Competition Among Refuging Sunfishes and Effects of Fish Density on Littoral Zone Invertebrates

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COMPETITION AMONG REFUGING SUNFISHES AND EFFECTS OF FISH DENSITY ON LITTORAL ZONE INVERTEBRATES[1]

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Abstract. In small lakes, juvenile sunfishes (Centrarchidae) commonly occupy vegetated habitats, reducing the risk of predation by piscivorous fish. Eight species of sunfish coexist in Lawrence Lake, Michigan, and the bluegill greatly dominates the fish fauna in terms of numbers and biomass. I hypothesized that the bluegill's use of the vegetation as a predation refuge could have a significant negative effect on the growth rates of other species occupying this habitat. A "target-neighbor" experimental design was used to test this hypothesis. Twelve 3-m^2 cages were arrayed linearly along the vegetated littoral zone of Lawrence Lake in 1986. Two juvenile pumpkinseeds (the "target" species) were placed into each cage, together with either 0, 2, 4, 6, 8, or 10 juvenile bluegills. Bluegill densities were randomly assigned to cages; average bluegill density in Lawrence Lake is equivalent to $\approx$5 fish per cage. Growth in mass over a 50-d period was used as a measure of competitive effect. Benthic invertebrates were also sampled from each cage to determine whether fish density significantly affected invertebrate size and abundance and whether invertebrate availability influenced sunfish growth.

Growth of both pumpkinseeds and bluegills declined linearly as a function of final bluegill density in the cages, indicating that the species were competing while occupying the vegetation refuge. Growth was positively related to the density of large invertebrate prey remaining at the end of the experiment. Using an optimal foraging model, I estimated the net energy return available to bluegills in each cage. Predicted net energy gains (in joules per second of foraging time) were also positively related to bluegill growth, indicating that prey availability directly influenced growth rates. Mean invertebrate size decreased significantly as fish density increased, owing to a reduction in the number of large invertebrates; the number of small prey showed no relationship to fish density. These results are consistent with a hypothesis of exploitative competition between juvenile sunfishes and indicate that the behavioral avoidance of predators by small fish can have significant effects on invertebrate size and abundance in littoral habitats.

Key words: benthic; competition; habitat; Lepomis; *littoral; Michigan; Osteichthyes; predation risk; refuge.*

INTRODUCTION

Predators have two major effects on prey populations: (1) they kill and consume prey, and (2) they modify prey behaviors. Studies that have examined the impact of predators on the population dynamics and interactions of their prey have for the most part only considered the first effect. However, a rapidly expanding literature demonstrates that predators influence prey behaviors (and even morphologies) in ways that can affect the resource use and competitive interactions of the prey (e.g., Kerfoot and Sih 1987). Numerous studies have suggested that predator-induced habitat shifts may result in competition for refuges or competition for resources within a refuge (e.g., Garrity and Levings 1981, Mittelbach 1981*a*, 1984*a*, Sih 1982, Power 1984). However, there appear to be no direct experimental tests of this idea nor has anyone explored the population consequences of competition among refuging prey.

The fish communities of small lakes and ponds offer an excellent opportunity to examine how predator-mediated habitat use may affect prey populations. Mittelbach (1981*a*) and Werner et al. (1983*a*) have shown that piscivorous fish (largemouth bass, *Micropterus salmoides*) restrict the habitat use of small bluegills (*Lepomis macrochirus*); in the presence of bass, small bluegills remain in or near dense vegetation, whereas in the absence of bass they shift to feeding in open habitats. Additional studies have shown that prey resources are often limiting in the vegetation refuge and that juvenile sunfish of several species share a significant fraction of these resources in common (Mittelbach 1984*a*, 1986). Interspecific competition among juvenile fishes may thus be intensified due to the bluegill's (and perhaps

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other species') behavioral response to predators. Mittelbach and Chesson (1987) present analytical models illustrating how such predator-induced competition among juveniles can lead to negative correlations in species' adult densities, even when adults of different species consume completely different foods. These two-species, two-life-stage models for fish reveal a richness of competitive effects not seen in conventional competition models, and have a number of interesting analogies to recently published models of competition between holometabolous insects (Prout 1986).

A critical step in evaluating whether predator-mediated shifts in habitat use may affect prey interactions is to determine whether prey compete when restricted to a refuge. This paper presents the results of a field experiment designed to measure competition between juvenile bluegills and pumpkinseeds (*L. gibbosus*) occupying the vegetated littoral zone of a natural lake. To determine whether competition between the sunfishes was resource based, I also examined the effects of fish density on the size and abundance of their benthic invertebrate prey and the relationship between fish growth rates and prey availability. The literature on the impact of fish on benthic invertebrates in lakes is equivocal. Here it is shown that an increase in fish density significantly decreased mean invertebrate size, due to a decrease in the density of large invertebrates, and that fish growth rates were directly correlated with prey availability.

METHODS

The experiment was conducted in Lawrence Lake, a 4.9-ha marl lake in southwest Michigan. Eight species of sunfish co-occur in Lawrence Lake, with the bluegill greatly dominating the fish fauna in terms of numbers and biomass (Werner et al. 1977). I hypothesized that the bluegill's use of the vegetation as a predation refuge adversely affects the growth rates of other species occupying this habitat. A "target-neighbor" experimental approach (sensu Goldberg and Werner 1983) was used to test this hypothesis. In this design, a few "target" individuals of one species are subjected to a range in density of their "neighbor" species to evaluate competitive effects. The pumpkinseed was used as the target species because it commonly co-occurs with the bluegill (Scott and Crossman 1973), and when small (<75 mm standard length), pumpkinseeds and bluegills both occupy the vegetation and feed on similar prey (Keast 1978, Mittelbach 1984*a*). Larger pumpkinseeds and bluegills, however, show little diet overlap in small Michigan lakes, with the bluegill feeding extensively on zooplankton and the pumpkinseed specializing on snails (Mittelbach 1984*a*).

