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STRONG EFFECTS OF FORAGING MINNOWS ON A STREAM BENTHIC INVERTEBRATE COMMUNITY¹

JAMES F. GILLIAM

*Behavioral Ecology Group, Department of Biological Sciences,
State University of New York at Albany, Albany, New York 12222 USA*

DOUGLAS F. FRASER

Department of Biology, Siena College, Loudonville, New York 12211 USA

AND

ALBERTO M. SABAT

*Behavioral Ecology Group, Department of Biological Sciences,
State University of New York at Albany, Albany, New York 12222 USA*

Abstract. Behavioral responses to piscivorous fish are known to alter the spatial distribution of small invertebrate-feeding fish in streams, producing concentrations of small fish in safer areas. We asked whether such variation in the local density of small juvenile creek chubs (*Semotilus atromaculatus*) would, in turn, produce local alterations in the stream benthic invertebrate community. Replicated treatments of 0, 2, and 6 juvenile chubs per 0.5-m² enclosure were established in a warm-water, soft-sediment stream. Over a 3-mo period, the presence of fish resulted in reductions of 79–90% in total invertebrate volume relative to the zero-fish treatments. Numbers were reduced 55–61%. The two major taxa, Oligochaeta and Isopoda, showed strong fish effects, and size distributions of these two taxa showed shifts to smaller sizes. Densities of less abundant taxa (e.g., Chironomidae, Sphaeriidae) showed no statistically significant fish effects. Evenness of the invertebrate community increased in the presence of fish.

No differences in invertebrate densities were detected between the two- and six-fish treatments; however, the above-sediment activity of Oligochaeta was reduced more in the six-fish treatment than in the two-fish treatment, and growth of the fish was slower in the six-fish treatment. Unlike previous experimental studies in stony streams, this experiment shows that foraging fish can significantly alter the behavior, population structure, and community structure of stream benthic invertebrates.

Key words: *community structure; Cyprinidae; eastern North America; experimental streams; fish; foraging; invertebrates; Isopoda; Oligochaeta; predation; Semotilus atromaculatus; streams.*

INTRODUCTION

Many studies have shown that mobile animals do not choose feeding sites randomly. Mobile animals often concentrate feeding activity in areas that yield a greater energy return (reviewed by Stephens and Krebs 1986), but such choices can be greatly modified by the presence of predators, which can cause mobile foragers to reduce use of hazardous areas (e.g., Cerri and Fraser 1983, Werner et al. 1983, Kotler 1984, Power et al. 1985, Sih 1986, Kneib 1987, Newman and Caraco 1987, Holbrook and Schmitt 1988, Rahel and Stein 1988). Since predators alter the spatial distribution and behavior of foragers, we might expect corresponding changes in a third trophic level, the resources of the forager. In this study we asked whether spatial variation in the density of juvenile minnows, whose distribution is known to be altered by predators, alters a stream benthic invertebrate community.

Changes in feeding rate or habitat use in the presence of predators is well documented for stream-dwelling fish. Upon appearance of a predator, stream fish usually reduce their feeding rate (Dill and Fraser 1984, Fraser and Gilliam 1987), and vulnerable individuals alter their habitat use patterns (Fraser and Cerri 1982, Power et al. 1985, Fraser et al. 1987, Gilliam and Fraser 1987, Power 1987, Schlosser 1987). Thus, spatial or temporal mosaics of safety to foraging fish (e.g., within and between pools, between pools and riffles, or across time) could indirectly create a corresponding mosaic in exploitation of the resources of the fish. Indeed, Power et al. (1985) found that herbivorous minnows chose to graze safer areas of a stream more heavily, producing lower algal densities in such regions.

Our own recent work has focused on the creek chub, *Semotilus atromaculatus*, a cyprinid fish that is widely distributed in running waters in eastern North America. The spatial distribution of juvenile chubs in streams is known to reflect both resource levels and predation hazard. In a field experiment, Fraser et al. (1987) found

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that small chubs avoided pools with predatory adult chubs. In an experimental field stream, Gilliam and Fraser (1987) found that small chubs preferred a safer feeding site over a more hazardous site if resources were equal in the sites, but also that chubs shifted to the more hazardous site if the resource level there exceeded a critical value predicted from a model. If resources are depletable, an extension of the model (Gilliam and Fraser 1988) predicts how resource levels would be structured by competitors foraging under predation hazard.

