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ORIGINAL PAPER

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Limiting similarity and the intensity of competitive effects on the mottled sculpin, Cottus bairdi, in experimental stream communities

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Abstract The identification of potential competitors has been driven by the concept of limiting similarity. Lacking are explicit tests of interaction strength among morphologically similar and dissimilar species. I used the mottled sculpin, *Cottus bairdi*, as a focal species in an artificial stream experiment designed to compare the effect of intraspecific competition to interspecific competition from two very different species: a congener, the Kanawha sculpin (*C. carolinae* ssp.), and an unrelated species, the fantail darter (*Etheostoma flabellare*). The differences in morphology between these two species generate specific predictions under limiting similarity regarding the likelihood of competition and its relative strength: the congener should be a more important potential competitor. Increased fish density had a strong effect on the multivariate response of survival and growth, and on the relative condition of *C. bairdi*, indicating competition. The effect of additional *C. bairdi* or Kanawha sculpins were roughly equal, but the effect of *E. flabellare* was significantly greater. The most important potential impact on *C. bairdi* came from interspecific competition by a species that is smaller and very different in morphology, contrary to predictions based on limiting similarity.

Key words Artificial streams · Competition · Fish · Limiting similarity · Streams

Introduction

The central goal of the study of competition is to determine the importance of competitive interactions in the evolution of new biological forms and in the structure of ecological communities. One of the central themes in the study of competition has been the theory of competitive exclusion (Gause 1934; Vandermeer 1972). The idea that species which utilize similar resources (members of a guild; Root 1967) cannot coexist without changes in niche use has guided our study of competitive interactions. An idea which has become almost inseparable from competitive exclusion is the concept of limiting similarity (MacArthur and Levins 1967). The theory of limiting similarity suggests that there is some maximum level of similarity between species that permits coexistence; similarity beyond that level will result in competitive exclusion (Abrams 1983). Though similarity is defined in terms of resource use, in practice similarity has often been synonymized with morphology, particularly the morphology of trophic structures (Hutchinson 1959). Recent studies have demonstrated that resource use and trophic structures can be independent; species with different morphologies and trophic structures compete exploitatively (Brown and Davidson 1977; Eadie and Keast 1982; Morin et al. 1988; Fauth et al. 1990). Thus, predicting competitive interactions based on taxonomy and morphology becomes problematic; we must test the idea that a species' strongest competitors are its closest relatives.

The potential importance of interspecific competition to a species depends upon the relative intensities of inter- and intraspecific competition (Volterra 1926; Lotka 1932; Gause 1934), and the degree (and consistency) of the asymmetry in interspecific competition coefficients (Aarssen 1983). These two components describe the potential for both competitive exclusion and for selection driven by interspecific (or intraspecific) competition. Thus, we need to focus on understanding the competitive relationships within communities from the perspective of these two important components (Aarssen 1983; Connell 1983).

We know little about the nature of competitive interactions or the role competitive interactions may play in the structure of stream communities. Benthic stream fish (here principally darters and sculpins) are strictly preda-

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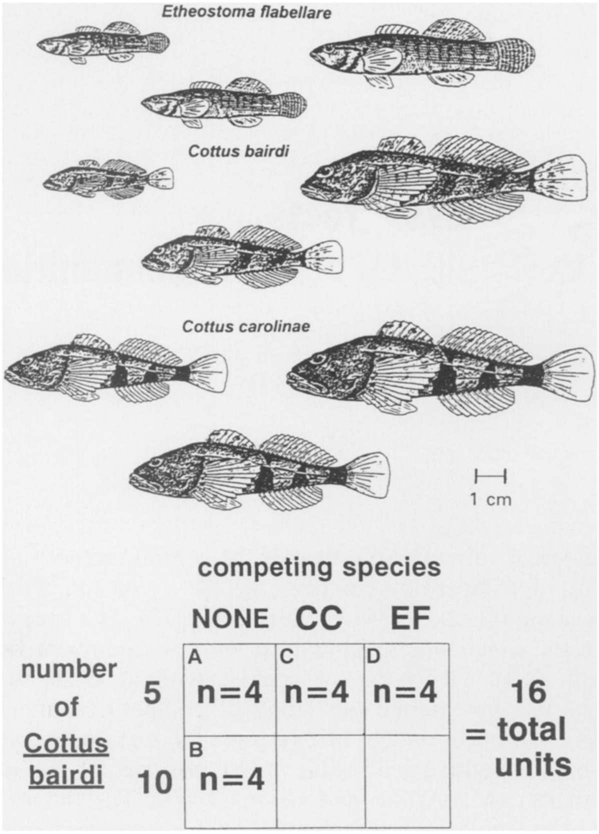