TABLE 1. Experimental design, showing numbers of bluegills placed (at random) into each of 12 cages containing two pumpkinseeds each.*

	Cage											
Species	1	2	3	4	5	6	7	8	9	10	11	12
Bluegill	8	4	2	4	10	6	10	6	0	0	8	2
Pumpkinseed	2	2	2	2	2	2	2	2	2	2	2	2

* All fish were lost during the experiment from cages 1 and 5; all pumpkinseeds were recovered from the other cages; number of marked bluegills recovered from the cages follow: cage 1, 0 bluegills; 2, 3; 3, 2; 4, 1; 5, 0; 6, 5; 7, 9; 8, 3; 9, 0; 10, 0; 11, 8; 12, 0. One unmarked bluegill (50 mm standard length) was recovered from cage 12 and was included in the final bluegill density.

The experiment was performed in 12 3-m^2 (1.7 × 1.7 m) cages arrayed linearly along the vegetated littoral zone of Lawrence Lake in $\approx$1.3 m of water. Cages were constructed of wood, enclosed on four sides by 0.1-mm mesh nylon netting buried in the sediment, and were without bottoms. Thin plastic bird netting (5-cm mesh) was placed over the top of each cage to eliminate possible predation by birds. Vegetation cover was continuous over the cage bottoms and was composed almost entirely of the bulrush *Scirpus subterminalis*, the predominant macrophyte in the lake (Rich et al. 1971). Each cage was stocked with two juvenile pumpkinseeds (mean length 52 mm; CV 5%), along with either 0, 2, 4, 6, 8, or 10 bluegills (mean length 49 mm; CV 4%) randomly assigned (Table 1). All fish lengths are reported as standard length, which is measured from the tip of the snout to the caudal terminus of the vertebral column. The average density of juvenile bluegills in the vegetated littoral of Lawrence Lake (based on seining estimates conducted in 1984 and 1985) is 1.6 fish/m^2; range 0.5–2.4 (= 4.8 fish per cage; range 1.5–7.2 fish). Juvenile pumpkinseeds are less abundant in Lawrence Lake, averaging the equivalent of $\approx$0.5 fish per cage. Two pumpkinseeds per cage were used in the experiment to allow for potential mortality and to provide a more accurate estimate of pumpkinseed growth. All experimental fish were marked with pelvic fin clips. Before adding fish, I attempted to remove all resident bluegills and pumpkinseeds by snorkeling in each cage and chasing the fish out through an open side. This method was quite effective for bluegills and pumpkinseeds (only four unmarked bluegills and pumpkinseeds were found at the end of the experiment, three of which were much smaller than the experimental fish). Other species, predominantly juvenile green sunfish (*Lepomis cyanellus*) and longear sunfish (*L. megalotis*), were not easily chased from the cages and occurred at approximately natural densities in the experiment (there were 2.3 ± 0.3 other fish per cage; $\bar{X} \pm 1$ SE).

The experiment was initiated on 9 July 1986 and terminated on 28 August 1986 by removing all fish from the cages with a net constructed from 0.6-cm mesh seine material attached to a 1.5 × 1.7 m metal frame which fit snugly inside the cages. The net could be operated by two people standing just outside the cages and each cage was seined repeatedly until no fish were collected in at least three successive hauls. Two

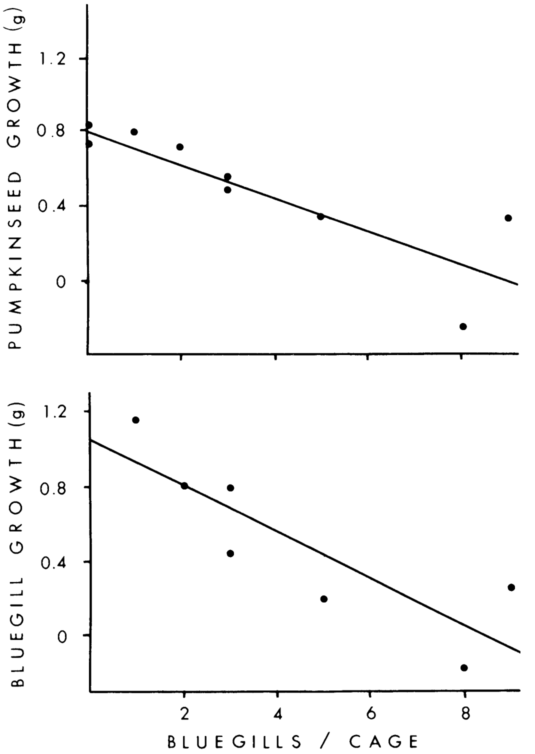

FIG. 1. Mean growth of bluegills and pumpkinseeds (grams live mass) over the 7 wk of the experiment, as functions of final bluegill densities in the experimental cages. Lines are least-squares linear regression: $Y = 0.80 - 0.09X$, $r^2 = 0.66$ for pumpkinseeds and $Y = 1.05 - 0.13X$, $r^2 = 0.73$ for bluegills. For both species the null hypothesis of a slope of 0 is rejected at $P < .01$.

cages (numbers 1 and 5, Table 1) were found to have holes in the netting at the end of the experiment and contained no bluegills or pumpkinseeds. In the other 10 cages, all of the original pumpkinseeds were recovered; bluegill recovery was 76% (averaged over all cages) and initial handling mortality probably accounted for most of the bluegills lost. Fish collected at the end of the experiment were examined for fin clips, measured for standard length, and weighed (wet mass). Growth in mass was used as a measure of competitive effect since considerable evidence indicates that fish growth rates are a good index of overall fitness (Werner 1986). Growth within a cage was calculated as the mean mass of bluegills or pumpkinseeds recovered at the end of the experiment minus their mean initial mass (initial masses determined by length-mass regressions).

If exploitative competition occurs between juvenile bluegills and pumpkinseeds, one would expect to find a negative relation between the density of fish in a cage and the density of invertebrate prey remaining at the end of the experiment. Also, one would expect a positive relation between the availability of prey in a cage and fish growth rates. To test for these relations, I sampled benthic invertebrates from the cages immediately before adding fish and immediately before removing them. Invertebrates were sampled by carefully climbing into each cage and taking two samples with a modified Gerking sampler (a 21.5-cm diameter Plexiglas cylinder with closing doors at the base and a Number 10 plankton net attached at the top; see Mittelbach 1981*b*, Merritt and Cummins 1984 for details of sampler design). The samples were gently washed into a series of three sieves (3.35-, 0.71-, and 0.25-mm mesh). Contents of the two largest sieves were sorted by hand and preserved in 10% formalin; contents of the smallest sieve were separated by using 20% $MgSO_4$ solution and preserved. Invertebrates were identified, counted, and measured under a dissecting microscope.

