantly on invertebrates (Olson, *in press*). Large bass were primarily piscivorous, and included all older age classes. Bass densities were quantified separately as catch-per-unit-effort (CPUE) for small bass (five lakes), and for large bass (seven lakes). CPUE's (numbers caught per seine) were estimated from an average of 32 ± 9 beach seines (23×1.8 m; 3.2-mm mesh) per lake taken from June through September 1990–1992 (there were no year effects: $F_{3,92} = 0.69$, $P > 0.10$ for small bass and $F_{2,56} = 0.99$, $P > 0.10$ for large bass). Densities of small bluegill (<75 mm SL) were also quantified as CPUE's in 1991.

Growth rates of small and large bass were back-calculated from scales of 1–5 yr old bass collected by seining and/or angling all seven lakes from 1990 to 1992. Bass were weighed (to the nearest gram) and measured (to the nearest millimetre of standard length), and five scales were taken just posterior to the depressed left pectoral fin. Impressions of these scales were made on acetate strips, and were projected with a microfiche reader. Distances from the focus to each annulus and scale edge were recorded from one non-regenerated scale per fish. Fish lengths at each age were back-calculated from these distances using the Fraser-Lee method (Tesch 1968) with an intercept of 16.5 mm SL (M. Olson, *unpublished data*). Lengths at age were converted to live mass using length–mass regressions developed for each lake (Olson 1993). Annual growth of YOY bass was estimated as mean mass at the end of their 1st yr for bass born between 1987 and 1990 (averages of each year, each based on an average of 19 fish, were averaged to get a single estimate per lake). Growth rates of large bass were estimated by first regressing natural log (change in mass through a year)

vs. natural log (mass at the start of that year) for each lake (average sample size = 105 bass per lake; year-to-year variation in growth rates was ignored). Growth rates were then standardized among lakes from these regressions using the mean size of a 3-yr-old bass (86 g).

RESULTS

Competition experiment

Fish growth and mortality.—There was significant mortality of both bluegill and bass during the experiment. In particular, only 14% of the stocked bass survived to the end of the experiment (Table 1), probably as a result of initial handling stress and predation by large invertebrates (e.g., *Anax*) while bass were small. Mortality of bass was density independent, and we recovered similar proportions of bass in all treatments ($F_{3,4} = 2.06$, $P > 0.10$). Recovery rates of bluegill were higher than bass. Assuming that survival rates of stocked and replacement bluegill were the same, 49% of the target bluegill and 79% of the neighbor bluegill survived to the end of the experiment. As was the case for bass, recovery rates of target bluegill were independent of density ($F_{3,4} = 0.54$, $P > 0.10$). Although mortality of bass and bluegill was higher than we expected, we could still assess competitive effects through comparisons of target growth rates among treatments because the mortality of each species was independent of density.

Increasing neighbor densities had strong negative effects on growth of both bass and bluegill. Initial bass sizes (mass) did not differ among treatments ($F_{3,4} = 3.39$, $P > 0.10$), but by the end of the experiment bass sizes were significantly different in all four treatments (Fig. 1A; $F_{3,4} = 278.60$, $P < 0.0001$). Bass growth was reduced through both intra- and interspecific competition. Strong intraspecific effects were also observed on bluegill growth and the final size of target bluegill was significantly lower at increasing bluegill densities (Fig. 1B; initial mass $F_{3,4} = 0.14$, $P > 0.10$, final mass: $F_{3,4} = 241.00$, $P < 0.0001$). Although final bluegill size appeared smaller in the Bass treatment compared with the Target treatment, the difference was not significant (Fig. 1B).

Low survivorship of bass made direct comparison of the relative strengths of intra- and interspecific competition problematic (i.e., neighbor densities in bass and low bluegill treatments were unequal by the end of the experiment). Therefore, as an alternative to ANOVA, we used a regression approach to express the predicted change in bluegill and bass growth as a function of bluegill or bass density (e.g., Goldberg and Werner 1983). Our first step was to develop empirical models that linearized the relationship between fish size and density. Using data from the six sections that varied in bluegill density (each replicate for the Target, Low Bluegill, and High Bluegill treatments), we first ex-

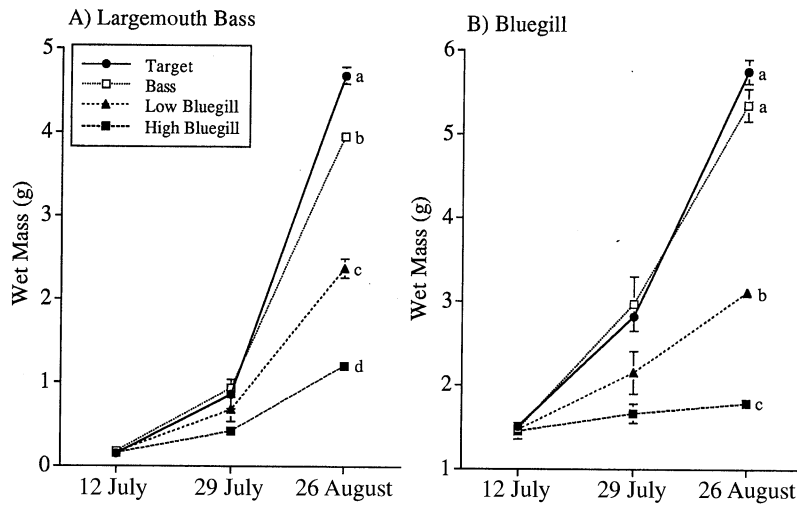


FIG. 1. Mean fish mass (± 1 SE) over time for bass (A) and target bluegill (B). Initial and intermediate masses were converted from standard length by regression; final mass was measured directly. For each species, different letters indicate mean final masses were significantly different ($P < 0.05$; Bonferroni T test).

examined the relationships of bluegill and bass growth with total bluegill density (targets and neighbors combined; target bass densities were ignored because they were similar in all six experimental units). Both log (final bass mass) and log (final bluegill mass) were linearly related to log (total bluegill density) across the three treatments (Fig. 2). These relationships, therefore, show the predicted effect of a change in bluegill density on bass and bluegill growth. If bass have the same per capita competitive effect as bluegill (i.e., bass and bluegill are equivalent competitors), then we would expect final bass and bluegill masses in the treatments with

added bass (Bass treatment) to fall along the regression lines in Fig. 2 (where "bluegill density" now represents the number of bluegill plus the number of neighbor bass in the treatment). If the points for this treatment lie above the line, then bass have less of a competitive effect than an equivalent density of bluegill; if the points fall below the line, then bass have stronger competitive effects. We estimated the number of "neighbor" bass as the difference between the number of bass recovered in each replicate of the Bass treatment and the mean in the other three treatments ($\bar{X} = 9.7$ bass).

