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Interspecific competition and qualitative competitive asymmetry between two benthic stream fish

William J. Resetarits, Jr.

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The mottled sculpin, *Cottus bairdi*, and the fantail darter, *Etheostoma flabellare*, are benthic fish common in small streams over much of eastern North America. Both juveniles and adults of these two species are closely associated in low elevation headwater streams in western Virginia. I explored the effects of competition between juveniles of the two species, and the effects of heterospecific adults on juvenile performance, in a controlled, replicated experiment in artificial streams. Effects of competition were determined for three measures of juvenile performance that can be potentially related to reproductive output, and hence, to population dynamics: survival, growth and relative condition.

Juveniles of *C. bairdi* and *E. flabellare* competed at densities well within the range observed in their natal streams. Adult *E. flabellare* had a positive effect on the survival of juvenile *C. bairdi*, the origin of which is unknown. Adult *C. bairdi* had no effect on juvenile *E. flabellare*. The most interesting result was that competition between juveniles of the two species was characterized by a qualitative asymmetry; *C. bairdi* responded with a reduction in growth, both in total length and mass, while *E. flabellare* responded with a decrease in relative condition, but no decrease in growth. These differences in response were clearly reflected in mass/length regressions. Unless responding variables can be precisely translated into quantitative effects on population dynamics, such qualitative asymmetries in competitive interactions greatly complicate the determination of competitive symmetry and the possible prediction of competitive outcomes, especially in species where *r* is difficult to determine directly.

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Understanding the nature of competitive interactions and their prevalence and importance in natural communities is critical to understanding the distribution and abundance of extant species and the processes which give rise to new species. Examining competition in a broad range of systems, including model systems (Lawton 1997, Morin 1997), allows us to explore the nature of competitive interactions and the ways in which species may respond to competition. The role of competition can be expected to vary by taxa, guild, trophic level, and type of habitat (Hairston et al. 1960, MacArthur 1972, Colwell 1984, Schoener 1986, Hairston 1989); by examining a variety of species and systems we can seek generalities regarding the way in which competition functions to affect individual species and the structure of communities, as well as how we approach our assay of the role of competition.

Our understanding of competitive interactions and their role in lotic systems is fairly cursory. Studies have documented competition in a variety of stream organisms (e.g. Barlocher 1980, McAuliffe 1984, Lamberti et al. 1987, Hemphill 1991, Resetarits 1991, 1995a, b), including stream fish, but the extent, importance and dynamics of competition in streams remains largely

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unexplored. Studies of competition in stream fish, with few exceptions (e.g. Fausch and White 1981, 1986, Fausch 1984, Resetarits 1995a), have been based on habitat segregation and measures of resource overlap (e.g., Paine et al. 1982, Matheson and Brooks 1983, Martin 1984, Greenberg 1991; see also Ross 1986 and references in Matthews and Heins 1987); few studies have measured competition directly. Indirect measures of competition rely on many assumptions regarding resource axes and their subdivision and are not satisfactory substitutes for direct measures of competitive effects (Hairston 1980). Thus, ecologists have increasingly turned to controlled experiments to assay competitive interactions (see Connell 1983, Schoener 1983, Sih et al. 1985, Hairston 1989, Goldberg and Barton 1992).

Assemblages of predatory benthic fish are an important component of many streams. They serve both as prey to larger organisms and as predators of smaller ones. Recent work has dramatically demonstrated the important role fish may play in the structure of stream communities (e.g., Gilliam et al. 1989, Power 1990, 1992, Flecker 1992, Gelwick and Matthews 1992; see also Northcote 1988); factors which affect the dynamics of fish populations and the structure of fish assemblages have potential effects at all trophic levels (Power 1992).

A previous study (Resetarits 1995a) examined the relative effects of intra- and interspecific competition (including competition from the fantail darter, *Etheostoma flabellare*) on the mottled sculpin, *Cottus bairdi*, in order to assay the role of morphological similarity in the strength of competitive interactions. The strength of competitive effects on *C. bairdi* were not correlated with morphological similarity (Resetarits 1995a). Field sampling in streams of the James River drainage in western Virginia, USA revealed that juveniles and small adults (hereafter referred to as juveniles) of these two species were abundant in the same habitats as larger adults, suggesting both the potential for interspecific competition among juveniles and possible interspecific interactions between juveniles and adults.

The juvenile stage of fish may be particularly important in population dynamics because generalized habitat and resource use enhances the possibilities for juvenile bottlenecks that are intensified by interspecific competition (Werner 1986, Persson 1988). This paper expands on previous work (Resetarits 1995a) to focus on the effects of interspecific competition from both juveniles and adults on the juvenile stage of these two species (*C. bairdi* and *E. flabellare*) and further explores aspects of competitive interactions among stream fish. I directly manipulated the competitive environment in replicated experimental streams and measured competition via effects on growth, condition, and survival.

Materials and methods

The species

Cottus bairdi is a medium sized (adult size range approximately 43–125 mm standard length [SL]) bottom-dwelling fish that occurs in a wide range of habitats across eastern North America (Lee 1980). In western Virginia, it occurs from high elevation, low fish diversity, cool-water streams characterized by native brook trout, to low elevation, high fish diversity, warm-water streams characterized by smallmouth bass (Burton and Odum 1945, Resetarits unpubl.). Both juvenile and adult mottled sculpins live in and among the cobbles of the stream bottom. Mottled sculpins may grow to 31–36 mm by the autumn of their first year (Bailey 1952, Ludwig and Norden 1969). All sizes of *C. bairdi* feed primarily on immature benthic insects, but take other arthropods, mollusks, small fish (including conspecifics), and fish eggs (Dineen 1951, Bailey 1952, Nagel 1980).

The fantail darter, *Etheostoma flabellare*, is a moderate-sized darter (70 mm SL maximum, adult size usually 30–60 mm) that occupies a variety of habitats in small headwater streams through moderate-size rivers (Pflieger 1975, Kuehne and Barbour 1983). In western Virginia, it occurs over essentially the same range of stream conditions as *C. bairdi* (Burton and Odum 1945). Hatchlings average 7 mm total length (TL) and may grow to 30 mm by November of their first year (Lake 1936). Both juvenile and adult *E. flabellare* live among the cobbles of the stream bottom where they feed on immature aquatic insects, copepods, amphipods and isopods (e.g., Karr 1964, Lotrich 1973, Small 1975). Like *C. bairdi*, *E. flabellare* is found in suitable streams across much of eastern North America (Lee 1980).

These two species are the numerically dominant benthic fish in lower elevation headwater streams in the James River drainage near Mountain Lake Biological Station (MLBS), western Virginia, USA. Juveniles and adults of both of these species reach high local densities ($>10\ \mathrm{m}^{-2}$) in Craig Creek and other local streams, and are the only benthic fish common in upper Craig Creek from ca 480 m to the source at ca 650 m, a distance of ca 20 km (pers. obs.). Adults and juveniles in Craig Creek occupy habitats ranging from riffles to quiet backwaters (pers. obs.).