Fig. 1 *Top:* General aspects of comparative morphology and size ranges (far left and far right, respectively) and means (center) for the three species used in the experiment (actual means and ranges in text). Both sculpins (*Cottus* species) are also much broader (dorso-ventrally compressed) than *Etheostoma flabellare*, further increasing the difference in mass/length ratios (see also Fig. 3). The figure illustrates the general relationships between body sizes without attempting to incorporate allometric changes in morphology, or key distinguishing characters; the latter are very fine-grained between the two *Cottus* species (Jenkins and Burkhead 1993). Drawings adapted from Pflieger (1975). *Bottom:* Diagram illustrating the experimental design (*CC Cottus carolinae* ssp., *EF Etheostoma flabellare*). CC streams received four *C. carolinae* ssp., EF streams received five *E. flabellare*. Contrast 1 compares A to B+C+D, contrast 2 compares B to C, and contrast 3 compares B to D. See text for description of contrast null hypotheses. Each treatment was replicated once in each of four spatial blocks

tory, live primarily on and in stream substrates, and are relatively sedentary. Most species feed primarily on in situ and drifting benthic invertebrates. They are abundant in a wide range of habitats, especially in smaller streams across eastern North America, and form an important component of stream communities. These characteristics (and others) make them good subjects in which to examine the nature of potential competition among stream fish. Studies of resource partitioning among benthic stream fish suggest that competition may be an important interaction (e.g., Matheson and Brooks 1983; Schlosser and Toth 1984; see also Ross 1986 and references therein). These studies have demonstrated patterns ranging from fine-grained partitioning of resources along food and habitat axes (Paine et al. 1982), or behavior, habitat and time axes (Greenberg 1991) to generalized food habits among species in diverse assemblages (Hansen et al. 1986).

I focused on the potential competitive environment experienced by a single species that is common in the streams of the New River Drainage in western Virginia. The mottled sculpin, *Cottus bairdi*, is a benthic predator which occurs in a broad range of habitats in clear, relatively swift streams. It was chosen as the focal species for this study because it occurs over a broad range of fish species richness, from very low diversity assemblages in the headwaters of mountain streams to relatively species rich assemblages at lower elevations (Burton and Odum 1945; W.J. Resetarits, personal observation). At the highest elevation sites, characterized by the presence of brook trout, it is the only benthic riffle fish present. As the streams descend the mountains, *C. bairdi* is joined in the benthic riffle habitat by a second species, the fantail darter, *Etheostoma flabellare*. *E. flabellare* is a smaller, morphologically dissimilar species that is closely associated with *C. bairdi* in areas where they co-occur. At lower elevations (in larger stream sections) *C. bairdi* co-occurs with a third species, the closely related but as yet undescribed Kanawha sculpin *C. carolinae* ssp. (Jenkins and Burkhead 1993). *C. bairdi* is closely associated with either one or both of these species throughout much of western Virginia (Burton and Odum 1945; W.J. Resetarits, personal observation). These two species provide interesting contrasts because of the differences in phylogenetic relatedness to *C. bairdi*, and accompanying differences in their size, shape and trophic morphology (Fig. 1).

Morphologically, *Cottus* are large-headed, stout-bodied, dorsoventrally compressed fishes with very wide gapes; *E. flabellare* is a smaller, distinctly fusiform fish with relatively small head and very limited gape. Kanawha sculpins are morphologically very similar, but on average larger, than *C. bairdi* in the streams sampled, while *E. flabellare* are considerably smaller (W.J. Resetarits, personal observation). All three species are highly predaceous, bottom-dwelling fish that occur in similar habitats and share similar habits (Jenkins and Burkhead 1993); all three may occupy a broad range of flow rates, depths, substrate types, etc., particularly in streams where riffle habitats are reduced or unavailable in some seasons (W.J. Resetarits, personal observation). They all feed primarily on benthic invertebrates, though larger sculpins will take fish, including conspecifics (e.g., Daiber 1956; Karr 1964; Nagel 1980; see also Jenkins and Burkhead 1993).