RESULTS

Density-dependent growth

Growth of both pumpkinseeds and bluegills declined linearly as a function of final bluegill density in the cages (Fig. 1), indicating that the concentration of juvenile bluegills in a vegetation refuge may lead to significant competition with other fishes. For both species, the null hypothesis of a regression slope of 0 is rejected at $P < .01$. Regression slopes do not differ between species (ANCOVA, $P > .20$), and within a cage, growth of bluegills and pumpkinseeds was significantly correlated ($r = 0.81$). In one of the cages (number 12), both of the original bluegills were missing at the end of the experiment. Therefore, the bluegill intraspecific regression is based on seven rather than the expected eight cages. Growth of pumpkinseeds in one cage (number 4) was clearly aberrant (mean growth -0.6 g, bluegill density = 1) and was eliminated as an outlier from the pumpkinseed regression (outlier test, $R_n = 2.76$, $\alpha = .01$; Tietjen et al. 1973, Draper and Smith 1980).

Multiple regressions were also conducted to examine whether the presence of other fishes within the cages significantly influenced the relations shown in Fig. 1. For the multiple regression of pumpkinseed growth as a function of bluegill density and the density of other sunfishes, bluegill density had a significant effect ($P < .05$) but the density of other fishes did not ($P > .50$). For the regression of bluegill growth as a function of bluegill density and the density of other sunfishes, the effect of bluegill density is not significant (although nearly so, $.07 > P > .05$) and the density of other fishes did not have a significant effect ($P > .20$). The lack of significant effects of other centrarchids on bluegill or pumpkinseed growth is probably a simple consequence of the nearly equal density of other fishes in all cages (range 1–5 fish, $\bar{X} = 2.3$).

If the observed competition between bluegills and pumpkinseeds is exploitative, one would expect to find the following relationships: (1) a negative effect of fish density on invertebrate size and/or abundance (i.e., prey depletion), and (2) a positive relationship between fish growth and prey availability (i.e., growth of sunfish is related to resources). Below, I first examine the effects of fish density on benthic invertebrates and then consider the relations between prey availability and fish growth rates.

Effects of fish on invertebrates

Sunfish are size-selective feeders (Werner and Hall 1974, 1977, Mittelbach 1981*a*, Werner et al. 1983*b*) and may be expected to affect the size of invertebrates present in a habitat. Earlier studies have shown that the average invertebrate size in ponds with bluegills is smaller than in ponds without fish (Hall et al. 1970, Crowder and Cooper 1982). To examine the impact of fish on the size of benthic invertebrates in Lawrence Lake, I calculated the mean lengths of all invertebrates sampled in the cases at the end of the experiment (excluding snails) and regressed these means against the number of bluegills and pumpkinseeds per cage. Snails were not included because most of the species and sizes of snails present were invulnerable to small bluegills and pumpkinseeds (Mittelbach 1984*a*). Because length–frequency distributions of invertebrates from each cage were distinctly lognormal, as has often been observed (Schoener and Janzen 1968, Werner 1977, Mittelbach 1981*b*), regressions were performed using both mean length and the mean of the log-transformed lengths. Fish density (X) had a significant negative effect on mean invertebrate length (Y) within a cage at the end of the experiment. The regression equation for mean invertebrate length (in millimetres) as a function of the number of bluegills and pumpkinseeds per cage is: $Y = 2.055 - 0.0431X$, $r^2 = 0.51$, H_0: slope = 0 rejected at $P < .01$. The equation for the mean of the log-transformed lengths is: $Y = 0.630 - 0.0269X$, $r^2 = 0.57$, H_0: slope = 0 rejected at $P < .01$. Invertebrate sizes at the beginning of the experiment (9 July) showed no relationship with fish density: $Y = 0.759 - 0.001X$, $r^2 = 0.01$, $P > .50$, for mean invertebrate length as a function of final fish density.

TABLE 2. Preference values (Manly/Chesson index) for Lawrence Lake bluegills feeding on vegetation-dwelling invertebrates. For both dates, preferences > .08 indicate positive selection for a given prey length.*

Mean prey length (mm)	22 May 1979	19 July 1979
	Preference	
0.5	.001	.003
1.5	.020	.018
2.5	.018	.004
3.5	.017	.015
4.5	.062	.050
5.5	0	.040
6.5	.073	.202
7.5	.055	.050
8.5	0	.202
9.5	.219	.050
10.5	.364	.202
>11.5	.171	.162

* Diet and prey data are from Mittelbach (1981*a*, Fig. 4b). Regression equations for preference as a function of prey length are: $Y = -0.050 + 0.022X$, $r^2 = 0.50$ for May and $Y = -0.018 + 0.017X$, $r^2 = 0.54$ for July. For both equations, the null hypothesis of a slope of 0 is rejected at $P < .01$.

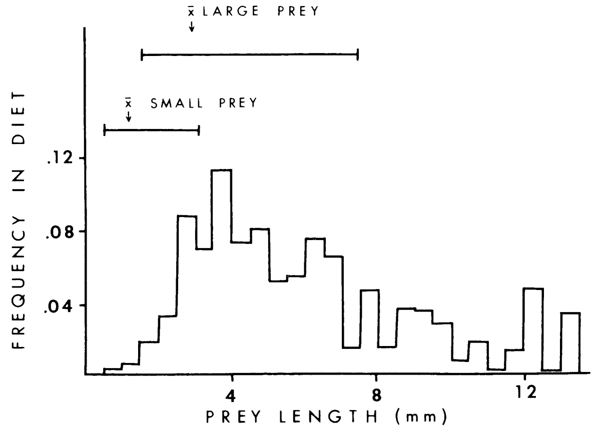

FIG. 2. Length distributions of prey found in the stomachs of 41 small bluegills and pumpkinseeds (50–75 mm standard length) collected from Lawrence Lake in May–August 1981. Symbols above the histogram indicate the mean and range of prey lengths sampled from the experimental cages in August 1986. Small prey were collected on a 0.25-mm mesh sieve and large prey on 0.71- and 3.35-mm mesh sieves.