Experimental stream system

The experiment was conducted in an array of 20 replicate experimental streams constructed below a large (ca 1 ha), spring-fed pond at MLBS. No fish occur in the creek feeding into the pond or elsewhere on MLBS, so the pond is permanently fish free.

Artificial streams were modelled after an earlier design (Resetarits 1991, 1995b) and modified specifically for studying benthic stream fish (Resetarits 1995a).

Individual streams were constructed from cattle feed bunks 3.35 m long, 0.69 m wide and 0.36 m deep and were located below the pond dam at an elevation of 1150 m. The array occupied an area of 7 × 21 m with streams packed as closely as possible to reduce uncontrolled variation. The canopy of vegetation over the array was left intact to simulate natural stream conditions. Streams were adjusted to a gradient of ca 4.0 cm/m, resulting in a shallow upstream end and a deeper downstream end. Each had a separate inflow pipe and control valve, and an adjustable drain pipe covered with a layer of 6-mm rigid plastic mesh and a second layer of 1.5-mm fiberglass screen. Flow rate into the experimental streams varied simultaneously and ranged between 30 and 60 l/min during the experiment. Outflow was collected and pumped back to the far side of the pond to conserve water. The experimental streams were designed to provide cover and microhabitat heterogeneity approximating conditions in Craig Creek and other nearby streams. Each stream received 300 kg of unwashed commercial sand, 300 kg of river gravel (ranging from 2–20 cm diameter), 4 l (packed) of leaf litter raked from the forest floor, and one large rock (ca 6000 cm^3) placed beneath the inflow. Streams were completely open to the environment to allow aerial colonization by insects and natural input of terrestrial drift organisms and litter. The design of the individual streams eliminated any direct communication between units, assuring their biological and statistical independence.

Experimental design

I used a randomized complete block, incomplete factorial design (see Fig. 1) partially crossing the presence/absence of juvenile *C. bairdi* (0 and 10 animals) (densities 0/m^2 and ca 5/m^2) with the presence/absence of juvenile *E. flabellare* (0 and 12 animals) (densities 0/m^2 and ca 6/m^2); the absence × absence (0 × 0) treatment was excluded. A third treatment was represented for each species; to streams with 12 *E. flabellare* I added three adult *C. bairdi*, and to streams containing 10 *C. bairdi* I added three adult *E. flabellare*. The five treatments were replicated once within each of four blocks (20 total units). Blocks consisted of the closest possible arrangement of five streams in the array. Treatments were assigned randomly within each block. All animals were weighed to the nearest 0.05 g, measured (total length [TL]) to the nearest 1.0 mm and assigned individually to numbered containers. They were then divided into size classes and an appropriate number of stratified random sets were generated; 12 each for juvenile *C. bairdi* and *E. flabellare*, and four each for adults of both species. Treatments were then randomly assigned to streams within blocks and sets of animals were randomly assigned to treatments within blocks. All animals used in this experiment were collected from upper Craig Creek, a first/second order tributary of the James River in Montgomery and Craig Counties, Virginia, between 4 and 9 June.

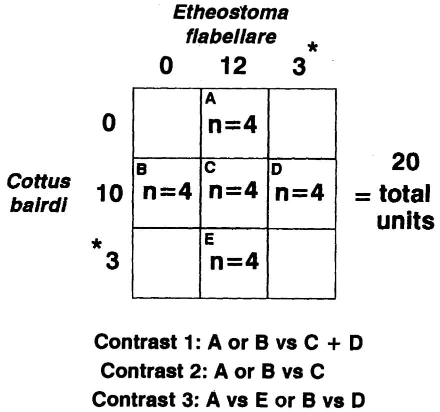

Fig. 1. Diagram of the experimental design and the three non-orthogonal a priori contrasts. Asterisk (*) indicates adults. Contrast 1 compares A to C + E (*E. flabellare*) or B to C + D (*C. bairdi*). Contrast 2 compares A to C (*E. flabellare*) or B to C (*C. bairdi*). Contrast 3 compares A to E (*E. flabellare*) or B to D (*C. bairdi*).

Juvenile *C. bairdi* ranged in initial total length from 46 mm to 68 mm and in initial mass from 0.95 g to 3.35 g (means; TL = 58.05 mm, mass = 2.26 g). Adult *C. bairdi* ranged from 74 mm to 87 mm TL and 5.35 g to 7.85 g (means; TL = 81.46 mm, mass = 6.63 g). Juvenile *E. flabellare* ranged in TL from 35 mm to 49 mm and in mass from 0.30 g to 0.95 g (means; TL = 41.51 mm, mass = 0.59 g). Adult *E. flabellare* ranged from 55 mm to 71 mm TL and from 1.45 g to 2.75 g in mass (means; TL = 60.79 mm, mass = 1.77 g).

The experiment began with addition of juvenile *C. bairdi* to blocks 1 and 2 on 7 June and blocks 3 and 4 on 10 June, juvenile *E. flabellare* to blocks 1 and 2 on 8 June and blocks 3 and 4 on 9 June, adult *C. bairdi* to all blocks on 11 June, and adult *E. flabellare* to all blocks on 12 June. The experiment was terminated with removal of all surviving fish on 12–15 August, after 60 d. The evening of 12 August the water was turned off and one block each night through 15 August was searched repeatedly using headlamps until no fish were collected in a full sweep of that block. Fish were held in aquaria and were weighed, measured, and preserved in 10% formalin within 24 h of removal. Streams were treated with 1.5 ml of rotenone on 15 August and the fish collected (< 5% of total) processed (as above) within two h. All surviving animals were thus removed and processed by 16 August.

Statistical analysis

Response variables for both *C. bairdi* and *E. flabellare* were survival, growth, and deviation in relative condition. Survival was angularly transformed before analysis. Growth was measured as both mean final TL and mean final mass; growth was based on overall stream means because individuals were not marked due to concerns over handling stress. Deviation in relative condition was the difference between the actual final mass for a given individual and the predicted mass based on mass/length regressions from the original samples of 307 *E. flabellare* and 314 *C. bairdi* that supplied experimental animals. A mean for each variable was calculated for each experimental stream and formed the units of analysis.

Survival and condition were analyzed by analysis of variance (ANOVA), and growth (mean final TL and mean final mass) was analyzed using analysis of covariance (ANCOVA) with mean initial TL as the covariate. Hypothesis testing used a priori contrasts. All ANOVA-based analyses were done within the PROC GLM procedure of PC-SAS (version 6.03, SAS Institute 1988) and used Type III sums of squares. Other data analysis used the Statgraphics system (version 3.0, Statistical Graphics Corporation 1988).