Material and methods

Experimental stream system

The experiment was conducted in an array of 16 replicate experimental streams constructed below a large (approximately 1 ha), spring-fed pond at Mountain Lake Biological Station (MLBS) in western Virginia. No fish occur in the creek feeding into the pond or elsewhere on MLBS, so the pond is permanently fish-free.

Individual streams were constructed from cattle feed bunks 3.35 m long, 0.69 m wide and 0.36 m deep (Resetarits 1991) and were located below the dam of the pond at an elevation of 1150 m. The stream array occupied an area of 7×21 m and consisted of four rows of streams packed as closely as possible to reduce uncontrolled variation. The canopy of vegetation over the array was left intact to emulate natural stream conditions. Streams were adjusted to a gradient of 3.3–4.5 cm/m, resulting in a shallow upstream end and a deeper downstream end. Each stream 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. Outflow was collected and pumped back to the far side of the pond to conserve water during summer months. The 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.

The experimental streams were designed to provide cover and habitat heterogeneity approximating that found in natural streams in the area. Each stream received 0.3 metric tons of unwashed commercial sand, 0.3 tons of commercial river gravel (ranging from 2–20 cm diameter), 4 l of packed leaf litter raked from the forest floor, and one large rock placed beneath the inflow. Flow rate into the experimental streams varied simultaneously and ranged between 30 and 60 l/min during the course of the experiment. All streams were started up at the same time and run continuously until the experiment was taken down.

Experimental design

I used a randomized complete block, incomplete factorial design with a total of four treatments, each replicated once within each of four blocks (16 total units; Fig. 1). The four treatments consisted of (1) five individuals of *C. bairdi* alone, (2) five *C. bairdi* plus an additional five *C. bairdi*, (3) five *C. bairdi* plus five individuals of *E. flabellare*, and (4) five *C. bairdi* plus four individuals of *C. carolinae*. The latter treatment contained only four individuals of *C. carolinae* because of the much larger average size of individuals used in the experiment (see below), which reflected the actual distribution of body sizes in field samples. I did not correspondingly increase the density of *E. flabellare* because I had no a priori expectation of how competitive effects might scale between *C. bairdi* and *E flabellare*, whereas I expected *Cottus* competitive effects to scale with body size across the size range represented here. The design involved a trade-off between simplicity of interpretation (i.e., holding densities constant) and biological reality (i.e., attempting to keep Kanawha biomass reasonable while not altering relative size relationships). The interpretation of the results remains relatively straightforward.

Blocks consisted of single rows in the stream array and treatments were assigned randomly within each block. All fish were collected from streams of the New River drainage in Giles County, Virginia. *C. bairdi* were taken from White Rocks Branch (a tributary of Big Stony Creek), an unnamed tributary of White Rocks Branch, and from Sinking Creek. *C. carolinae* were also taken from Sinking Creek, and *E. flabellare* were collected from Wolf Creek. Animals were weighted to the nearest 0.05 g on a portable field balance (Ohaus Model C151), measured to the nearest 0.01 mm using digital calipers (Mitutoyo), placed individually in numbered containers, ordered by size, and then randomly assigned into the appropriate number of size-stratified sets. Streams were randomly assigned treatments and the size-stratified sets of each species were then randomly assigned to the appropriate streams.

Body size varied both within and among the species used in the experiment, reflecting both the relative sizes of the three species in the natural streams and the intraspecific body size distributions (Fig. 1). *C. bairdi* used in the experiment ranged in initial standard length (SL) from 35.6 mm to 76.5 mm and in initial mass from 0.70 g to 9.20 g (means: SL=55.18 mm, mass=3.60 g). *C. carolinae* ranged from 61.7 mm to 84.6 mm SL and from 3.80 g to 11.40 g in mass (means: SL=73.19, mass=7.74 g). *E. flabellare* ranged in SL from 37.7 mm to 64.4 mm and in mass from 0.65 g to 3.00 g (means: SL=46.87 mm, mass=1.32 g).