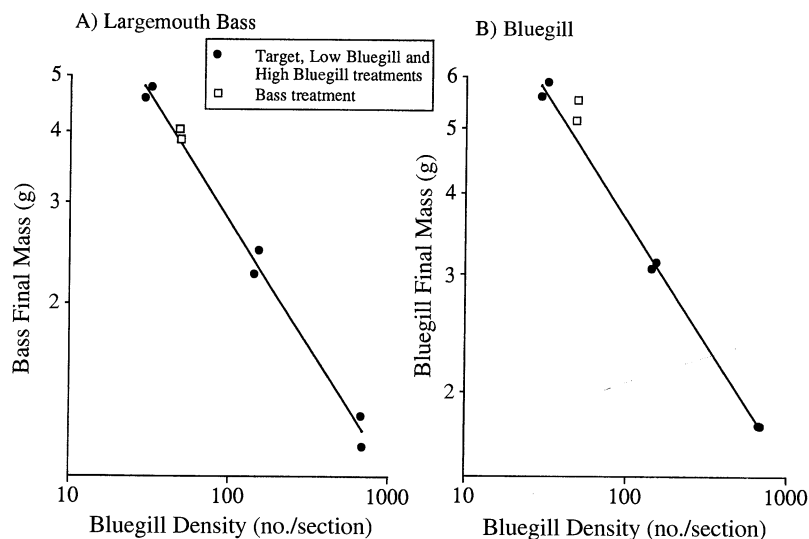


FIG. 2. Linear regressions of final masses of all bass (A) and target bluegill (B) vs. final bluegill density (targets and neighbors). Regression lines are based on six points from the target, Low Bluegill, and High Bluegill treatments: (A) Bass growth: $\log_{10} Y = 1.34 - 0.437(\log_{10} X)$, $r^2 = 0.990$, (B) Bluegill growth: $\log_{10} Y = 1.31 - 0.375(\log_{10} X)$, $r^2 = 0.996$. Open squares represent final masses in bass treatments as a function of bluegill and "neighbor" bass densities above the nominal target density of bass (9.7 bass/section).

TABLE 2. Taxonomic diet compositions of bass and bluegill at the end of the experiment. Numbers represent mean percent contribution by mass for all sections. Means for each section were based on an average sample size of 8 bass, 18 target bluegill, and 20 neighbor bluegill (the latter were collected only from Low and High Bluegill sections). Small cladocerans represent *Diaphanosoma* and *Ceriodaphnia*. Bass prey represent the combined totals of *Simocephalus*, dipteran pupae, and baetid, coenagrionid, aeschnid, and libellulid nymphs. Snails were represented by *Gyraulus parvus* and *Physa* spp.

Prey category	Bass	Target bluegill	Neighbor bluegill
	Mean \pm 1 SE	Mean \pm 1 SE	Mean \pm 1 SE
Bass prey	72.11 \pm 6.27	17.19 \pm 1.90	21.83 \pm 3.57
Calanoid copepods	15.18 \pm 6.09	5.69 \pm 2.73	1.53 \pm 1.01
Chironomids	4.14 \pm 1.14	52.15 \pm 3.58	47.20 \pm 2.17
Small cladocerans	2.10 \pm 0.69	10.01 \pm 2.97	6.15 \pm 1.47
Snails	0.00 \pm 0.00	0.50 \pm 0.21	1.05 \pm 0.27
Miscellaneous	6.56 \pm 1.34	14.69 \pm 3.54	22.33 \pm 3.69

Final bass sizes in bass treatments fell very near the line describing bluegill competitive effects (Fig. 2A), and cannot be distinguished as outliers ($P > 0.10$: Grubbs and Beck 1972 [cited in Gill 1978]), indicating that the effects of intra- and interspecific competition on bass growth were similar. For bluegill, interspecific competition had less of an effect than intraspecific competition because final masses in the presence of additional bass were clearly above the line (Fig. 2B; analysis of residuals indicates that both points are outliers from the regression at $P < 0.05$).

In our original design, we had planned to compare the magnitude of the population level effect of bluegill (vs. bass) on YOY bass growth by comparing bass growth in the High Bluegill treatment with bass growth in the Bass treatment. However, due to low survivorship of bass this comparison was no longer appropriate. Fortunately, we were still able to examine population level effects of bluegill using the Low Bluegill treatment (in this comparison final bluegill neighbor densities were $\approx 7\text{--}8\times$ higher than final bass neighbor densities). Bass growth was much lower in the Low Bluegill treatment compared to the Bass treatment (Fig. 1A), suggesting that the reduction in bass growth due to interspecific competition from the bluegill population relative to that from intraspecific competition among bass will be much stronger on a lake-wide basis.

Fish diets.—Across treatments, the percentage composition by mass of different prey taxa was very consistent for both bass and bluegill (Olson 1993). In contrast, there were marked changes in the sizes of prey consumed in the different treatments. When feeding in the open water, bass relied heavily on calanoid copepods (which made up 88% of their open-water prey by mass), whereas bluegill fed more on cladocerans (64% by mass for targets, 80% by mass for neighbors). Calanoid copepods were also consumed by bluegill, but at a much lower proportion (Table 2). In the vegetation, bass had relatively narrow diets. They utilized a total of 11 prey types, and of those, 6 were predominant. Insect nymphs (of the families Baetidae, Coenagrionidae, Aeschnidae, and Libellulidae), *Simocephalus*, and dipteran pupae together constituted 91% of the prey mass eaten by bass in this habitat. Bluegill had much

broader diets when feeding in vegetation, consuming 10 of the 11 prey types found in bass diets as well as six others. Chironomid larvae dominated bluegill diets, and no other prey taxa comprised $>10\%$ of the total prey mass. Only $\approx 20\%$ of bluegill diets came from the six categories that were most abundant in bass stomachs (Table 2: Bass prey).