Specific hypotheses were tested using three non-orthogonal a priori contrasts testing three null hypotheses (see Fig. 1); Contrast 1 for juveniles of each species tested the null hypothesis of no interaction (juvenile *C. bairdi* raised alone vs juvenile *C. bairdi* raised with adult *E. flabellare* and juvenile *C. bairdi* raised with juvenile *E. flabellare*; B vs C + D, Fig 1, or juvenile *E. flabellare* raised alone vs juvenile *E. flabellare* raised with adult *C. bairdi* and juvenile *E. flabellare* raised with juvenile *C. bairdi*; A vs C + E, Fig. 1), Contrast 2 tested the null hypothesis of no competition between juvenile *E. flabellare* and juvenile *Cottus bairdi* (responses of juveniles of each species alone vs responses in competition with heterospecific juveniles; B vs C for *C. bairdi*, A vs C for *E. flabellare*, Fig. 1), and Contrast 3 tested the null hypothesis that juveniles of each species were unaffected by heterospecific adults (responses of juveniles of each species alone vs responses when raised with heterospecific adults; B vs D for *C. bairdi*, A vs E for *E. flabellare*, Fig. 1). These three non-orthogonal contrasts explore hypotheses regarding species interactions from the perspective of juvenile *C. bairdi* and *E. flabellare*. This experiment (via contrasts) tests hypotheses of interaction vs no interaction; the additive design and unequal juvenile densities are appropriate for these specific hypotheses.

Results

Responses of adult *C. bairdi* and *E. flabellare*

Survival was high for adults of both species; 83% (10/12) of the adult *E. flabellare* and 92% (11/12) of the adult *C. bairdi* survived, with at least 2 of 3 surviving in each stream. Growth response differed between the two species. Mean mass and mean total length (TL) for adult *C. bairdi* stayed relatively constant, from an initial TL of 82.00 $\pm$ 4.0 mm ($\bar{X} \pm \mathrm{SD}$) to a final TL of 81.36 $\pm$ 4.84 mm ($\mathrm{df} = 22$, $t = 0.34$, $p = 0.73$) and an initial mass of 6.64 $\pm$ 0.78 g to a final mass of 6.24 $\pm$ 0.54 g ($\mathrm{df} = 22$, $t = 1.41$, $p = 0.17$). Growth was significantly positive for adult *E. flabellare*, mean TL increasing from 60.17 $\pm$ 2.29 mm to 63.40 $\pm$ 1.17 mm ($\mathrm{df} = 21$, $t = 4.03$, $p = 0.0007$), and mean mass from 1.72 $\pm$ 0.20 g to 2.21 $\pm$ 0.26 g ($\mathrm{df} = 21$, $t = 5.07$, $p = 0.00006$).

Responses of *C. bairdi*

Survival was high for juvenile *C. bairdi* in all treatments (mean = 0.82), ranging from 0.7 to 0.93 (Fig. 2a). The results from a priori contrasts are as follows (see Statistical analysis above and Fig. 1). *Etheostoma flabellare* (juvenile and adult; Contrast 1) had a significant positive effect on survival ($F_{1,6} = 7.41$, $p = 0.035$, Table 1, Fig. 2a), a significant negative effect on final total length ($F_{1,5} = 8.40$, $p = 0.034$, Table 1, Fig. 2b), and a significant negative effect on mean final mass ($F_{1,5} = 7.67$, $p = 0.039$, Table 1, Fig. 2c). There was no effect of *E. flabellare* on relative condition (Table 1, Fig. 2d). Juvenile *E. flabellare* (Contrast 2) had a significant negative effect on mean final TL ($F_{1,5} = 7.23$, $p = 0.043$, Table 1, Fig. 2b), and a nearly significant negative effect on mean final mass ($F_{1,5} = 6.01$, $p = 0.058$, Table 1, Fig. 2c). Juvenile *E. flabellare* had no effect on survival (Table 1, Fig. 2a) or relative condition (Table 1, Fig. 2d). Adult *E. flabellare* (Contrast 3) had a significant positive effect on survival ($F_{1,6} = 11.86$, $p = 0.014$, Table 1, Fig. 2a), and nearly significant negative effect on both mean final TL ($F_{1,5} = 5.54$, $p = 0.065$, Table 1, Fig. 2b) and mean final mass ($F_{1,5} = 5.57$, $p = 0.065$, Table 4, Fig. 2c). Adult *E. flabellare* had no effect on relative condition (Table 1, Fig. 2d).

These results provide evidence to reject the null hypothesis from Contrast 1, that *E. flabellare* have no effect on *C. bairdi*, as well as evidence to reject the null hypothesis from Contrast 2, that juvenile *E. flabellare* have no effect on juvenile *C. bairdi*. Similarly, we reject the null hypothesis for Contrast 3, no effect of adult *E. flabellare*, because they had a positive effect on the survival and possibly a negative effect on growth of juvenile *C. bairdi*, though the latter was not significant.

Responses of *E. flabellare*

Survival was moderately high for juvenile *E. flabellare* in all treatments, (mean = 0.58) ranging from 0.52 to 0.65 (Fig. 3a). The results from a priori contrasts are as follows (see Statistical Analysis above and Fig. 1).