C. bairdi were added to the experiment on 14 June followed by the addition of *E. flabellare* and *C. carolinae* on 15 June. The experiment was terminated with the removal of all animals on 8–9 September, after 87 days. Beginning on the evening of 8 September the water was turned off to all streams and each stream was searched repeatedly using a headlamp until no more animals were collected in a full sweep of the 16 streams. The streams were then treated with 1.5 ml of Rotenone to assure that any animals remaining in the gravel and sand were brought to the surface. Fish were held in aquaria and were weighed. measured, and preserved in 10% formalin within 24 h of removal. Fish captured using Rotenone (<5% of total) were processed within 2 h. All introduced animals were removed and processed by 10 September.

Statistical analysis

Response variables for the focal species, *C. bairdi*, were survival, growth, and deviation in relative condition. Percentage survival was arcsine square-root transformed before analysis. Growth was measured both as change in mean SL and change in mean mass. Deviation in relative condition was calculated as the difference between the actual final mass for a given individual (a given SL) and the mass predicted for that individual (SL) from the regression of initial mass on initial SL for the 100 *C bairdi* used in this experiment. A mean for each response variable was calculated for each experimental unit and these formed the units of analysis.

Data were analyzed using analysis of variance (ANOVA), and multivariate analysis of variance (MANOVA), within the PROC GLM procedure of PC-SAS (version 6.03; SAS Institute 1988). Hypothesis testing was accomplished using a priori contrasts testing three hypotheses; contrast 1 tested the null hypothesis of no effect of fish density on *C. bairdi* (1× *C. bairdi* versus all other treatments, A versus B+C+D; Fig. 1); contrast 2 tested the null hypothesis of no difference between the effect of additional *C. bairdi* and the addition of *C. carolinae* (2× *C. bairdi* versus *C. carolinae*, B versus C; Fig. 1); contrast 3 tested the null hypothesis that addition of five *C. bairdi* or *E. flabellare* had equal effects on *C. bairdi* (2× *C. bairdi* versus *E. flabellare*, B versus D; Fig. 1). I concentrated on the responses of the focal species (*C. bairdi*) because the limited number of experimental units did not allow for adequate replication of a full factorial design. Contrast 1 determines whether competition is a factor for the focal species; contrasts 2 and 3 allow me to determine the relative strengths (given the caveat of unequal densities in contrast 2) of intra- and intraspecific competition from the perspective of this focal species.

There were three components in the multivariate response: survival, Δ SL (mean change in standard length) and Δ mass (mean change in mass). Each component of the multivariate response was analyzed individually using univariate analysis of variance, and the three together were analyzed using MANOVA. Wilk's λ was used as the test criterion for MANOVA analyses. Relative condition was analyzed with a univariate ANOVA on the deviation from predicted values. All analyses were interpreted using type III sums of squares.

Results

Main effects

Survival of *C. bairdi* was high in all treatments (mean= 84%), ranging from 75% in the *C. carolinae* treatment to 95% in the 1× *C. bairdi* treatment (Fig. 2). BLOCK was not significant in the ANOVAs of *C. bairdi* survival, Δ SL, Δ mass (Table 1), relative condition (Table 2), or the MANOVA of survival, Δ SL and Δ mass (Table 1).