To examine more closely the effect of fish density on invertebrate populations and the effect of invertebrate density on fish growth rate, it is crucial to know what prey types and sizes bluegills and pumpkinseeds actually consume. An earlier study of juvenile bluegill and pumpkinseed diets in Lawrence Lake (Mittelbach 1984*a* and unpublished data) showed that five taxa: Amphipoda, Chironomidae, Ephemeroptera, Trichoptera, and Zygoptera, together made up >90% of the average seasonal diets (by dry mass) of bluegills 50–75 mm feeding in the vegetation. Pumpkinseeds 50–75 mm had diets very similar to the bluegill except for the addition of Ceratopogonidae and some small physid snails. Mittelbach (1981*a*) further demonstrated that bluegills feed preferentially on larger invertebrates. Selectivities (Manly/Chesson index; Chesson 1978, 1983) calculated for bluegills (50–100 mm) feeding in the vegetation of Lawrence Lake during the spring and summer of 1979 were positively related to the length of the invertebrates eaten (Table 2). Thus, one would predict that any effect of sunfish density on invertebrate abundance would be greatest on larger instars of the five invertebrate groups listed above. To examine this prediction, I analyzed separately the densities of large and small prey using individuals collected on the large sieves (0.71- and 3.35-mm mesh) and on the small sieve (0.25-mm mesh). All of the prey trapped on the two larger sieves were in the range of prey sizes eaten by 50–75 mm bluegills and pumpkinseeds in Lawrence Lake, while prey collected on the small sieve were gen-

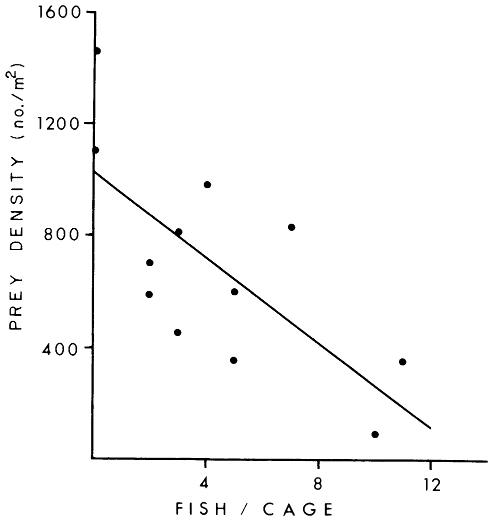

FIG. 3. Final prey densities in the experimental cages as a function of the number of bluegills and pumpkinseeds in the cage: $Y = 1025 - 75.6X$, $r^2 = 0.51$, H_0: slope = 0 rejected at $P < .01$. Prey are defined as invertebrate taxa that made up >90% of the diet by dry mass of small bluegills in Lawrence Lake (i.e., Amphipoda, Chironomidae, Ephemeroptera, Trichoptera, and Zygoptera). Only prey large enough to be retained on a 0.71-mm mesh sieve are included.

erally at the lower end of the range of prey sizes eaten by these fish (Fig. 2). Note that some prey sizes in the diets of bluegills and pumpkinseeds from the lake ranged above those sampled from the experimental cages. This was probably due to two factors: (1) the fish collectively sampled a larger volume of habitat than I did, and (2) some of the fish were collected in May and early June, when large invertebrates are more common in Lawrence Lake (Mittelbach 1981*b*).

There was a significant negative relation between the density of large prey in a cage (combining the five prey taxa) and the number of bluegills and pumpkinseeds in that cage (Fig. 3). An examination of the density of all centrarchids in the cages (i.e., bluegills, pumkinseeds, and other sunfishes) showed the regression between prey density and total fish density also to be significant: $Y = 1163 - 71.6X$, $r^2 = 0.47$, H_0: slope = 0 rejected at $P < .02$. The density of small prey (i.e., those from the 0.25-mm sieve) in a cage was not related to fish density; regression of final small prey numbers as a function of fish density: $Y = 60.41 + 0.96X$, $r^2 = 0.03$, $P > .50$. Densities of the individual prey taxa (Amphipoda, Ephemeroptera, etc.) were also examined as functions of fish density. Four of the five taxa showed declining densities with increasing fish numbers (Table 3), though the individual regression slopes were usually not significant.

Prey densities outside the cages were not sampled at the end of the experiment; therefore I cannot directly estimate the effect of caging on the invertebrate community. However, prey densities in the vegetation of Lawrence Lake were sampled from May to August in an intensive study conducted in 1979 (Mittelbach 1981*b*). These invertebrate samples were collected and processed in exactly the same way as in 1986. On 13 August 1979 the average density of large prey in Lawrence Lake was 780 prey/m² (eight replicate samples), which can be compared to final prey densities in the cages on 27 August 1986 (Fig. 3). A density of 780 large prey/m², coupled with the ambient bluegill density in Lawrence Lake (≈5 fish/cage, see Methods), falls close to the regression line for prey density vs. fish density measured in the cages (Fig. 3), suggesting that the cages themselves did not have a major impact on the way fish affected invertebrate densities.

Growth in response to prey availability

Ideally, one would like to relate the dynamics of fish growth to prey availability over the course of the experiment. However, repeated sampling of prey and fish in the cages would have destroyed the habitat. Therefore, I used the density of large prey sampled from each cage at the end of the experiment (i.e., organisms collected on the 0.71- and 3.35-mm sieves) as one estimate of prey availabilities in the different cages. The density of these large invertebrates was positively related to the growth rate of the fish (Fig. 4). In contrast, the density of small prey showed no relation to fish growth: $Y = 0.79 - 0.0001X$, $r^2 = 0.03$, $P > .50$. Prey densities are of course only a rough measure of prey availabilities because the rates at which fish encounter prey are determined both by prey size and prey density, as well as other factors (O'Brien 1979, Mittelbach 1981*a*). Therefore, I also used an optimal foraging model of the type developed by Charnov (1976) to calculate predicted net energy gains (joules per second of foraging time) for bluegills feeding on the total distribution of invertebrate sizes available in each cage at the end of the experiment. The optimal foraging model incorporates both prey size and abundance in calculating predicted prey encounter rates and handling times, and then determines net energy gains available from a given prey distribution. The model used has been described and tested in detail by Mittelbach (1981*a*) and Werner et al. (1983*b*). Therefore, I will only present a brief outline of it below.