The above experimental work establishes a link between predation hazard and the spatial distribution of foraging fish in streams. However, previous experimental work casts strong doubt on the reality of a link to the third trophic level: i.e., between the presence of foraging fish and measurable alterations of the benthic invertebrate community. Experimental manipulations of fish density in stony streams have usually failed to detect any measurable effects of the presence or absence of fish on stream benthic invertebrate communities (e.g., Allan 1982, Reice 1983, Flecker and Allan 1984, Culp 1986, Reice and Edwards 1986; but see Flecker 1984). In this study, we manipulated the density of juvenile creek chubs in experimental sections of a meandering, soft-sediment stream, to test whether results of previous studies, all of which were conducted in stony streams with apparently higher flow rates, apply to streams of this type.

MATERIALS AND METHODS

Experimental streams

We studied the impact of fish on benthic macroinvertebrates in a warm-water, second-order stream. The stream, located in Albany County, New York, originates 2.7 km west of the study area, from which it continues eastward for another 1.9 km before entering the Hudson River. Between its origin and our study area, the stream meanders (gradient = 19 m/km) first through open fields for 1.6 km and then through 1.1 km of mature deciduous forest. The stream may be classified as a depositing-type stream (Hynes 1974). Over most of its course the bed is composed primarily of silt and mud, although there are some erosional stretches with stones and gravel present. The experimental section of the stream consisted of two parallel wooden channels (14.4 m long, 0.42 m wide, and 0.31 m high with wooden bottoms) laid directly into the bed of the stream. These experimental streams were located downstream of a collecting pool. Water was fed from the collecting pool into the experimental streams through intake pipes, 7.5 cm in diameter, with current maintained at 1–4 cm/s. The up- and downstream ends were screened with 3-mm mesh hardware cloth to prevent entry by indigenous fish.

During a colonization period between November 1985 and July 1986, the experimental streams were

without fish and otherwise undisturbed. The channels developed a natural substratum, ≈ 10 cm deep, consisting of muddy silt, leaves, twigs, and other small organic debris, in which a fauna typical of rich soft substrata developed: i.e., tubificid worms, isopods (*Asellus*), and chironomids (Hynes 1970, 1974). Samples from the muddy bottom of the collecting pool showed the same major taxa (see Results). Other substrata (e.g., stones, leaf packs with abundant plecoptera), present in other sections of the natural stream, were not included in this study. Each experimental stream was divided into 12 compartments, each 1.2×0.4 m. Wooden dividers completely separated the sediments between adjacent compartments, and water flowed between compartments through 3-mm mesh screens at the tops of the dividers. At the beginning of the experiment (August 1986) each compartment was lined with an insert of 3-mm mesh hardware cloth, 80 cm high. The hardware cloth insert prevented escape by fish during torrential rains when the water level sometimes rose to the tops of the wooden channels.

Experimental protocol

We used a randomized block design to test for the effect of young foraging creek chubs on the benthic invertebrate fauna during the period 11 August to 12 November 1986. In 18 pools of the natural stream, the mean (\pm SE) density of creek chubs that were 20–80 mm in total length (Age 0 and I in the autumn) was 5.62 ± 1.09 fish/m² (D. F. Fraser, *personal communication*), which is equivalent to 2.8 fish per compartment in the experimental streams. We bracketed this density by establishing three densities of chubs: zero, two, or six per compartment. Because there were other size classes of creek chubs and also other species in the natural stream, notably blacknose dace, *Rhinichthys atratulus*, at densities similar to those of chubs, these densities were very conservative in asking whether the chubs measurably influenced the invertebrate fauna. The three treatments (zero, two, or six fish) were assigned by random number table to compartments, within each of six blocks (front, middle, or back of each of the two streams) to control for possible differences between streams or positions within a stream. Thus, each treatment was replicated six times.

Forty-eight creek chubs (35–48 mm total length, $\bar{X} \pm$ SE = 41.6 ± 0.44) were stocked into the experimental streams on 11 August. The fish were measured to the nearest 0.5 mm and randomly assigned to treatments. To test for density-dependent growth, the fish were remeasured on 11 September and 12 November, at the end of the experiment.

The benthic invertebrate fauna was sampled on 11 September and 12 November. A core of the substratum, 7.5 cm in diameter, was taken at random coordinates in each compartment. The core was taken to the wooden bottom of the stream, a sediment depth of ≈ 10 cm. The sample was sieved through a 0.3-mm

mesh, and preserved in 70% ethanol. Invertebrates were picked from the remaining particulate matter under a dissecting microscope, and the length and width of each invertebrate was measured to the nearest 0.1 mm. The volumes of approximately cylindrical invertebrates (e.g., Oligochaeta and Chironomidae) were computed as volume = $\pi(r^2 \times \text{length})$. Volumes of remaining prey were calculated from unpublished length–volume regressions. Chironomids were mounted on slides for further identification.