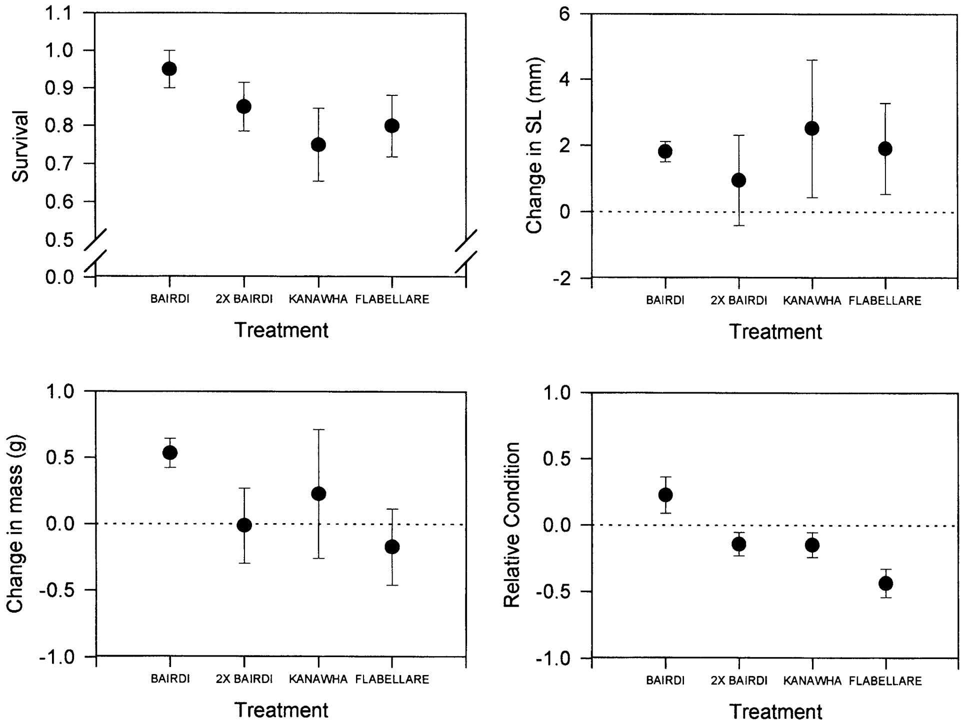

Fig. 2 Responses of *Cottus bairdi* by treatment for survival, change in standard length (SL), change in mass, relative condition

Table 1 MANOVA and individual ANOVAs for responses of *Cottus bairdi.* A priori contrasts test the following null hypotheses: (1) no effect of fish density, (2) no difference between *C. carolinae* ssp. treatment and 2× *C. bairdi* treatment, (3) effect of *C. bairdi* and *E. flabellare* on *C. bairdi* are equal (*SL* standard length)

MANOVA (survival, Δ SL, Δ mass)

Source of Variation	*df*	Wilks' λ	*F*	*P*
Contrast 1	3, 7	0.1647	11.83	0.004
Contrast 2	3, 7	0.8182	0.52	0.683
Contrast 3	3, 7	0.3396	4,54	0.046
Block	9, 17.2	0.2018	1.78	0.146
Treatment	9, 17.2	0.0996		

Source of variation	*df*	SS	MS	*F*	*P*
ANOVA of survival					
Contrast 1	1	0.2436	0.2436	4.42	0.065
Contrast 2	1	0.0274	0.0274	0.50	0.499
Contrast 3	1	0.0076	0.0076	0.14	0.719
Block	3	0.4159	0.1386	2.52	0.124
Treatment	3	0.2710	0.0903		
Error	9	0.4957	0.0551		
Total	15	1.1826			
ANOVA of Δ SL					
Contrast 1	1	0.0009	0.0009	0.00	0.993
Contrast 2	1	4.9401	4.9401	0.51	0.491
Contrast 3	1	1.8351	1.8351	0.19	0.672
Block	3	11.4732	3.8244	0.40	0.758
Treatment	3	5.0200	1.6733		
Error	9	86.3859	9.5984		
Total	15	102.8791			
ANOVA of Δ mass					
Contrast 1	1	0.8023	0.8023	1.60	0.238
Contrast 2	1	0.1149	0.1149	0.23	0.644
Contrast 3	1	0.0508	0.0508	0.10	0.758
Block	3	0.3907	0.1302	0.26	0.853
Treatment	3	1.1252	0.3751		
Error	9	4.5237	0.5026		
Total	15	6.0396			

Table 2 ANOVA for the deviation from predicted condition for individuals of *Cottus bairdi*

Source of variation	ANOVA of relative condition				
	df	SS	MS	*F*	*P*
Contrast 1	1	0.6641	0.6641	11.40	0.008
Contrast 2	1	0.0001	0.0001	0.00	0.976
Contrast 3	1	0.1659	0.1659	2.85	0.126
Block	3	0.0341	0.0114	0.20	0.897
Treatment	3	0.8813	0.2938		
Error	9	0.5241	0.0582		
Total	15	1.4395			