As a result of these differences in prey use, dietary overlap, calculated by Schoener's index (1975), averaged only 0.32 ± 0.014 ($\bar{X} \pm 1$ SE) between bass and target bluegill and 0.29 ± 0.054 for bass and neighbor bluegill (target and neighbor bluegill had very similar diets: overlap, $\bar{x} = 0.81 \pm 0.035$). Diet overlaps did not vary among treatments (bass and target bluegill: $F_{3,4} = 0.16$, $P > 0.10$, bass and neighbor bluegill: $F_{1,3} = 2.92$, $P > 0.10$).

Resource dynamics—open water habitat.—To better understand how bluegill exerted a strong competitive effect on bass despite relatively little overlap in diet, we examined changes in prey abundance and size structure through time for both the open-water and vegetation habitats. Strong treatment effects were observed through time on invertebrates found in the open water (Fig. 3). Total densities of zooplankton diverged through time among treatments (initial densities: $F_{3,4} = 2.16$, $P > 0.10$; final densities: $F_{3,4} = 231.83$, $P < 0.0001$). By the end of the experiment, zooplankton densities were significantly lower in the High Bluegill treatment compared with the Low Bluegill treatment or with Target and Bass treatments (Fig. 3A; Bonferroni T test separated treatments into three groups at $P < 0.05$). Zooplankton densities also varied through time as a result of changes in species composition within the zooplankton community (Olson 1993). In general, large-bodied zooplankters (e.g., *Chaoborus* and *D. pulex*) were replaced by smaller bodied species (e.g., *Diaphanosoma* and *Ceriodaphnia*), leading to a decrease in mean zooplankton body size over time in all treatments (Fig. 3B). There was also a divergence in mean size among treatments (Fig. 3B; initial mean size: $F_{3,4} = 1.02$, $P > 0.10$, final mean size: $F_{3,4} = 94.94$, $P < 0.0005$), due in part to differences in mean size of the two dominant zooplankton taxa (Table 3).

Changes in the density and size-structure of zoo-

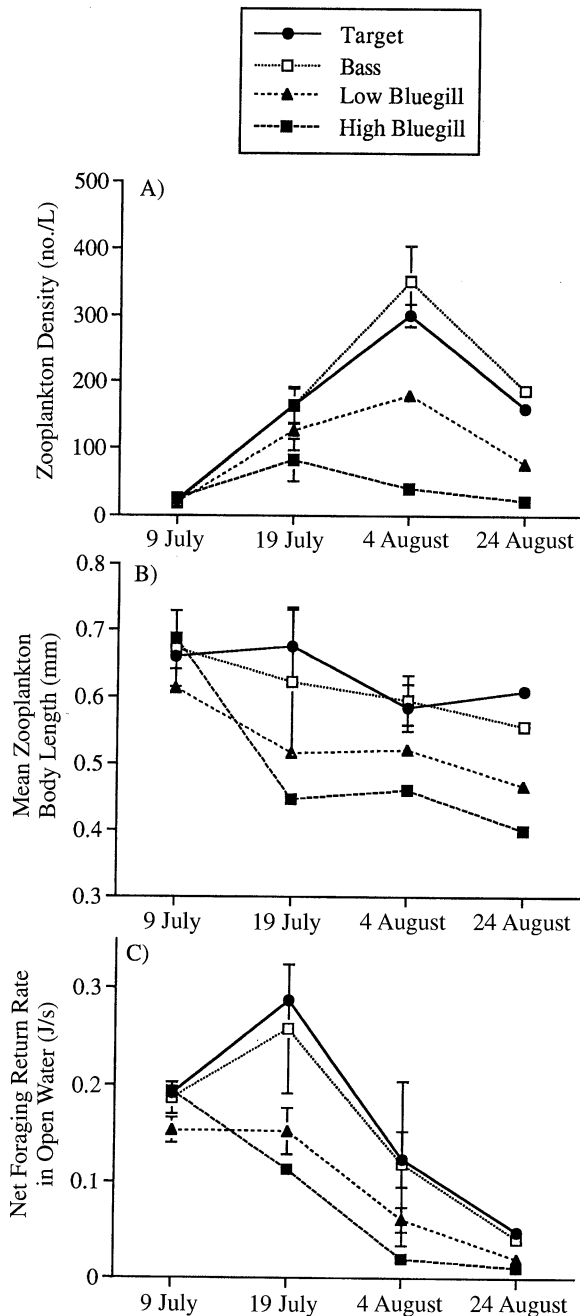


FIG. 3. Dynamics of the open water invertebrate community. (A) Mean zooplankton density (± 1 SE; $n = 2$) over time for all taxa combined. (B) Mean zooplankton body length (± 1 SE; $n = 2$) over time. Means are based on all zooplankton regardless of species identity. (C) Mean foraging return (± 1 SE; $n = 2$) over time for a bluegill feeding in the open water.

plankton had important effects on resource quality (i.e., energy gain). A foraging model developed for bluegill demonstrated a general decline in predicted foraging return rates in all treatments, and a divergence in foraging return rates among treatments (Fig. 3C; initial

foraging return rate: $F_{3,4} = 2.74$, $P > 0.10$, final foraging return rate: $F_{3,4} = 9.14$, $P < 0.03$). This decline was driven primarily by changes in zooplankton size; foraging return rates decreased in some cases even when zooplankton densities increased (e.g., compare density [Fig. 3A] and foraging returns from 19 July to 4 August). Bluegill therefore had a significant negative effect on the quality of their resource through time. Presumably, they had a similar effect on planktonic resources used by bass. For example, in addition to their effect on cladocerans, increasing bluegill density also led to a decrease in mean size of calanoid copepods, which were an important prey item in bass diets (Table 2).