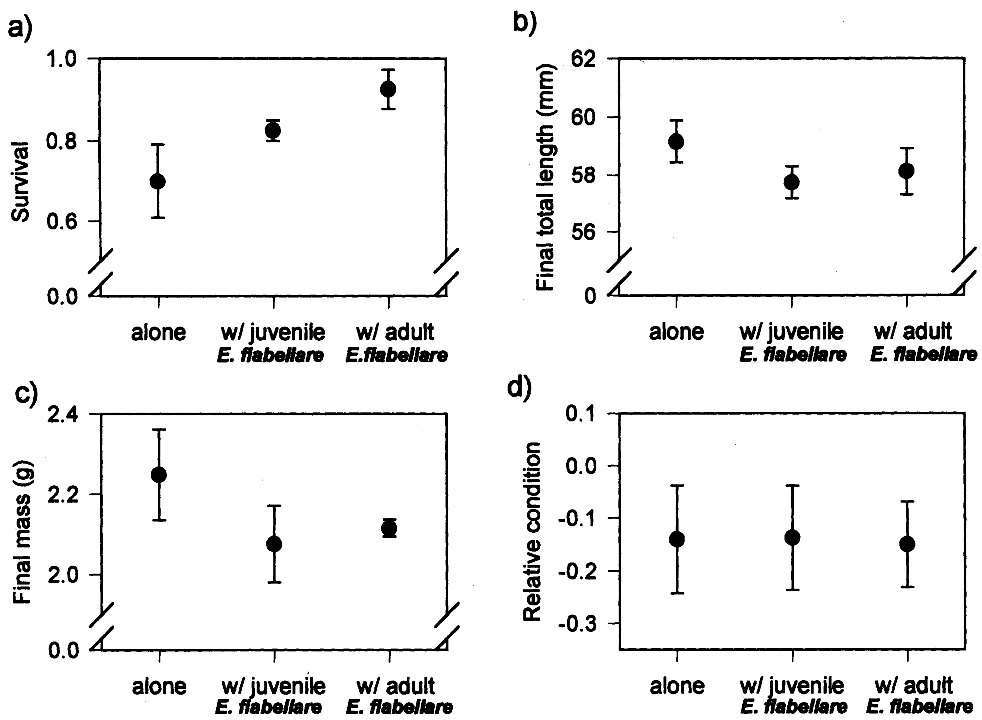

Fig. 2. Responses (mean ± 1 SE) of juvenile *Cottus bairdi* by treatment for (a) survival, (b) mean final TL, (c) mean final mass, and (d) relative condition. The baseline for relative condition is the regression line of mass on length for 314 wild-caught *Cottus bairdi* from Craig Creek (see text and Fig. 4a).

Neither juvenile nor adult *Cottus bairdi* had any effect on the survival or growth of juvenile *E. flabellare* (Table 2, Fig. 3). Evidence for an effect of *C. bairdi* on juvenile *E. flabellare* comes only from the ANOVA of relative condition. *Cottus bairdi* juveniles and adults (Contrast 1) had a nearly significant negative effect on relative condition ($F_{1,6} = 5.02$, $p = 0.066$, Table 2, Fig. 3d) resulting primarily from a significant negative effect of juvenile *C. bairdi* (Contrast 2) ($F_{1,6} = 7.24$, $p = 0.036$, Table 2, Fig. 3d). Adults themselves (Contrast 3) had no effect on relative condition.

Evidence to reject the null hypothesis of no interaction between the two species (from the perpective of *E. flabellare*) comes strictly from the effect of juvenile *C. bairdi* on relative condition of juvenile *E. flabellare*.

Patterns of response to interspecific competition

The clearest result is that juveniles of the two species compete with one another at realistic densities, and competition was detected using ecological variables potentially related to population dynamics. Juveniles of the two species, however, responded to interspecific competition in strikingly different ways. Mass/length regressions for *C. bairdi* alone and *C. bairdi* with juvenile *E. flabellare* were virtually identical ($t = 0.613$, $p > 0.05$, two-tailed test for homogeneity of slopes, Fig. 4a), and fell below the regression line based on the field sample. There was no difference between the condition of *C. bairdi* alone and with juvenile *E. flabellare*; juvenile *C. bairdi* responded to competition from juvenile *E. flabellare* by decreasing their growth in terms of both mass and TL.

In contrast, juvenile *E. flabellare* responded to competition from juvenile *C. bairdi* with a decline in condition relative to *E. flabellare* raised alone. These individual differences translate into significantly different mass/length regressions for juvenile *E. flabellare* in the presence of *C. bairdi* and juvenile *E. flabellare* alone ($t = 4.73$, $p < 0.001$, two-tailed test for homogeneity of slopes, Fig. 4b). Both regression lines fell above the line based on the field sample. Juvenile *E. flabellare* responded to competition from juvenile *C. bairdi* by adjusting their length-specific mass relationship.

Discussion

Densities of juvenile fishes can be high in natural populations, and density-dependent processes (including interspecific competition) may be most likely at this stage where the range of potential food and habitat resources are limited by size, gape, physical capabilities (e.g. swimming ability), and vulnerability to predators (e.g., Werner et al. 1983, Fraser and Emmons 1984, Mittlebach 1984, Werner 1986, Schlosser 1987, 1988,

Table 1. ANOVAs and ANCOVAs for the responses of juvenile *C. bairdi*. A priori contrasts test the following null hypotheses: 1) no effect of *E. flabellare*, 2) no effect of juvenile *E. flabellare*, 3) no effect of adult *E. flabellare*. Survival values were arcsine square root transformed before analysis.

ANOVA of survival

Source	df	Type III SS	Mean square	*F*	*P*
Contrast 1	1	0.1688	0.1688	7.41	0.035
Contrast 2	1	0.0368	0.0368	1.62	0.251
Contrast 3	1	0.2702	0.2702	11.86	0.014
Block	3	0.1750	0.0583	2.56	0.151
Treatment	2	0.2763	0.1382		
Error	6	0.1367	0.0228		
Total	11	0.5880			

ANCOVA of mean final TL

Source of variation	dF	Type III SS	Mean square	*F*	*P*
Contrast 1	1	5.6194	5.6194	8.40	0.034
Contrast 2	1	4.8310	4.8310	7.23	0.043
Contrast 3	1	3.7064	3.7064	5.54	0.065
Mean initial TL	1	2.7125	2.7125	4.06	0.100
Block	3	12.4605	4.1535	6.21	0.039
Treatment	2	5.7122	2.8561		
Error	5	3.3430	0.6686		
Total	11	22.2518			

ANCOVA of mean final mass

Source of variation	dF	Type III SS	Mean square	*F*	*P*
Contrast 1	1	0.0973	0.0973	7.67	0.039
Contrast 2	1	0.0762	0.0762	6.01	0.058
Contrast 3	1	0.0707	0.0707	5.57	0.065
Mean initial TL	1	0.0756	0.0756	5.96	0.059
Block	3	0.0911	0.0304	2.39	0.185
Treatment	2	0.0975	0.0487		
Error	5	0.0634	0.0127		
Total	11	0.3286			

ANOVA of relative condition

Source	df	Type I SS	Mean square	*F*	*P*
Contrast 1	1	0.00002	0.00002	0.00	0.971
Contrast 2	1	0.00002	0.00002	0.00	0.971
Contrast 3	1	0.00017	0.00017	0.01	0.921
Block	3	0.22779	0.07593	4.75	0.050
Treatment	2	0.00034	0.00017		
Error	6	0.09590	0.01598		
Total	11	0.32403			

Persson and Greenberg 1990). Competition induced mortality can directly affect recruitment, while variation in juvenile growth may affect reproductive output via changes in size and age at first reproduction. Variation in growth may also indirectly affect survival by increasing the time spent at smaller, more vulnerable size-classes (Wilbur et al. 1983, Werner and Gilliam 1984, Tonn et al. 1986). Similarly, effects on condition may increase susceptibility to predators, disease, parasites and overwintering stress. Thus, events early in life-history can dramatically affect population dynamics and assemblage structure in fish (Persson 1988).