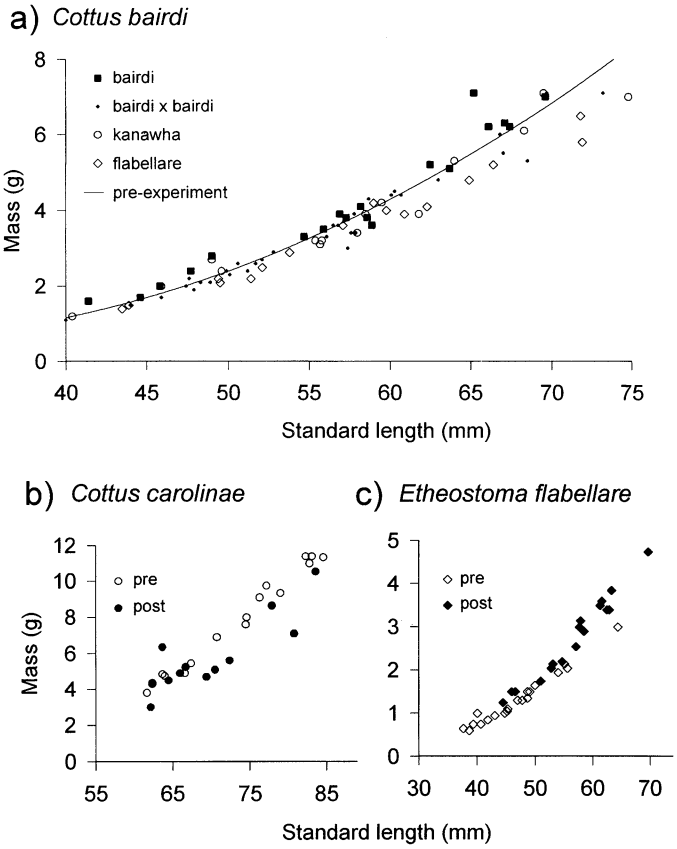

Fig. 3 **a** Condition of *Cottus bairdi* by treatment. *Solid line* is the initial regression of all *C. bairdi* entering the experiment. **b** *Cottus carolinae* ssp. initial (*pre*) and final (*post*) condition, and **c** *Etheostoma flabellare* initial (*pre*) and final (*post*) condition

A priori hypotheses

The contrasts employed in this experiment tested three null hypotheses with respect to *C. bairdi* (Fig. 1); (1) that there was no effect of fish density on *C. bairdi* (no competition), (2) that *C. bairdi* or *C. carolinae* had (approximately) equal effect on *C. bairdi* (densities were not equal), and (3) that *C. bairdi* or *E. flabellare* had equal effect on *C. bairdi* (densities were equal). Contrasts 2 and 3 test the relative intensity (for *C. bairdi*) of intra- versus interspecific competition for the two different competitors. The results from the three contrasts describe the competitive environment experienced by *C. bairdi* in the experimental streams.

There was a trend toward decreasing survival with increased fish density (contrast 1, P=0.065; Table 1; Fig. 2), and a highly significant reduction in the multivariate response of growth and survival under conditions of increased fish density (MANOVA contrast 1, P=0.004; Table 1; Fig. 2). Increased fish density also resulted in a highly significant decrease in relative condition of *C. bairdi* (contrast 1, P=0.004; Table 2; Fig. 2). Contrast 2 was not significant for any of the univariate or the multivariate responses; the effect of adding *C. carolinae* was not significantly different from the effect of adding additional *C. bairdi* (Tables 1, 2; Fig. 2). However, adding *E. flabellare* was significantly different from adding additional *C. bairdi* (MANOVA contrast 3, P=0.046; Table 1; Fig. 2). The effect of *E. flabellare* on *C. bairdi* was significantly greater than that of an equivalent number of *C. bairdi* in spite of the much lower average mass of *E. flabellare*.

There was a strong effect of both intra- and interspecific competition on *C. bairdi* in the experimental streams, and the strength of the effect depended on the species. The two species of *Cottus* were similar in their competitive effects, whereas *E. flabellare* had a greater effect on *C. bairdi* than either *C. bairdi* or its larger congener *C. carolinae*. This effect is more impressive when the difference in size between *C. bairdi* and *E. flabellare* is considered.