The effects of a reduction in prey size were directly reflected in fish diets. Regression analyses of log (zooplankton size) found in bass and target bluegill stomachs vs. log (bluegill density) indicated that bass and bluegill always fed on the largest zooplankton available, and zooplankton size in the diet decreased across the gradient in bluegill density (Fig. 4). As also observed for growth rates, per capita impacts of bluegill predation on zooplankton size structure were not constant, but were strongest at low density and decreased as density increased.

Resource dynamics—vegetation habitat.—In addition to their impact on zooplankton, fish also affected invertebrates associated with the vegetation. These effects were limited to soft-bodied prey; bluegill had no observable effect on either density or mean size of snails (density: $F_{3,4} = 1.46$, $P > 0.10$; size: $F_{3,4} = 1.17$, $P > 0.10$). Therefore, all subsequent analyses on vegetation-dwelling prey were restricted to soft-bodied invertebrates.

Treatment effects on vegetation-dwelling invertebrates were observed primarily through changes in prey size-structure; fish had little effect on prey density (Fig. 5A; initial density: $F_{3,4} = 1.37$, $P > 0.10$, final density $F_{3,4} = 1.91$, $P > 0.10$; see Olson 1993 for responses by individual taxa). Invertebrate body lengths decreased over time, and also diverged among treatments (Fig. 5B; initial mean length: $F_{3,4} = 0.25$, $P > 0.10$, final mean length $F_{3,4} = 14.07$, $P < 0.02$). When the experiment ended, prey were smallest in the Low and High Bluegill treatments, and largest in the Target and Bass treatments (Fig. 5B; Bonferroni T test separated treatments into two groups at $P < 0.05$). These differences were driven by changes in the abundance of large prey. Invertebrates > 6.0 mm in length were significantly less abundant in Low and High Bluegill treatments compared with Target and Bass treatments ($F_{3,4} = 9.77$, $P < 0.03$; Bonferroni T test separated treatments into two groups at $P < 0.05$), creating a truncated size-frequency distribution and thus a lower mean. Many different prey taxa contributed to this result. *Simoecephalus*, baetid nymphs, and larval leptocerids, tanypodids, and chironomids were all smaller in treatments with bluegill neighbors (Table 3). The reduction

TABLE 3. Final mean body lengths in millimetres (± 1 SE; $n = 2$) of the major zooplankton and littoral invertebrate taxa that showed significant treatment effects (small-bodied cladocerans: $F_{3,4} = 41.40$, $P < 0.002$; calanoid copepods: $F_{3,4} = 34.54$, $P < 0.003$; baetid nymphs: $F_{3,4} = 8.61$, $P < 0.05$; leptocerid larvae: $F_{3,4} = 7.27$, $P < 0.05$; tanypodid larvae: $F_{3,4} = 9.23$, $P < 0.05$; *Simocephalus*: $F_{3,4} = 41.47$, $P < 0.05$, and chironomid larvae which were marginally significant: $F_{3,4} = 5.52$, $P < 0.07$).

Prey type	Target	Bass	Low bluegill	High bluegill
	Mean ± 1 SE	Mean ± 1 SE	Mean ± 1 SE	Mean ± 1 SE
Zooplankton				
Small cladocerans	0.54 \pm 0.002	0.55 \pm 0.02	0.48 \pm 0.003	0.47 \pm 0.003
Calanoid copepods	0.94 \pm 0.04	0.89 \pm 0.02	0.66 \pm 0.02	0.63 \pm 0.03
Littoral invertebrates				
<i>Simocephalus</i>	1.88 \pm 0.05	1.93 \pm 0.01	1.76 \pm 0.03	1.49 \pm 0.03
Baetid nymphs	3.30 \pm 0.18	3.32 \pm 0.02	3.12 \pm 0.02	2.73 \pm 0.02
Leptocerid larvae	3.75 \pm 0.05	3.61 \pm 0.15	3.19 \pm 0.23	2.89 \pm 0.09
Tanypodid larvae	5.37 \pm 0.16	5.10 \pm 0.09	4.60 \pm 0.27	4.23 \pm 0.06
Chironomid larvae	8.38 \pm 0.21	8.38 \pm 0.52	7.01 \pm 0.44	6.71 \pm 0.25

in prey size in Low and High Bluegill treatments resulted in a lower predicted foraging return available to bluegill in the vegetation habitat as the experiment progressed (Fig. 5C; initial foraging return rate: $F_{3,4} = 2.74$, $P > 0.10$, final foraging return rate: $F_{3,4} = 9.76$, $P < 0.03$).

When available prey sizes decreased, there was a corresponding reduction in the sizes of prey eaten by bass and bluegill. Mean body lengths of littoral invertebrates in the stomachs of both species declined across the gradient of bluegill density (Fig. 6A). Diet analyses also showed that bluegill ate larger littoral prey than

bass, and that bass fed on the same-sized prey as in the environment (Fig. 6A). However, bass fed on only a subset of available prey types, and for these prey the pattern of size selection was very different. For those prey groups accounting for 90% of bass diets in the littoral zone (Table 2), sizes also decreased with bluegill density ($F_{3,4} = 53.53$, $P < 0.0001$); however, bass consumed prey larger than in the environment or in bluegill stomachs (Fig. 6B). Bluegill fed on prey that were smaller than or equal in size to those in the environment (Fig. 6B), but were still able to reduce overall prey size-structure.

Field patterns in bass and bluegill

As would be expected if the two species fed on a common resource when small, annual growth of YOY bass (i.e., size at age one) and small bluegill growth (expressed as yearly change in mass [grams per year]: see Mittelbach and Osenberg 1993) were positively correlated across a series of local lakes ($r = 0.93$, $n = 7$, $P < 0.003$). Furthermore, bass size at age 1 declined with small bluegill density (Fig. 7A: $r = -0.92$, $n = 7$, $P < 0.005$). These effects were observed despite the fact that diet overlaps in natural populations of bass and bluegill were slightly lower than observed in the pond experiment (overlaps by Schoener's index [1975] averaged 0.30 in the experiment and about 0.20 in the lakes).