TABLE 3. Linear regression equations for the densities (individuals/m²) of five prey taxa as a function of the total number of bluegills and pumpkinseeds per cage. Prey densities apply to organisms large enough to be retained by a 0.71-mm mesh sieve. $N = 12$ for each equation.

Prey group	Intercept	Slope	r^2	P*
Amphipoda	412.1	−42.2	.35	<.05
Trichoptera	69.6	−6.5	.32	<.06
Ephemeroptera	370.6	−17.8	.23	<.11
Zygoptera	143.1	−7.7	.11	>.20
Chironomidae	19.2	1.6	.01	>.50

* Test of H_0: slope = 0.

The following equation was used to predict net energy intake (E_n) per unit foraging time (T) for a 50-mm bluegill:

$$E_n/T = \frac{\left[\sum_{i=1}^{n} \lambda_i E_i\right] - C_s}{1 + \sum_{i=1}^{n} \lambda_i H_i}, \qquad (1)$$

where $E_i = Ae_i - C_h H_i$, and A = the assimilable fraction of the energy content of prey size i, e_i = energy content of prey size i (in joules), C_h = energy costs of handling prey (in joules per second), H_i = handling time of prey size i (in seconds), C_s = energy costs of searching (in joules per second), and λ_i = number of prey of size i encountered per second of search. To estimate encounter rates of vegetation-dwelling prey, I performed a number of experiments using bluegills as predators and coenagrionid (damselfly) nymphs as prey in 214-L aquaria containing live macrophytes (100 *Elodea* stems/m^2). Approximately 100 experiments were conducted using nine bluegills (21–115 mm) and various combinations of damselfly densities and sizes (see Mittelbach 1981*a* for details). A multiple regression equation was fit to the data to predict encounter rates with prey (λ_i) as a function of prey length and density and length of the fish. For a 50-mm bluegill the encounter rate equation is: $\log \lambda_i = -4.726 + 0.779 \log D + 1.045 \log L$ ($n = 110$, $R^2 = 0.58$), where D = prey density (number per cubic metre) and L = prey length (millimetres). Prey handling times (H_i) were a function of the relative size of predator and prey, and for a 50-mm bluegill feeding on prey ≥ 2.25 mm in length, handling times can be described by the following equation: $H = 0.639e^{0.199}$ ($n = 112$, $r^2 = 0.92$). For prey <2.25 mm, handling time is constant at 1 s (Mittelbach 1981*a*). The energy costs of searching for and handling prey (C_s and C_h) were estimated using the data of Wohlschlag and Juliano (1959) and the swimming speeds exhibited by bluegills searching for and handling prey in the laboratory experiments. The energy content of prey (e_i) was determined by converting prey lengths to dry masses and then multiplying by the appropriate energy equivalents (Cummins and Wuycheck 1971, Mittelbach 1981*a*).

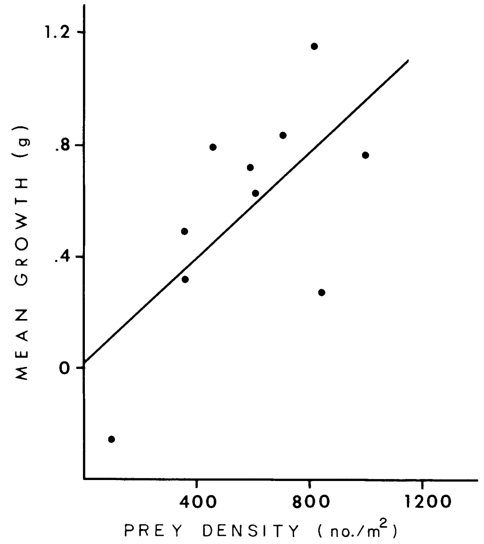

FIG. 4. Mean growth of bluegills and pumpkinseeds in the experimental cages as a function of final prey density in a cage. Prey are defined as in Fig. 3 legend. The fitted regression equation is $Y = 0.0226 + 0.0009X$, $r^2 = 0.43$, H_0: slope = 0 rejected at $P < .05$. Some caution should be taken in evaluating the significance of this regression as it is due largely to the influence of a single point.

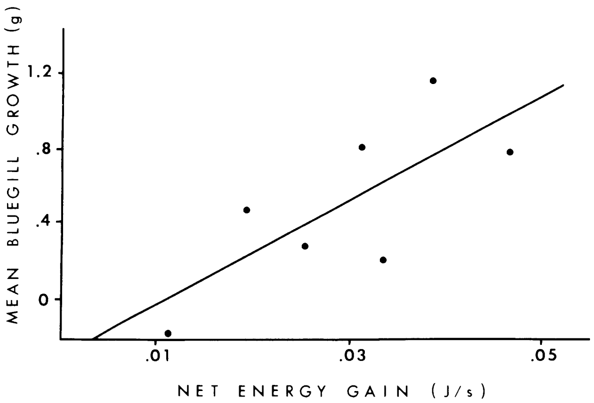

FIG. 5. Mean growth of bluegills in the experimental cages as a function of the predicted net foraging gain (J/s) for a 50-mm bluegill. Net foraging gains were calculated by using the optimal foraging model described in Mittelbach (1981*a*) and the distribution of invertebrate sizes available in each cage (see Results: Growth in Response to Prey Availability for details). The fitted regression equation is $Y = -0.336 + 28.675X$, $r^2 = 0.57$, H_0: slope = 0 rejected at $P < .05$.

Eq. 1 can be used to determine a bluegill's optimal diet and maximum energy gain by ranking available prey sizes from highest to lowest profitability (E_i/H_i) and then adding prey sizes to the diet until E_n/T is maximized. Predicted optimal diets for 50-mm bluegills in each of the cages at the end of the experiment included all the available prey sizes. Therefore, the predicted net energy gain in each cage is simply a function of prey encounter rates, handling times, and energy contents, minus the energy costs of searching and handling. These predicted net energy gains were compared with the actual growth of the bluegills over the course of the experiment. A significant positive relation was found between these two factors (Fig. 5), indicating that growth rates in the cages were directly related to prey availability.