In this experiment, juveniles of *C. bairdi* and *E. flabellare* competed in experimental streams at densities well within the range observed in their natal streams, while adult *E. flabellare* facilitated survival of juvenile *C. bairdi*. The sign reversal in the effect of *E. flabellare* with changing life stage adds complexity to the interaction between these two species and supports the idea that the net effect of species on one another, even for generalist predators such as these (and even without the complication of intraguild predation), must be integrated over the entire size/stage range (Polis 1984, Werner and Gilliam 1984, Resetarits 1995b).

This positive effect of adult *E. flabellare* on juvenile *C. bairdi* is intriguing, and contrasts sharply with the lack of response of juvenile *E. flabellare* to adult *C. bairdi*, most of which were large enough to prey on them. Adult *E. flabellare* must either influence intraspecific density-dependent processes which affect mortality, or have indirect positive effects on survival of juvenile *C. bairdi* via the food web; the actual mechanism cannot be resolved with the available data. Positive effects (facilitation) between potential competitors are not uncommon among plants (Goldberg and Barton

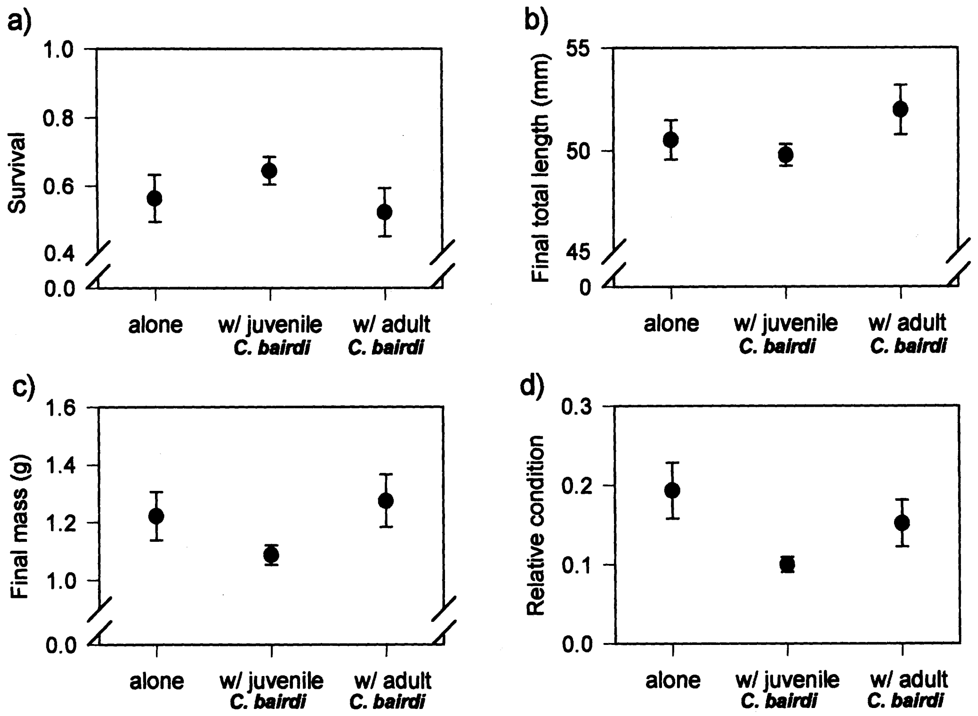

Fig. 3. Responses (mean ± 1 SE) of juvenile *Etheostoma flabellare* by treatment for (a) survival, (b) mean final TL, (c) mean final mass, and (d) relative condition. The baseline for relative condition is the regression line of mass on length for 307 wild-caught *Etheostoma flabellare* from Craig Creek (see text and Fig. 4b).

1992), and examples have begun to surface in animals (e.g., Kotler et al. 1992, Soluk 1993).

Perhaps the most interesting result of this experiment is that the effects of competition manifested themselves differently in the two species. Juvenile *C. bairdi* responded to juvenile *E. flabellare* with decreased growth in both length and mass, but no variation in relative condition or survival, while juvenile *E. flabellare* responded to juvenile *C. bairdi* with a decrease in relative condition, but no variation in either growth or survival. Detecting responses to competition in both species was highly dependent on choosing the appropriate response variables, and the qualitative asymmetry detected focuses attention on an intriguing issue. Both are negative responses to competitors, clearly fitting the pattern of −/− interactions that classically defines competition. However, it is difficult to judge the potential symmetry, since the responding variables were qualitatively different, and have associated with them different levels of potential reproductive cost. At the simplest level (from an ecological perspective), these may be their characteristic initial responses to reduced energy, reflecting differences in their respective developmental programs. Juvenile *E. flabellare* may preferentially allocate resources into increased length, while juvenile *C. bairdi* may require a tighter balance between length and mass. Alternatively, the two responses may be hierarchical, with decreased length-specific mass (condition) preceding decreased growth in length. Although the proximate causes and the ultimate consequences of the different response patterns are unknown, both responses can affect reproductive output. Until we can translate those responses into the common currency of population growth rate, the qualitative asymmetry prevents our assessing the relative intensity of competition experienced by the two species and the potential for quantitative asymmetry.

Determining the relative intensity of intra-versus interspecific competition (Gause 1934) and the symmetry of competitive interactions (Aarssen 1983) are critical to determining the potential for competitive exclusion, and hence, for understanding the role of competition in species coexistence, species diversity and community structure (Aarssen 1983, Connell 1983, Ågren and Fagerström 1984, Resetarits 1995a, b). The ongoing debate on the meaning of 'competitive ability' clearly illustrates the importance of competitive symmetry within the framework of competition theory (e.g. Aarssen 1983, Thompson 1987, Tilman 1987, Grace 1993). Qualitative asymmetries, where species differ in their responding variables, may be a general problem for determining symmetry/asymmetry in systems of competition. A typical assumption in studies of competition is that equivalent responses in specific variables, such as growth or survival, indicate equivalent effects on population dynamics, since for most long-lived organisms determination of population growth rate is difficult. That assumption is itself tenuous, as we seldom

Table 2. ANOVAs and ANCOVAs for the responses of juvenile *E. flabellare*. A priori contrasts test the following null hypotheses: 1) no effect of *C. bairdi*, 2) no effect of juvenile *C. bairdi*, 3) no effect of adult *C. bairdi*. Survival values were arcsine square root transformed before analysis.