Although an increase in density of small bluegill was negatively correlated with YOY bass growth, large piscivorous bass grew better in lakes with more abundant bluegill (Fig. 7B: $r = 0.90$, $n = 7$, $P < 0.005$). This resulted in a negative correlation between the growth rates of small and large bass ($r = -0.93$, $n = 7$, $P < 0.003$) and contrasting patterns of growth and density for the two stages (Fig. 7C and D). Bass size at age 1 was negatively correlated with density of YOY bass (Fig. 7C: $r = -0.95$, $n = 5$, $P < 0.01$), whereas growth of large bass was positively correlated with the density of large bass (Fig. 7D: $r = 0.87$, $n = 7$, $P < 0.02$).

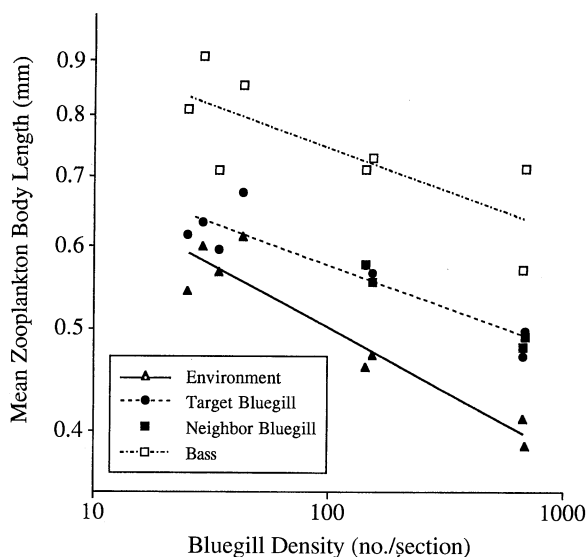


FIG. 4. Mean body length of zooplankton consumed by bass, target bluegill, or available in the environment on the last date, as a function of bluegill density. Mean prey sizes of neighbor bluegill are included on the figure but were not used to calculate regressions. All three regressions are significant ($P < 0.05$: environment: $\log_{10} Y = -0.058 - 0.121(\log_{10} X)$, $r^2 = 0.90$; bass: $\log_{10} Y = 0.034 - 0.081(\log_{10} X)$, $r^2 = 0.588$; target bluegill: $\log_{10} Y = -0.077 - 0.081(\log_{10} X)$, $r^2 = 0.837$).

This pattern of negative density dependence in the early life stage, but positive density dependence in the later life stage, is consistent with a mixed competition/predation interaction between stage-structured species.

DISCUSSION

Competition between predator and prey

Ontogenetic niche shifts in diet and/or habitat use of a species can dramatically change the nature of its interactions with other species. This study and its companion paper (Olson, *in press*) document how the interaction between largemouth bass and bluegill changes from competition to predation as bass grow in size (see also Gilliam 1982). The timing of the bass' ontogenetic shift from feeding on invertebrates to feeding on fish is very dynamic in natural lakes and has important consequences for the bass/bluegill interaction. For example, if competition between juvenile bluegill and YOY bass is weak and bass grow well on invertebrates, they quickly become large enough to be piscivorous, and their diet shifts from invertebrates to almost exclusively YOY fish (Olson, *in press*). Thus, the competitive stage ends quickly, and leads to an early shift to piscivory that further enhances growth rates (Olson, *in press*). However, if competition with bluegill is strong, it can reduce growth rates to a point where bass are not large enough to consume fish. Competition with bluegill will continue and may even be intensified by the arrival of YOY bluegill into the littoral zone. In this case, competition prolongs the duration of the invertebrate-feeding stage and, as a result, bass are smaller at the end of the growing season and may show reduced over-winter survival (Davies et al. 1982, Gutreuter and Anderson 1985).

Piscivory was not possible in our pond experiment (i.e., YOY bluegill were not present), and bass fed on invertebrates for the entire experiment regardless of their size. Therefore, competitive effects of bluegill were probably underestimated because the invertebrate-feeding stage lasted the same length of time in all treatments. If the larger bass in low-density treatments had been allowed to shift to piscivory, competitive effects of bluegill on bass growth may have been even more pronounced.

Bluegill had strong competitive effects on themselves and bass through their impacts on invertebrates in both open water and vegetation habitats. This was driven primarily by changes in invertebrate size (particularly in the vegetation where bluegill had no observable effect on overall invertebrate densities). Prey size is an important determinant of resource quality for fish (Paloheimo and Dickie 1966, Mittelbach and Osenberg 1993), and the major effect of bluegill in the pond experiment was to reduce the abundance of the largest, most profitable invertebrates.

Our experiment also suggested that competition between juvenile bluegill and YOY bass was asymmetric.