The relationships shown in Figs. 4 and 5, in combination with the evidence for prey depletion, support the hypothesis that juvenile bluegills and pumpkinseeds were competing exploitatively. However, it is possible that interference between bluegills and pumkinseeds may also account for some of the density dependence observed in the growth rates of these two species. To test for this, I conducted a partial correlation analysis to separate the effects of fish density and prey abundance on the average growth rates of bluegills and pumpkinseeds in the experiment. The analysis examined the effect of total fish density on the mean growth of bluegills and pumpkinseeds in a cage, while holding the effects of prey density constant; it also examined the effect of prey density on the mean growth of bluegills and pumpkinseeds, while holding the effects of fish density constant. The partial correlation coefficient for the effect of fish density on fish growth is -0.74 and for the effect of prey density on fish growth is 0.42 (the simple correlation coefficients for these relationships are -0.83 and 0.65, respectively). Neither partial correlation is significant ($P > .05$). Thus, neither fish density nor final prey density alone accounts for the observed growth in the cages, and the analysis does not allow one to eliminate either mode of competition as potentially occurring. Indeed, both interference and exploitation may have been involved in the cages. Evidence from other studies, however, suggests that competition between these species is primarily exploitative (Werner and Hall 1976, 1979). There is no comparable field evidence for interference between juvenile bluegills and pumpkinseeds and no aggressive interactions were observed between fish in the cages. Laboratory studies with juvenile bluegills also show no interference effects on foraging rates at fish densities <8 individuals/m^2 (Mittelbach 1984*b*).

Discussion

Evidence from both observational and experimental studies demonstrates that juvenile bluegills and pumpkinseeds compete while restricted to the vegetation refuge. For example, earlier work showed that the growth of small bluegills and pumkinseeds in small Michigan lakes was only $\approx \frac{1}{2}$ to $\frac{1}{6}$ that of these same species stocked at low densities in nearby experimental ponds (Mittelbach 1986). Also, observational data on the growth of bluegills and pumpkinseeds from seven Michigan lakes showed a significant negative relationship between yearly growth of these species within a lake and the density of bluegills and pumpkinseeds in the lake (all data for fish ≤ 75 mm; Osenberg et al. 1988). Finally, the above observational studies, suggesting interspecific competition, were strongly supported by the experimental work reported here (see also Mittelbach 1986 for additional experimental evidence of intraspecific competition in juvenile bluegills).

Various studies have suggested that prey species compete for resources within a refuge (e.g., Morse 1980, Garrity and Levings 1981, Mittelbach 1981*a*, 1984*a*, Sih 1982, Power 1984); however, in all cases direct evidence of competition is lacking. For the bluegill, the studies by Mittelbach (1981*a*) and Werner et al. (1983*a*) demonstrate that small fish are concentrated in the vegetated littoral zone in response to predation risk. Here I show that one consequence of this predator avoidance behavior may be competition among juvenile fishes. Thus, for these size-structured populations, the presence of predators may actually intensify interspecific competition early in their life history. How often predator avoidance intensifies or structures the timing of interspecific competition in other systems remains to be seen. I suspect that it may occur rather often among motile species whose vulnerability to predation depends strongly on size or age, and when refuges represent a limited fraction of the available habitat. Clearly, the action of predators in intensifying competition at certain stages in a species' life history differs widely from the conventional view that predators primarily reduce interspecific competition, either by removing superior competitors or by lowering total demand for resources. While piscivores no doubt lower the density of bluegills and pumpkinseeds in Lawrence Lake, interspecific competition still occurs at the densities of fish found in the vegetation refuge. A significant goal for future research is to tease apart the direct effects of predators on prey densities from the indirect effects of predators on prey behaviors (e.g., habitat choice), and ask how each of these factors contributes to community dynamics.

Unfortunately, it is difficult to predict the ultimate consequences of predator avoidance and juvenile competition to the bluegill and pumpkinseed populations. One can show mathematically that strong juvenile or larval competition between two species can result in negative correlations in adult densities, even when the adults of two species use completely separate resources (Mittelbach and Chesson 1987). Thus, for the bluegill and pumpkinseed, it is likely that their common response to predators as juveniles links their population dynamics, when otherwise they would function independently. Werner and Hall (1977, 1979) have also shown that if bluegills and pumpkinseeds are allowed to segregate by habitat, competition between them is greatly reduced. However, there is no way to predict accurately the potential resource use by juvenile bluegills and pumpkinseeds in the absence of predators. If, for example, both small bluegills and pumpkinseeds were to shift to feeding on zooplankton when predators were removed, the species may continue to compete, although the interaction would be for a different set of resources. Sorting out the population- and community-level effects of predator-mediated behaviors is clearly a major challenge. Large-scale field manipulations of predator abundance provide one logical avenue for evaluating the consequences of predator-induced competition to species dynamics.

In the Lawrence Lake cages, increases in fish density significantly decreased the density of large invertebrates present (Fig. 3) and mean invertebrate length. Other studies that have examined the impact of fish on lentic invertebrate densities have reported either no significant effects (Thorp and Bergey 1981*a, b,* Hanson and Leggett 1986), decreased invertebrate densities with fish (Ball and Hayne 1952, Morin 1984*a, b*), or variable effects (Hall et al. 1970, Crowder and Cooper 1982, Gilinsky 1984, Hershey 1985). Many of these seemingly contradictory results may be resolved by recognizing that fish are often size-selective predators and are therefore expected to affect large and small invertebrates differently.

Several studies conducted in fishless ponds and a lake with a depauperate fish fauna, demonstrate that introduced fish can have a profound impact on the size structure of benthic invertebrate communities. For example, in an early study of the effect of bluegill predation on pond invertebrates, Hall et al. (1970) found a significant negative correlation between the standing stock of all benthic invertebrate taxa weighing >0.01 mg dry mass and the standing stock of introduced bluegills. In contrast, the authors reported no demonstrable effect of fish on the total biomass of benthic invertebrates. Hall et al. (1970) concluded that the strongest effect of fish was a reduction in the abundance of large, motile organisms, and that body size was better than taxonomic group as a descriptor of invertebrate response. Crowder and Cooper (1982) similarly found that when bluegills were added to fishless ponds, the mean size of invertebrates decreased relative to fishless controls; they attributed this decrease in mean prey size to a reduction in the abundance of certain large, motile invertebrates (e.g., *Hyalella,* Zygoptera) in the presence of fish. Total invertebrate biomass decreased with the addition of fish, despite an increase in abundance of small invertebrates in the presence of bluegills. In an observational study, Post and Cucin (1984) examined the littoral zone invertebrates of Little Minnow Lake, Algonquin Park, Ontario, before and after the accidental introduction of yellow perch, *Perca flavescens* (the lake supported only hatchery-reared salmonids and some minnows before perch were added). After the introduction of yellow perch, the mean mass of benthic invertebrates decreased $\approx 50\%$ and total benthic biomass declined $\approx 60\%$. Of the nine invertebrate taxa examined, five decreased significantly in total biomass and eight decreased significantly in mean mass, but none decreased significantly in density.