Condition of competing *Cottus carolinae* and *Etheostoma flabellare*

Survival was high for both of the competing species: 75% of the *C. carolinae* survived the experiment (12 of 16), and 85% of the *E. flabellare* (17 of 20) survived. Although my experimental design did not allow a rigorous, direct test of the responses of *C. carolinae* and *E. flabellare*, I gained insight into the environment experienced by these two species by examining the condition of the survivors relative to that of the animals originally introduced into the experiment (Fig. 3). For this exploratory analysis only, I used each pre- or post-experiment measurement as the unit of analysis in an analysis of covariance (ANCOVA) with standard length (SL) as the covariate. This removed the variance due to length prior to comparing pre- and post-experiment mass. The covariate

SL was significant at the 0.0001 level for each species. *C. carolinae* survivors showed a highly significant decrease in condition compared to the initial population ($F_{1,25}$=7.87, P=0.01; Fig. 3b). In contrast, *E. flabellare* survivors showed a highly significant increase in condition relative to the initial population ($F_{1,34}$=12.59, P=0.001; Fig. 3c). For comparison, Fig. 3a shows the individual condition by treatment for all surviving *C. bairdi*. Only *C. bairdi* at low density consistently fell on or above the regression line for initial condition. This suggests that the competitive environments experienced by *C. bairdi* at increased density and by competing *Cottus* were similarly severe, but that the competitive environment experienced by *E. flabellare* was relatively benign by comparison. This supports the hypothesis that *E. flabellare* is a strong performer (perhaps superior competitor) under the conditions present in the experimental streams.

Discussion

Competition was a significant factor in the performance of *C. bairdi* in the experimental stream communities. Both intraspecific competition, resulting from an increase in *C. bairdi* densities, and interspecific competition, resulting from the addition of similar numbers of heterospecific competitors, had strong effects on performance in *C. bairdi*. The measures of performance used in this experiment, survival, growth, and condition, are direct measures of the effect of competition. Variables related to size (length, mass, and condition), are known to have strong effects on both survival (Werner and Gilliam 1984) and fecundity (Bagenal 1978) in fish [fecundity is strongly correlated with size in *C. bairdi* (Nagel 1980)]. Thus, effects of competition on growth and condition (in addition to direct effects on survival) can translate directly into effects on fitness.

The intensity of the competitive effect was strongly dependent on the species identity of the competitor. From the perspective of the focal species, *C. bairdi*, the competitive effects of an additional individual of *C. carolinae* and *C. bairdi* are of similar magnitude; addition of five *C. bairdi* was virtually identical to the addition of four *C. carolinae*, suggesting a slightly higher per capita effect of the larger *C. carolinae*. The decreased relative condition of the surviving *C. carolinae* relative to the original population (Fig. 3b) suggests that the competitive interaction may have been reciprocal. In contrast, *E. flabellare* had a significantly stronger effect on *C. bairdi*. *E. flabellare* grew considerably during the experiment and the condition of the survivors exceeded that of the original population (Fig. 3c). *C. bairdi* and *C. carolinae* each grew relatively less and declined in mean condition under competition. The ecological significance of these results is more striking when one considers the differences in size, as illustrated in Fig. 1 (see also Fig. 3).

Although the design of the experiment did not allow a direct test of the asymmetry of the competitive interactions, it is clear that competing fish species are not identical from the perspective of *C. bairdi*.. The two species of *Cottus* are similar in their competitive effects; thus, the intensity of intra- and interspecific competition are approximately equal for *C. bairdi* when competing with *C. carolinae*. In contrast, the intensity of competition from *E. flabellare* is significantly greater than intraspecific competition. If the reciprocal effect of *C. bairdi* on *E. flabellare* is not equivalent (asymmetric competition), *E. flabellare* could locally exclude *C. bairdi*. If the competitive interaction is symmetric, but the intensity of interspecific competition is greater than intraspecific competition for both species, the carrying capacity of each will be reduced by a factor related to their relative abundances (Hairston 1980). Because of its smaller size, *E. flabellare* has the potential to be more abundant at a given level of available resources, further increasing its potential impact on *C. bairdi* (Persson 1985). In competition between species of similar sizes and morphologies, size has frequently been shown to be strongly correlated with competitive ability (e.g., Brown and Munger 1985; Fausch and White 1986; Southerland 1986). In this system, the larger member of the species pair, *C. carolinae*, does have a slightly stronger per capita effect than *C. bairdi*, suggesting that competitive ability does scale with body size in this species pair. However, the strongest competitive effect is produced by the smallest of the three species involved, *E. flabellare*, which also is quite dissimilar morphologically (Fig. 1).