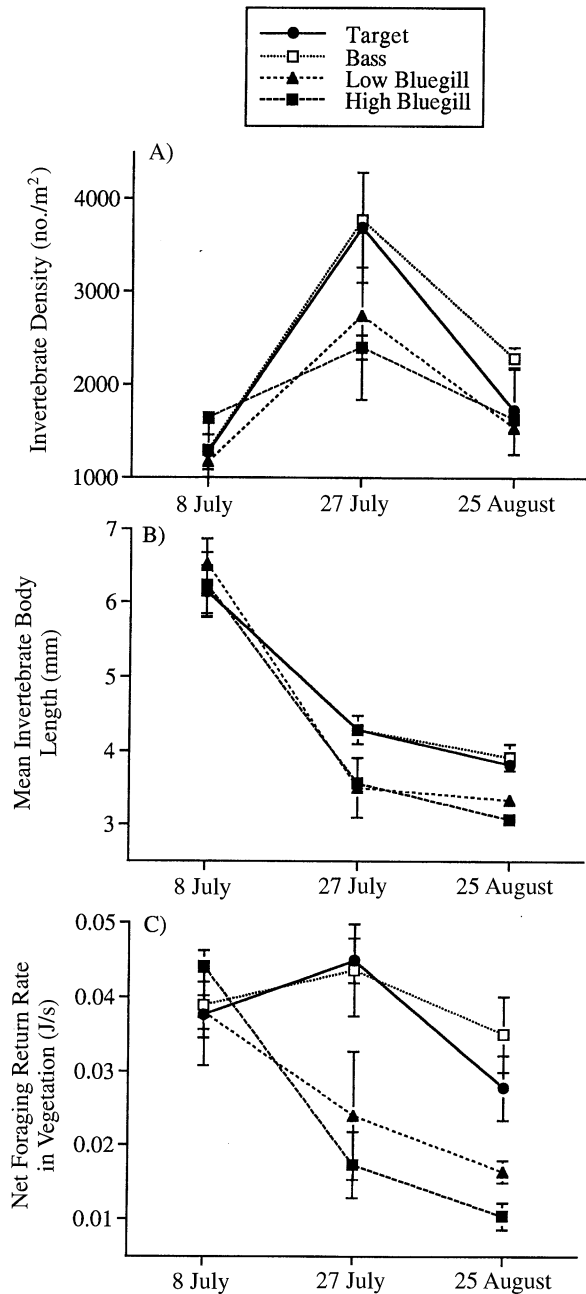


FIG. 5. Dynamics of the soft-bodied littoral invertebrate community. (A) Mean density (± 1 SE; $n = 2$) of all taxa combined. (B) Changes in mean body length (± 1 SE; $n = 2$) of all taxa combined. (C) Mean foraging rates (± 1 SE; $n = 2$) over time for a bluegill feeding in the littoral zone.

For fish sizes used in the experiment, bass and bluegill had similar effects on bass, whereas bass had a weaker effect on bluegill than bluegill had on themselves. One explanation for the observed asymmetry is that bluegill were competitively superior by virtue of their larger initial size. If bass and bluegill of similar sizes had been used in the experiment, then perhaps the inter-

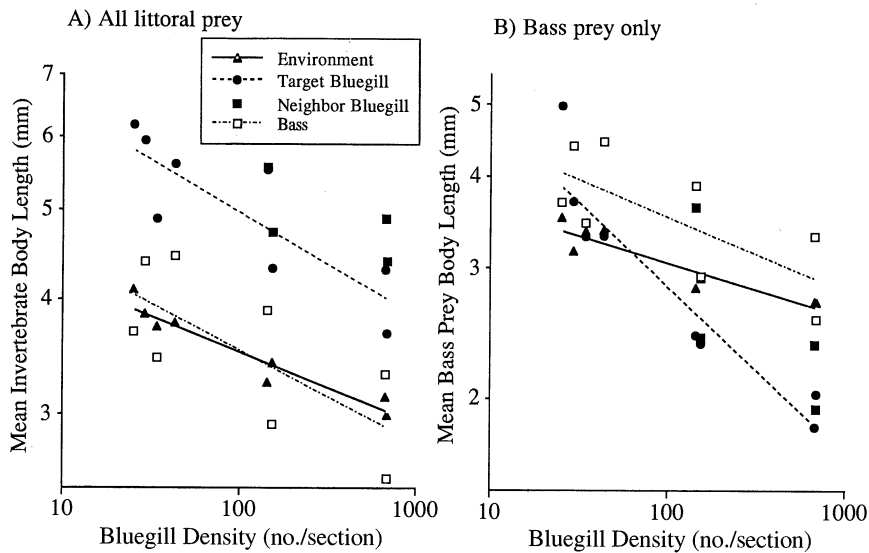


FIG. 6. Mean sizes of littoral prey consumed by bass, target bluegill, or available in the environment on the last date, as a function of bluegill density. Mean prey sizes of neighbor bluegill are included on the figure but were not used to calculate regressions. (A) All invertebrate taxa. All three regressions are significant ($P < 0.05$: environment: $\log_{10}Y = 0.698 - 0.077(\log_{10}X)$, $r^2 = 0.92$; bass: $\log_{10}Y = 0.747 - 0.100(\log_{10}X)$, $r^2 = 0.53$; bluegill: $\log_{10}Y = 0.921 - 0.112(\log_{10}X)$, $r^2 = 0.72$). (B) Bass prey only (*Simocephalus*, dipteran pupae, baetid nymphs, coenagrionid nymphs, libellulid nymphs, and aeschnid nymphs). All regressions are significant ($P < 0.05$: environment: $\log_{10}Y = 0.630 - 0.073(\log_{10}X)$, $r^2 = 0.89$; bass: $\log_{10}Y = 0.747 - 0.100(\log_{10}X)$, $r^2 = 0.53$; bluegill: $\log_{10}Y = 0.905 - 0.226(\log_{10}X)$, $r^2 = 0.87$.)