ANOVA of survival

Source	df	Type III SS	Mean square	*F*	*P*
Contrast 1	1	0.0014	0.0014	0.05	0.837
Contrast 2	1	0.0228	0.0228	0.74	0.422
Contrast 3	1	0.0074	0.0074	0.24	0.642
Block	3	0.0769	0.0256	0.84	0.521
Treatment	2	0.0574	0.0287		
Error	6	0.1839	0.0306		
Total	11	0.3182			

ANCOVA of mean final TL

Source of variation	dF	Type III SS	Mean square	*F*	*P*
Contrast 1	1	0.1803	0.1803	0.04	0.848
Contrast 2	1	0.7888	0.7888	0.18	0.691
Contrast 3	1	2.4925	2.4925	0.56	0.488
Mean initial TL	1	2.5972	2.5972	0.58	0.479
Block	3	9.2004	3.0668	0.69	0.596
Treatment	2	5.7494	2.8747		
Error	5	22.2362	4.4472		
Total	11	42.0892			

ANCOVA of mean final mass

Source of variation	dF	Type III SS	Mean square	*F*	*P*
Contrast 1	1	0.0058	0.0058	0.22	0.656
Contrast 2	1	0.0323	0.0323	1.25	0.314
Contrast 3	1	0.0022	0.0022	0.09	0.781
Mean initial TL	1	0.0097	0.0097	0.37	0.567
Block	3	0.0689	0.0230	0.89	0.507
Treatment	2	0.0533	0.0266		
Error	5	0.1290	0.0258		
Total	11	0.2729			

ANOVA of relative condition

Source	df	Type I SS	Mean square	*F*	*P*
Contrast 1	1	0.0121	0.0121	5.02	0.066
Contrast 2	1	0.0174	0.0174	7.24	0.036
Contrast 3	1	0.0034	0.0034	1.42	0.279
Block	3	0.0122	0.0041	1.70	0.266
Treatment	2	0.0175	0.0087		
Error	6	0.0144	0.0024		
Total	11	0.0441			

know whether 10% decreases in the individual growth or survival of species A and B produce identical demographic effects. However, comparisons become even more difficult and lose much of the weight of logic when responses differ qualitatively. To assess competitive symmetry or asymmetry under such conditions, we must quantitatively assess population growth rate itself; this is a daunting proposition for many species.

For example, in a study of competition between larvae of two species of salamander, the two were declared competitive equals because the strength of intra- and interspecific competition were equivalent for individuals of both species (Fauth et al. 1990). The effects of intra- and interspecific competition on *individuals* were equal, leading to the assumption that effects on *populations* were equal. This often necessary assumption is rendered far more problematic by a clear qualitative asymmetry; larval sirens, *Siren intermedia*, responded to intra- and interspecific competition with reduced growth, but not survival, while larval newts, *Notophthalmus viridescens*, responded with reduced survival, but not growth. Strong asymmetry in the actual competition coefficients, resulting from the impact of a single newt or siren on siren population dynamics being greater than the effect of a single siren or newt on newt population dynamics (possibly because components of 'competitive ability' may differ; see e.g. Aarssen 1983, Thompson 1987, Tilman 1987, Grace 1993), could lead directly to seemingly equal competitors being unequally represented in the community. The smaller population would face a greater risk of local extinction due to stochastic events, predation, other competitors, etc., potentially leading to local extinction (essentially competitive exclusion). If characteristic responses to density-dependent processes differ, even if the response of individuals to inter- and intraspecific competition are

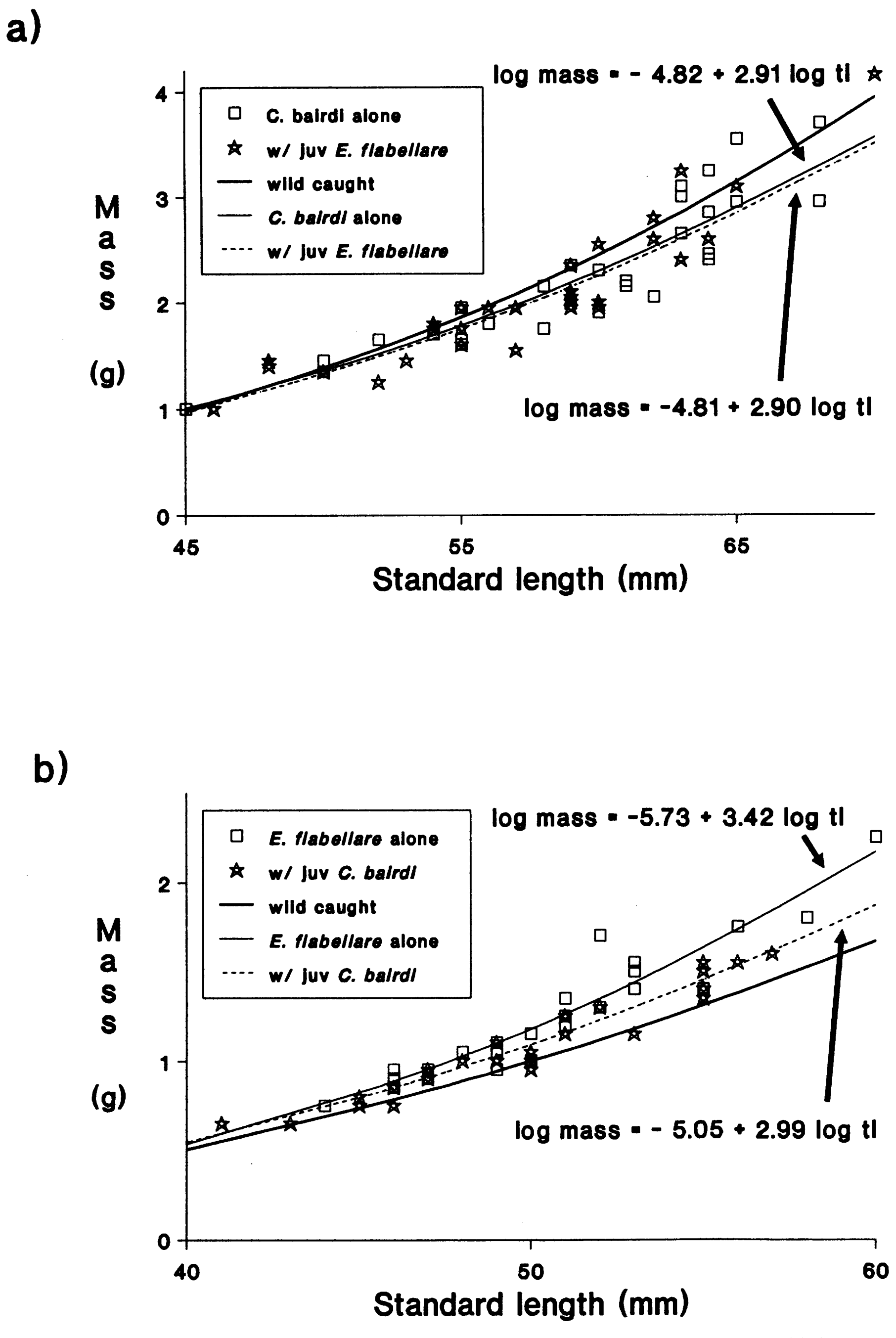

Fig. 4. Plot of mass–length relationships (condition) for a) *C. bairdi*, and b) *E. flabellare*. Heavy solid lines are the regressions for initial field samples of each species (314 *C. bairdi* and 307 *E. flabellare*) from which the experimental animals were taken. Solid lines are the post-experiment regressions for juveniles of each species when raised alone; broken lines are the post-experiment regression lines for juveniles of each species when raised together (see text).

equal, population level consequences are far less likely to be equal.