Identification of *E. flabellare* as a significant potential competitor of *C. bairdi* is further evidence of the limitations of the concept of limiting similarity (Hutchinson 1959; MacArthur and Levins 1967; see Abrams 1983 for a review) as a basis for identifying and ranking potential competitors (Brown and Davidson 1977; Morin et al. 1988; Fauth et al. 1990). The idea that competitive exclusion is most likely to occur among closely related species has recently been called into question (Aarssen 1983; Agren and Fagerstrom 1984; Keddy 1989). Similar species are likely to overlap to a greater degree in their resource use, but they are also more likely to be similar in their competitive abilities (Aarssen 1983; Agren and Fagerstrom 1984). Competitive interactions between species which are dissimilar in morphology are frequently strongly asymmetric (Williams 1981; Morin and Johnson 1988; Persson 1988; Bristow 1991; Resetarits 1991, 1995; but see Fauth et al. 1990 for a counter-example), presumably as a result of markedly different capabilities resulting from differing evolutionary histories (Keddy 1989). The potential impact (including the potential for competitive exclusion) of a competitor depends not only on the degree of overlap in exploited resources but also on the intensity of the competition for those shared resources and the degree of asymmetry in the competitive interaction. In my experiment, although morphology would predict that the two species of *Cottus* would have the greatest degree of resource overlap, the relative intensities of intra- and interspecific competition are so similar that it is difficult to imagine consistent asymmetry occurring in this competitive interaction. In contrast, competition from *E. flabellare* satisfies the first basic criterion for competitive exclusion; interspecific competition is stronger than intraspecific competition (Gause 1934), and it has the potential to be consistently asymmetric, which would satisfy the second criterion (Aarssen 1983). Even if the interaction is symmetric the significantly stronger per capita impact of *E. flabellare* implicates this species as an important factor in the ecology of *C. bairdi*

The possible chink in the armor of this study is that the mechanism of competition, exploitative versus interference, is not known with certainty, although it is difficult to imagine that exploitation does not play a major role. The theory of limiting similarity was designed to apply only to pure exploitative competition (MacArthur and Levins 1967), so is it simply a straw man in this case? In attempting to understand the distribution and abundance of species, the important parameters are the net effects of species on one another; we seldom enjoy the luxury of knowing the exact mechanism(s) of competition (Schoener 1983) or of interspecific interactions in general (Polis et al. 1989). Yet, we have gone about identifying potential competitors and testing competition almost wholly within the framework (constraint) of limiting similarity. Our slowness to move beyond studying competition among closely related species, and our resulting inability to address whether closely related species, infact, compete more strongly, is less a failure of limiting similarity than a failure to recognize the very restricted circumstances under which it truly applies. The definitive tests of limiting similarity in situations of pure exploitative competition remain to be carried out, but the general utility of the theory for predicting competitive interactions is being challenged by the growing body of data on competition between morphologically dissimilar species (e.g., Brown and Davidson 1977; Eadie and Keast 1982; Morin et al. 1988; Fauth et al. 1990; Resetarits 1991, 1995).

Our view of the distribution of competitive interactions within communities has been constrained by a rather narrow interpretation of niche theory, limiting similarity and the theory of competitive exclusion (Aarssen 1983; Abrams 1983; Agren and Fagerstrom 1984). Data continue to accumulate which question our ability to predict a priori the strength of competitive interactions based on commonly used criteria related to similarity of morphology or overall resource use. Only by directly measuring the relative intensity of intra- and interspecific competition, the relative impacts of different competing species, and the degree of asymmetry of competitive interactions in a broad range of species and systems can we begin to understand the dimensions of competition and bring about a more rigorous, predictive, and less constrained formulation of competition theory.

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