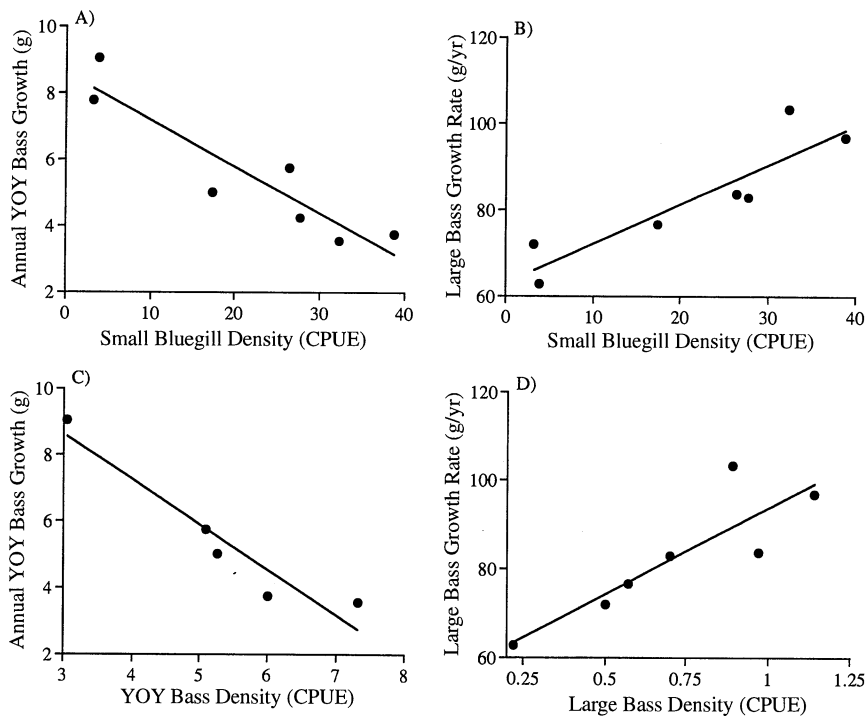


FIG. 7. Bass growth rates in natural populations as a function of bluegill and bass densities. (A) Annual growth of young-of-year (YOY) bass vs. small bluegill density. (B) Large bass growth vs. small bluegill density. (C) Annual growth of YOY bass vs. YOY bass density. (D) Large bass growth vs. large bass density. CPUE = catch-per-unit-effort.

action would have been more symmetrical. However, bass and bluegill of similar size do not consume similar resources; bass only feed on invertebrates when they are small (Applegate and Mullen 1966, Heidinger 1975). Consequently, diet overlap and thus potential for competition is highest between smaller bass and larger bluegill. Our experiment used bass and bluegill of different sizes to reflect the likely competitive interaction in natural systems, and under these conditions competition was asymmetric.

The observed asymmetry in bass and bluegill competition is consistent with model predictions of Polis et al. (1989) for mixed competition/predation interactions (which they term intra-guild predation). In their model, asymmetry is required for the coexistence of predator and prey, assuming the predator can survive on the shared resource (which bass can do: Hodgson and Kitchell 1987). Otherwise, prey will be excluded by the dual forces of competition and predation. This model, however, does not include stage-structure in the prey population, and other models have demonstrated that stage-structure can stabilize otherwise unstable interactions (Mittelbach and Chesson 1987, Murdoch et al. 1987).

Asymmetric competition between predator and prey is also predicted from laboratory feeding performance studies (between bass and bluegill: Werner 1977; between Eurasian perch (*Perca fluviatilis*) and roach (*Rutilus rutilus*): Persson 1987, 1988). These studies suggest that fish face a morphological trade-off in feeding on prey that are large or small relative to their own body size. Because piscivores spend much of their lives feeding on relatively large prey (up to half their own body length: Timmons et al. 1980), young (i.e., small) piscivores are not morphologically adapted for capturing small prey. Prey fish (like bluegill or roach) differ in that they feed from a narrower range of relative prey sizes through their ontogeny, and thus can be morphologically adapted to this prey, making them much more efficient than their predator. Based on these differences in efficiency, bluegill are predicted to be superior competitors to bass (Werner 1977).

Limitations set by bass morphology may restrict their diets to a subset of available prey in the invertebrate community. In this experiment, bass fed on fewer types of prey than bluegill, and tended to specialize on a smaller number of prey taxa (e.g., calanoid copepods, *Simocephalus*, ephemeropteran and odonate nymphs). These are generally active, mobile prey for which the bass morphology is well suited (Werner 1977, Wine-miller and Taylor 1987). Interestingly, on this subset of prey, bass appear to be more effective than bluegill. Bass ate larger prey than bluegill in all treatments, and there is evidence to suggest that encounter rates on one of these prey (baetid nymphs) are higher for bass than bluegill (Gilliam 1982). Bluegill use a slower, more deliberate foraging strategy than bass (Mittelbach

1981a, Gilliam 1982), and thus may be less effective at feeding on elusive prey.

Therefore, the mechanism of competitive asymmetry between juvenile bass and bluegill is not the same as predicted by Werner (1977). Rather than being driven by differences in efficiency when feeding on shared prey, asymmetric competition appears to be the result of differences in diet (niche) overlap (Colwell and Fuentes 1975). The bass niche is included within the bluegill's; almost all of the prey types found in bass diets were also found in bluegill, whereas only 20% of bluegill prey by mass came from those categories important to bass. Bluegill, on the other hand, have many prey types (e.g. chironomids, leptocerids, tanypodids) that are rarely or never consumed by bass. Thus, even if bluegill and bass share preferences for the same prey (sensu Rosenzweig 1991) a wide variety of other prey taxa offer bluegill a competitive refuge. Chironomids are especially important because they are the dominant prey type in bluegill diets and are one of the most abundant invertebrate taxa in the littoral zone (Mittelbach 1981b). Asymmetric competition also occurs between bluegill and congeneric green sunfish (*Lepomis cyanellus*) through a mechanism analogous to the one we propose for the bass-bluegill system (Werner and Hall 1977, 1979).

Even though bluegill fed on smaller shared prey than bass, they still had strong impacts on the size-structure of these invertebrates. In this regard, bluegill can be viewed as "effect competitors" (Goldberg 1990). Through the occasional consumption of large prey, or by eating prey while prey are small and preventing their recruitment to larger sizes (see Taylor 1980, Barry and Tegner 1990), bluegill reduce the abundance of large prey for bass. Unlike bluegill, bass had very little effect on invertebrate size-structure, particularly on invertebrates important to bluegill. Mittelbach (1988) also found that bluegill were strong effect competitors on other centrarchids, mediated primarily through their impact on the abundance of large prey.