The above studies were conducted in fish-poor or fishless systems, where it may be argued that the effect of introduced fish should be especially dramatic. In studies conducted in ponds and lakes containing fish, however, the same general effects of fish predation were evident; e.g., fish had a significant negative effect on the abundance of large invertebrates (often decreasing mean invertebrate size), but appeared to have no consistent effect on total invertebrate numbers. Morin (1984*a, b*) found clear effects of fish predation on the size composition of dragonfly larvae in a North Carolina pond, where the exclusion of fish produced a shift from assemblages dominated by a small species to assemblages dominated by species of intermediate size. Thorp and Bergey (1981*a, b*) detected no significant effects of fish predation on invertebrate densities; however, they did not examine the effects of fish on invertebrate size-structure nor attempt to classify the invertebrate community on the basis of body size (except for the Chironomidae, where they found no fish effects). Gilinsky (1984) also examined a pond invertebrate community using experimental cages with and without fish. In this study, fish significantly affected the densities of some benthic invertebrates; however, the patterns were quite complicated because some invertebrate species increased and others decreased, and the effects of fish predation varied with the season. Like Thorp and Bergey (1981*a, b*), Gilinsky examined species densities without looking at size distributions or separating the invertebrate community into large and small forms. Hanson and Leggett (1986), who also examined only total invertebrate numbers and biomass, found no effects of fish density. It is likely that any impact of fish on the density of large individuals will be masked when looking only at total invertebrate numbers, due to the inclusion of small size classes, which are generally much more abundant in the community (Mittelbach 1981*b*).

In the present study, fish had a strongly negative effect on the densities of large invertebrates, but no effect on the densities of small prey. The lack of effect on the abundance of small invertebrates in Lawrence Lake is in contrast to the findings of Crowder and Cooper (1982), who found that the number of small invertebrates increased in the presence of fish. Gilinsky (1984) also noted that the density of small chironomids (subfamily Chironominae) increased in the presence of fish, probably as a response to a reduction in larger chironomid species. Some of the differences between my work and these other studies may be due to the relatively short duration of the present experiment (50 d), which limited the time available for small invertebrates to respond to a reduction in the number of larger individuals. It is also possible that the differential response of small invertebrates between this study and that of Crowder and Cooper (1982) was due to differences in the invertebrate communities between fishless ponds (Crowder and Cooper's study) and lakes with fish.

The present study is significant because it experimentally examined the effects of fish on benthic invertebrates in a natural lake, where both predator and prey have co-occurred for many generations. Most other studies have either considered the effects of introduced fish in a previously fishless system, or were conducted in man-made ponds and reservoirs. As judged by the present study, it is clear that fish can affect invertebrate assemblages in a potentially coevolved system; however, these effects were manifested largely through changes in population size structure (at least in the short term). Based on the above studies, I suggest that fish in lentic systems have: (1) strong effects on benthic invertebrate size structure, (2) little or no effect on benthic invertebrate species richness (except perhaps between fish and fishless systems), and (3) variable effects on total invertebrate densities. These conclusions are in general agreement with Thorp's (1986) recent survey of the literature.

Although predator avoidance by small fish clearly has significant effects on interspecific competition and the structure of the benthic invertebrate community, other community-level effects are likely as well. For example, it was shown in a pond study that small bluegills fed extensively on open-water zooplankton when piscivorous fish were removed (Werner et al. 1983*a*), and in Lawrence Lake the predicted energy returns for small bluegills were often twice as high in open water as in vegetation (Mittelbach 1981*a*). Thus, if piscivorous fish were absent, small bluegills (and perhaps other species) would likely shift out of the vegetation to feed on zooplankton. This change in foraging intensity in the open water can have dramatic effects on the plankton. A. Turner and G. G. Mittelbach (*personal observation*) have demonstrated such an effect in a recent pond experiment, where bluegills were stocked with and without largemouth bass. In this experiment, zooplankters such as *Daphnia, Diaphanosoma,* and *Chaoborus* were strongly favored in the presence of largemouth bass, whereas calanoid copepods were negatively affected. These changes in the zooplankton were the result of changes in bluegill foraging behaviors and not changes in bluegill densities due to the bass. Thus, it is likely that piscivores affect community organization at many levels and that these effects go well beyond the simple consumption of prey. In fact, to paraphrase Zaret (1980), the indirect effects of predators in modifying prey behaviors may turn out to be more important than the relatively small percentage of prey they actually consume.

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LITERATURE CITED

Ball, R. C., and D. W. Hayne. 1952. Effects of the removal of the fish population on the fish-food organisms of a lake. Ecology **33**:41–48.

Charnov, E. L. 1976. Optimal foraging: attack strategy of a mantid. American Naturalist **110**:141–151.

Chesson, J. 1978. Measuring preference in selective predation. Ecology **59**:211–215.

———. 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology **64**:1297–1304.

Crowder, L. B., and W. E. Cooper. 1982. Habitat structural complexity and the interaction between bluegills and their prey. Ecology **65**:894–908.

Cummins, K. W., and J. C. Wuycheck. 1971. Caloric equivalent for investigations in ecological energetics. Internationale Vereinigung für theoretische und angewandte Limnologie, Mitteilungen **18**:1–158.

Draper, N. R., and H. Smith. 1980. Applied regression analysis. Second edition. John Wiley and Sons, New York, New York, USA.

Garrity, S. D., and S. C. Levings. 1981. A predator-prey interaction between two physically and biologically constrained tropical rocky shore gastropods: direct, indirect and community effects. Ecological Monographs **51**:267–286.

Gilinsky, E. 1984. The role of fish predation and spatial heterogeneity in determining benthic community structure. Ecology **65**:455–468.

Goldberg, D. E., and P. A. Werner. 1983. Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. American Journal of Botany **70**:1098–1104.