Since responses to competition can be species-specific (e.g. Fauth et al. 1990, this study), and non-lethal effects of competition (like those of predation) may be very subtle, detection of such responses and their unequivocal ascription to competition require experiments. However, even in controlled experiments, assay of competition remains problematic because we often do not know what variables are critical and, further, what types and magnitudes of effect are meaningful from a population perspective (see Grace 1995). Qualitative asymmetries greatly exacerbate the already daunting problems associated with predicting the outcome and impact of competitive interactions.

Understanding the role of competition in natural communities remains a difficult task that requires a plurality of approaches. Artificial communities are especially useful tools with which to study species interactions in habitats and species assemblages which are difficult to manipulate (such as streams and stream fish) but may harbor a wealth of information on the nature of ecological processes. The demonstration of ecological processes in artificial communities can delineate the potential interactions in their natural models, and describe the potential range of responses to those processes (Morin 1997, Resetarits and Fauth 1997). The demonstration of competitive interactions between juveniles of *C. bairdi* and *E. flabellare*, along with the positive effect of adult *E. flabellare* on juvenile *C. bairdi*, suggest that interactions between these species are potentially complex and may play an important role in the population dynamics of both species. Similarly, the demonstration of qualitative asymmetry in the competitive interactions suggests differences in the responses we might expect in natural communities, and draws attention to a widespread issue that has been largely overlooked but is critical to our understanding the dynamics of competitive interactions.

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References

Aarssen, L. W. 1983. Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. – Am. Nat. 122: 707–731.

Ågren, G. I. and Fagerström, T. 1984. Limiting dissimilarity in plants: randomness prevents exclusion of species with similar competitive abilities. – Oikos 43: 369–375.

Bailey, J. E. 1952. Life history and ecology of the sculpin *Cottus bairdi punctulatus* in southwestern Montana. – Copeia 1952: 243–255.

Barlocher, F. 1980. Leaf-eating invertebrates as competitors of aquatic hyphomycetes. – Oecologia 47: 303–306.

Burton, G. W. and Odum, E. P. 1945. The distribution of small stream fish in the vicinity of Mountain Lake, Virginia. – Ecology 26: 182–194.

Colwell, R. K. 1984. What's new? Community ecology discovers biology. – In: Price, P. W., Slobochikoff, C. N. and Gaud, W. S. (eds), A new ecology: novel approaches to interactive systems. Wiley, New York, pp. 387–396.

Connell, J. H. 1980. Diversity and the coevolution of competitors, or the ghost of competition past. – Oikos 35: 131–138.

– 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. – Am. Nat. 122: 661–696.

Dineen, C. F. 1951. A comparative study of the food habits of *Cottus bairdi* and associated species of Salmonidae. – Am. Midl. Nat. 46: 640–645.

Fausch, K. D. 1984. Profitable stream positions for salmonids: relation specific growth rate to net energy gain. – Can. J. Zool. 62: 441–451.

– and White, R. J. 1981. Competition between brook trout (*Salvelinus fontinalis*) and brown trout (*Salmo trutta*) for position in a Michigan stream. – Can. J. Fish. Aquat. Sci. 38: 1220–1227.

– and White, R. J. 1986. Competition among juveniles of coho salmon, brook trout, and brown trout in a laboratory stream, and implications for Great Lakes tributaries. – Trans. Am. Fish. Soc. 115: 363–381.

Fauth, J. E., Resetarits, W. J., Jr. and Wilbur, H. M. 1990. Interactions between larval salamanders: a case of competitive equality. – Oikos 58: 91–99.

Flecker, A. S. 1992. Fish trophic guilds and the structure of a tropical stream: weak direct vs. strong indirect effects. – Ecology 73: 927–940.

Fraser, D. F. and Emmons, E. E. 1984. Behavioral responses of blacknose dace (*Rhinichthys atratulus*) to varying densities of predatory creek chub (*Semotilus atromaculatus*). – Can. J. Fish. Aquat. Sci. 41: 364–370.

Gause, G. F. 1934. The struggle for existence. – Williams and Wilkins, Baltimore, MD.

Gelwick, F. P. and Matthews, W. J. 1992. Effects of an algivorous minnow on temperate stream ecosystem properties. – Ecology 73: 1630–1645.

Gilliam, J. F., Fraser, D. F. and Sabat, A. M. 1989. Strong effects of foraging minnows on a stream benthic invertebrate community. – Ecology 70: 445–452.

Goldberg, D. E. and Barton, A. M. 1992. Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants. – Am. Nat. 139: 771–801.

Grace, J. B. 1993. The effect of ahabitat productivity on competition intensity. – Trends Ecol. Evol. 8: 229–230.

– 1995. On the measurement of plant competition intensity. – Ecology 76: 305–308.

Greenberg, L. 1991. Habitat use and feeding behavior of thirteen species of benthic stream fishes. – Environ. Biol. Fish. 31: 389–402.

Hairston, N. G. 1980. The experimental test of an analysis of field distributions: competition in terrestrial salamanders. – Ecology 61: 817–826.

– 1989. Ecological experiments: purpose, design, and execution. – Cambridge Univ. Press, Cambridge.

– , Smith, F. E. and Slobodkin, L. B. 1960. Community structure, population control, and competition. – Am. Nat. 94: 421–425.

Hemphill, N. 1991. Disturbance and variation in competition between two stream insects. – Ecology 72: 864–872.

Karr, J. R. 1964. Age, growth, fecundity and food habits of fantail darters in Boone County, Iowa. – Proc. Iowa Acad. Sci. 71: 274–280.

Kottler, B. P., Blaustein, L. and Brown, J. S. 1992. Predator facilitation: combined effect of snakes and owls on the foraging behavior of gerbils. – Ann. Zool. Fenn. 29: 199–206.

Kuehne, R. A. and Barbour, R. W. 1983. The American darters. – Univ. Press of Kentucky, Lexington, KY.

Lake, C. T. 1936. Life history of the fan-tailed darter, *Catonotus flabellaris flabellaris*. – Am. Midl. Nat. 17: 816–830.

Lamberti, G. A., Feminella, J. W. and Resh, V. H. 1987. Herbivory and intraspecific competition in a stream caddisfly population. – Oecologia 73: 75–81.