Consequences for stage-structured dynamics

Our experiment demonstrated the mechanisms of resource-based competition between juvenile bluegill and YOY bass and suggested that in natural systems interspecific competition with bluegill can potentially have strong effects on YOY bass growth. Data collected from the lake survey supports this prediction: bass size at the end of their 1st yr showed a striking decline across a gradient in small bluegill density. In addition, growth rates of YOY bass and small bluegill were positively correlated, suggesting a similar response to a gradient in resources. An alternative explanation for the among-lake variation in growth of YOY bass is that the intensity of intraspecific competition varies among lakes. For example, because bass and bluegill densities are positively correlated ($r =$

0.91, $n = 5$, $P < 0.05$), growth of YOY bass is negatively correlated with YOY bass density (Fig. 7C). Thus, the influences of intraspecific and interspecific competition are confounded in the lake survey. However, the results of the competition experiment indicate that the among-lake variation in growth of YOY bass is better explained by interspecific competition with bluegill rather than intraspecific competition among bass, due to the greater density of bluegill and the equivalent per capita effects of bass and bluegill (Fig. 2A).

Contrary to the effect of bluegill on small bass, growth rates of large bass were greatest in lakes with high densities of small bluegill, consistent with observations that bluegill are important prey in large bass diets (Swingle and Smith 1940, Dillard and Novinger 1975). Therefore, bass populations are split into two stages that respond very differently to changes in bluegill abundance (see Osenberg et al. 1992 for a related example involving competition between bluegill and pumpkinseed sunfish).

Bluegill populations, like bass, are also stage-structured; small bluegill feed on invertebrates in the littoral zone, whereas large bluegill (>75 mm SL) feed on zooplankton in the open water (Mittelbach 1981a, 1984). Variation in bluegill growth and density among lakes appears to be driven by variation in zooplankton productivity (Mittelbach and Osenberg 1993, Osenberg et al. 1994); lakes with higher zooplankton productivity have higher densities of both small and large bluegill. An increased density of small bluegill intensifies competition for littoral invertebrates, which lowers growth rates of YOY bass (and small bluegill) and delays the bass' shift to piscivory (Olson, *in press*). Because over-winter mortality is size-dependent (Davies et al. 1982, Gutreuter and Anderson 1985), increased competition can potentially limit per capita recruitment rates of bass to the piscivorous stage. This potential cost is countered by the enhanced growth of large bass, which feed on small bluegill. An increase in large bass growth is predicted to result in increased production rates of bass, because fecundity is strongly correlated with size in fish (Carlander 1977, Bagenal 1978). Large bass densities increase with increasing bluegill density (Olson 1993), suggesting that the stock-recruitment curve is monotonic (Mittelbach and Chesson 1987). However, if the bass' density response is dampened by a recruitment bottleneck in the invertebrate feeding stage, densities would only partially respond to the increase in bluegill density.

In our study lakes, both bass and bluegill show stage-structured responses consistent with an increase in the productivity of the second stage's resource (zooplankton for bluegill and young bluegill for bass). This increase enhances growth and fecundity of adults, which leads to increased interspecific competition between bass and bluegill in the first stage. As a result, growth rates of small bass decrease. The divergent responses

between stages generate patterns that are very different from non-structured populations. Decreased recruitment rates (a result of lower growth and higher mortality in the first stage) weaken the coupling between the numerical response of large fish and their resources. Instead, densities partially respond, and bass and bluegill both show the unusual pattern of a positive correlation between growth and density in the second stage. Furthermore, decreased recruitment dampens a consumer's impact on its resource and as a result, overall densities (and biomasses) of bass and bluegill increase in parallel.

Positive correlations in biomass of adjacent trophic levels differ from predicted patterns for simple non-structured food chains. If populations have no size- or stage-structure, a model developed by Oksanen et al. (1981) predicts that increases in productivity result in increases only in alternate trophic levels (starting with the top level), and no correlation in biomass of adjacent trophic levels. In the bass-bluegill system, however, increased productivity intensifies competition between small bass and bluegill and prevents a complete response in density of the top trophic level (i.e., bass). Bass biomass does increase, but not enough to prevent bluegill from increasing as well. This is an expected result when predator death rates increase (e.g., via decreased recruitment rates imposed by juvenile bottlenecks) across a gradient in productivity (McCauley et al. 1988, Mittelbach et al. 1988). Stage-structure in bluegill also generates a positive correlation between bluegill and zooplankton biomass (expressed as a predicted foraging return rate: Mittelbach et al. 1988, Mittelbach and Osenberg 1993). As a result, three adjacent trophic levels show increased biomasses across a gradient in productivity.

Positive correlations in biomass are not an automatic result of a competitive stage between adjacent trophic levels, however. If the negative effect of competition is stronger than the positive effect of predation, a negative correlation would be expected. Negative correlations have been found between biomasses of roach and their predator, Eurasian perch, in Scandinavian lakes (Persson et al. 1988, 1992). Roach compete with small perch directly for zooplankton and also have an indirect negative effect by intensifying competition between small and larger perch (Persson 1987, Persson and Greenberg 1990). With increasing lake productivity, roach become more abundant and their negative effect on perch imposes a severe bottleneck on recruitment that actually reduces the number of piscivorous perch. As a consequence, overall perch biomass decreases with increasing productivity. One reason the negative effect outweighs the positive effect is that perch spend several years in the invertebrate feeding stage before they are large enough to switch to piscivory. Bass differ from perch in that they are piscivorous after their 1st yr (if not sooner). Because most of their lives are spent as predators, it is not surprising that the

net effect of bluegill is positive. Nevertheless, in both systems, stage-structure and juvenile competition play a critical role in generating patterns that are very different from predator-prey systems that lack population structure.

Recognition of the importance of body size can dramatically alter the way we view species interactions (Murdoch et al. 1987, Osenberg et al. 1992, 1994, Murdoch 1994). In the bass-bluegill system, size-dependent processes play a major role in creating stage structure and determining patterns of growth and abundance of both species. Therefore, within a system that has been classically thought of as a predator-prey interaction, the two species interact through a variety of processes that result in unexpected patterns of growth and density. These patterns, although not predicted by conventional models, can be understood by explicitly considering processes that operate within distinct life history stages. Because most populations are size- or stage-structured, with dynamics that are governed by stage-specific processes (Werner and Gilliam 1984, Nisbet et al. 1989), further advancements in the understanding of natural systems will require more explicit study of the way in which life history features and population structure influence dynamics of interacting species.

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