Hall, D. J., W. E. Cooper, and E. E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnology and Oceanography **15**:839–928.

Hanson, J. M., and W. C. Leggett. 1986. Effect of competition between two freshwater fishes on prey consumption and abundance. Canadian Journal of Fisheries and Aquatic Sciences **43**:1361–1372.

Hershey, A. E. 1985. Effects of predatory sculpin on the chironomid communities in an arctic lake. Ecology **66**:1131–1138.

Keast, A. 1978. Feeding interrelations between age groups of pumpkinseed sunfish (*Lepomis gibbosus*) and comparisons with the bluegill sunfish (*L. macrochirus*). Journal of the Fisheries Research Board of Canada **35**:12–27.

Kerfoot, W. C., and A. Sih. 1987. Predation. New England University Press, Hanover, New Hampshire, USA.

Merritt, R. W., and K. W. Cummins. 1984. An introduction to the aquatic insects of North America. Second edition. Kendal/Hunt, Dubuque, Iowa, USA.

Mittelbach, G. G. 1981*a*. Foraging efficiency and body size: a study of optimal diet and habitat use by bluegills. Ecology **62**:1370–1386.

———. 1981*b*. Patterns of invertebrate size and abundance in aquatic habitats. Canadian Journal of Fisheries and Aquatic Sciences **38**:896–904.

———. 1984*a*. Predation and resource partitioning in two sunfishes (Centrarchidae). Ecology **65**:499–513.

———. 1984*b*. Group size and feeding rate in bluegills. Copeia **1984**:998–1000.

———. 1986. Predator-mediated habitat use: some consequences for species interactions. Environmental Biology of fishes **16**:159–169.

Mittelbach, G. G., and P. L. Chesson. 1987. Predation risk: indirect effects on fish populations. Pages 315–332 *in* W. C. Kerfoot and A. Sih, editors. Predation. New England University Press, Hanover, New Hampshire, USA.

Morin, P. J. 1984*a*. The impact of fish exclusion on the abundance and species composition of larval odonates: results of short-term experiments in a North Carolina pond. Ecology **65**:53–60.

———. 1984*b*. Odonate guild composition: experiments with colonization history and fish predation. Ecology **65**:1866–1873.

Morse, D. H. 1980. Behavioral mechanisms in ecology. Harvard University Press, Cambridge, Massachusetts, USA.

O'Brien, W. J. 1979. The predator-prey interaction of planktivorous fish and zooplankton. American Scientist **67**:572–581.

Osenberg, C. W., E. E. Werner, G. G. Mittelbach, and D. J. Hall. 1988. Growth patterns in bluegill (*Lepomis macrochirus*) and pumpkinseed (*L. gibbosus*) sunfish: environmental variation and the importance of ontogenetic niche shifts. Canadian Journal of Fisheries and Aquatic Sciences **45**:17–26.

Post, J. R., and D. Cucin. 1984. Changes in the benthic community of a small precambrian lake following the introduction of yellow perch, *Perca flavescens*. Canadian Journal of Fisheries and Aquatic Sciences **41**:1496–1501.

Power, M. E. 1984. Depth distributions of armored catfish: predator-induced resource avoidance? Ecology **65**:523–529.

Prout, T. 1986. The delayed effect on fertility of preadult competition: two-species population dynamics. American Naturalist **127**:809–818.

Rich, P. H., R. G. Wetzel, and N. V. Thuy. 1971. Distribution, production, and the role of aquatic macrophytes in a southern Michigan marl lake. Freshwater Biology **1**:3–21.

Schoener, T. W., and D. H. Janzen. 1968. Notes on environmental determinants of tropical versus temperate insect size patterns. American Naturalist **102**:207–224.

Scott, W. B., and E. J. Crossman. 1973. Freshwater fishes of Canada. Fisheries Research Board of Canada, Ottawa, Ontario, Canada.

Sih, A. 1982. Foraging strategies and the avoidance of predation by an aquatic insect, *Notonecta hoffmanni*. Ecology **63**:786–796.

Thorp, J. H. 1986. Two distinct roles for predators in freshwater assemblages. Oikos **47**:75–82.

Thorp, J. H., and E. A. Bergey. 1981*a*. Field experiments on responses of a freshwater, benthic macroinvertebrate community to vertebrate predators. Ecology **62**:365–375.

Thorp, J. H., and E. A. Bergey. 1981*b*. Field experiments on interactions between vertebrate predators and larval midges (Diptera:Chironomidae) in the littoral zone of a reservoir. Oecologia (Berlin) **50**:285–290.

Tietjen, G. L., R. H. Moore, and R. J. Beckman. 1973. Testing for a single outlier in simple linear regression. Technometrics **15**:717–721.

Werner, E. E. 1977. Species packing and niche complementarity in three sunfishes. American Naturalist **111**:553–578.

———. 1986. Species interactions in freshwater fish communities. Pages 344–358 *in* J. Diamond and T. J. Case, editors. Community ecology. Harper and Row, New York, New York, USA.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983*a*. An experimental test of the effects of predation risk on habitat use in fish. Ecology **64**:1540–1548.

Werner, E. E., and D. J. Hall. 1974. Optimal foraging and size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). Ecology **55**:1042–1052.

Werner, E. E., and D. J. Hall. 1976. Niche shifts in sunfishes: experimental evidence and significance. Science **191**:404–406.

Werner, E. E., and D. J. Hall. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). Ecology **58**:869–876.

Werner, E. E., and D. J. Hall. 1979. Foraging efficiency and habitat switching in competing sunfishes. Ecology **60**:256–264.

Werner, E. E., D. J. Hall, D. R. Laughlin, D. J. Wagner, L. A. Wilsmann, and F. C. Funk. 1977. Habitat partitioning in a freshwater fish community. Journal of the Fisheries Research Board of Canada **34**:360–370.

Werner, E. E., G. G. Mittelbach, D. J. Hall, and J. F. Gilliam. 1983*b*. Experimental tests of optimal habitat use in fish: the role of relative habitat profitability. Ecology **64**:1525–1539.

Wohlschlag, D. E., and R. O. Juliano. 1959. Seasonal changes in bluegill metabolism. Limnology and Oceanography **4**:195–209.

Zaret, T. M. 1980. Predation and freshwater communities. Yale University Press, New Haven, Connecticut, USA.