Lawton, J. H. 1997. Ecological experiments with model systems: the Ecotron facility in context. – In: Resetarits, Jr., W. J. and Bernardo, J. (eds), Issues and perspectives in experimental ecology. Oxford Univ. Press, Oxford, in press.

Lee, D. L. 1980. *Cottus bairdi*. – In: Lee, D. S. et al. (eds), Atlas of North American freshwater fishes. North Carolina State Museum of Natural History, Raleigh, NC.

Lotrich, V. A. 1973. Growth, production, and community composition of fishes inhabiting a first-, second-, and third-order stream of eastern Kentucky. – Ecol. Monogr. 43: 377–397.

Ludwig, G. M. and Norden, C. R. 1969. Age, growth and reproduction of the northern mottled sculpin (*Cottus bairdi bairdi*) in Mt. Vernon creek, Wisconsin. – Milw. Public Mus. Occas. Pap. Nat. Hist. 2: 1–67.

MacArthur, R. M. 1972. Coexistence of species. – In: Behnke, J. (ed.), Challenging biological problems. Oxford Univ. Press, New York, pp. 253–259.

Martin F. D. 1984. Diets of four sympatric species of *Etheostoma* (Pisces: Percidae) from southern Indiana: interspecific and intraspecific multiple comparisons. – Environ. Biol. Fish. 11: 113–120.

Matheson, R. E., Jr. and Brooks, G. R., Jr. 1983. Habitat segregation between *Cottus bairdi* and *Cottus girardi*: an example of complex inter- and intraspecific resource partitioning. – Am. Midl. Nat. 110: 165–176.

Matthews, W. J. and Heins, D. C. (eds) 1987. Community and evolutionary ecology of North American stream fishes. – Univ. of Oklahoma Press, Norman, OK.

McAuliffe, J. R. 1984. Competition for space, disturbance, and the structure of a benthic stream community. – Ecology 65: 894–908.

Mittlebach, G. G. 1984. Predation and resource partitioning in two sunfishes (Centrarchidae). – Ecology 65: 499–513.

Morin, P. J. 1997. Realism, precision, and generality in experimental ecology. – In: Resetarits, Jr., W. J. and Bernardo, J. (eds), Issues and perspectives in experimental ecology. Oxford Univ. Press, Oxford, in press.

Nagel, J. W. 1980. Life history of the mottled sculpin, *Cottus bairdi*, in northeastern Tennessee. – Brimleyana 4: 115–121.

Northcote, T. G. 1988. Fish in the structure and function of freshwater ecosystems: a "top-down" view. – Can. J. Fish. Aquat. Sci. 45: 361–379.

Paine, M. D., Dodson, J. J. and Power, G. 1982. Habitat and food resource partitioning among four species of darters (Percidae: *Etheostoma*) in a southern Ontario stream. – Can. J. Zool. 60: 1635–1641.

Persson, L. 1988. Asymmetries in competitive and predatory interactions in fish populations. – In: Ebenman, B. and Persson L. (eds), Size-structured populations: ecology and evolution. – Springer-Verlag, Berlin, pp. 203–218.

– and Greenberg, L. A. 1990. Juvenile competitive bottlenecks: the perch (*Perca fluviatilis*)-roach (*Rutilus rutilus*) interaction. – Ecology 71: 44–56.

Pflieger, W. L. 1975. The fishes of Missouri. – Missouri Dept of Conservation, Jefferson City, MO.

Polis, G. A. 1984. Age structure component of niche width and intraspecific resource partitioning: can age groups function as ecological species? – Am. Nat. 123: 541–564.

Power, M. E. 1990. Effects of fish in river food webs. – Science 250: 411–415.

– 1992. Habitat heterogeneity and the functional significance of fish in river food webs. – Ecology 73: 1675–1688.

Resetarits, Jr., W. J. 1991. Ecological interactions among predators in experimental stream communities. – Ecology 72: 1782–1793.

– 1995a. Limiting similarity and the intensity of competitive effects on the mottled sculpin, *Cottus bairdi*, in experimental stream communities. – Oecologia 104: 31–38.

– 1995b. Competitive asymmetry and coexistence in size-structured populations of brook trout and spring salamanders. – Oikos 73: 188–198.

– and Fauth, J. E. 1997. From cattle tanks to Carolina Bays: the utility of model systems for understanding natural communities. – In: Resetarits, Jr., W. J. and Bernardo, J. (eds), Issues and perspectives in experimental ecology. Oxford Univ. Press, Oxford, in press.

Ross, S. T. 1986. Resource partitioning in fish assemblages: a review of field studies. – Copeia 1986: 352–388.

SAS Institute. 1988. SAS/STAT User's Guide, Release 6.03 Ed. – SAS Inst. Inc., Cary, NC.

Schlosser, I. J. 1987. The role of predation in age- and size-related habitat use by stream fishes. – Ecology 68: 651–659.

– 1988. Predation risk and habitat selection by two size classes of a stream cyprinid: experimental test of a hypothesis. – Oikos 52: 36–40.

Schoener, T. W. 1983. Field experiments on interspecific competition. – Am. Nat. 122: 240–285.

– 1986. Kinds of ecological communities – ecology becomes pluralistic. – In: Diamond, J. M. and Case, T. J. (eds), Community ecology. Harper and Row, New York, pp. 467–479.

Sih, A., Crowley, P., McPeek, M., Petranka, J. and Strohmeier, K. 1985. Predation, competition, and prey communities: a review of field experiments. – Annu. Rev. Ecol. Syst. 16: 269–311.

Small, J. W. 1975. Energy dynamics of benthic fishes in a small Kentucky stream. – Ecology 56: 827–840.

Soluk, D. A. 1993. Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. – Ecology 74: 219–225.

Statistical Graphics Corporation. 1988. Statgraphics User's Guide. – Statistical Graphics Corporation, Rockville, MD.

Thompson, K. 1987. The resource ratio hypothesis and the meaning of competition. – Funct. Ecol. 1: 297–303.

Tilman, D. 1987. On the meaning of competition and the mechanisms of competitive superiority. – Funct. Ecol. 1: 304–315.

Tonn, W. M., Paszkowski, C. A. and Moermond, T. C. 1986. Competition in *Umbra-Perca* fish assemblages: experimental and field evidence. – Oecologia 69: 126–133.

Werner, E. E. 1986. Species interactions in freshwater fish communities. – In: Diamond, J. and Case, T. J. (eds), Community ecology. Harper and Row, New York, pp. 344–358.

– and Gilliam, J. F. 1984. The ontogenetic niche and species interactions in size-structured populations. – Annu. Rev. Ecol. Syst. 15: 393–425.

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

Wilbur, H. M., Morin, P. J. and Harris, R. N. 1983. Salamander predation and the structure of experimental communities: anuran responses. – Ecology 64: 1423–1429.