On the 11 September sampling date, we collected six random core samples from the natural collecting pool. The purpose of these samples was to assess whether the experimental streams had been colonized by the same major taxa as occurred in the natural stream. Unlike the six replicates of the experimental treatments, the six cores from the pool did not represent independent treatment replicates (i.e., these were subsamples taken from a single pool). We therefore did not conduct statistical tests of differences between the cores from the pool and those from the zero-, two-, and six-fish experimental treatments.

Data analysis

Oligochaetes were frequently fragmented in the samples, and exact counts were not possible; therefore our main analyses are by invertebrate volume rather than number. For each sampling date, the effect of treatment (zero, two, or six fish) on the volume of each invertebrate taxon was initially analyzed by an analysis of variance on $\log(x + 1)$ -transformed data with stream and position in the stream (front, middle, back) as blocking factors. Block effects were never significant ($P > .05$), and subsequent analysis omitted blocks as a factor. Two planned orthogonal contrasts were computed. Contrast 1 (the “fish effect”) asked whether the zero-fish treatment differed from those containing fish: i.e., (zero-fish) vs. (two- plus six-fish). Contrast 2 (the “density effect”) asked whether the two- and six-fish treatments differed from each other. Contrasts were evaluated with two-tailed t tests on log-transformed data (the transformation successfully homogenized variances). Untransformed means and standard errors are reported in the text.

Invertebrate abundance by number was analyzed in the same way, but fragmentation of oligochaetes in the samples necessitated a way of estimating the number of worms in a sample (usually $>50\%$ of the oligochaete mass was fragmented). We estimated the number of oligochaetes in a sample as $n = v/m$, where v is the total volume of oligochaetes (fragmented and whole) in the sample, and m is the mean of the individual volumes of any whole worms present in samples of the same treatment and date. Obviously, these estimates would be biased by nonrandom fragmentation. Counts of other taxa are exact.

The effects of treatment on evenness (J') and richness (S) of the invertebrate community were analyzed by

the same orthogonal contrasts as above. J' and S were calculated for each replicate, with $J' = H'/H_{\max}$, where $H' = -\sum p_i \ln p_i$, $H_{\max} = \ln S$, and p_i = proportion of a sample (by volume) composed of taxon i . We calculated J' at the taxonomic level of family.

Tubificid oligochaetes often respire by waving their posterior portions in the water column, and we have observed that, in aquaria, creek chubs are more likely to attack protruding worms than those retracted below the surface. Once attacked, protruding worms usually temporarily retract below the sediments. We estimated above-sediment activity of the oligochaetes as follows. On 12 August, in each compartment we marked an area, 25×25 mm, in which oligochaetes were abundant. Once a day in midmorning, on 12 d between 12 and 29 August, an assistant scored the activity of the majority of worms in each area as retracted or protruding. We defined “activity” of the worms at each of the three treatments as $p = (\text{number of observations scored “protruding”})/(\text{total number of observations})$. Treating p as a binomial parameter, we calculated 95% confidence intervals on p by the method of Fisher and Yates (Zar 1984).

RESULTS

Invertebrate densities

The total volume of invertebrates per sample was significantly reduced by fish on both the September and the November sampling dates (Table 1). The reductions were 79–90% in the two- and six-fish treatments compared to the zero-fish treatment on each date, and the “fish effect” was statistically significant for each date (Contrast 1, $P < .05$ for each date separately). However, the total invertebrate volume did not differ between the two- and six-fish treatments (Contrast 2, $P = .26$ for September and $P = .75$ for November).

Table 1 shows that the most abundant (by volume) invertebrate taxa in the absence of fish were oligochaetes ($>95\%$ Tubificidae, primarily *Limnodrilus udekemianus*) and isopods (*Asellus*). Together, these taxa comprised 91% of the volume in the zero-fish treatments in September and 83% in November. Substantial reduction in the presence of fish was apparent for both oligochaetes and isopods (Contrast 1, $P < .05$ for each taxon on each date, except $P = .07$ for isopods in November). However, neither oligochaete density nor isopod density differed significantly between the two- and six-fish treatments (orthogonal contrast 2, $P > .48$ for each taxon on each date). The volumes of bivalves (family Sphaeriidae, 0.9–2.7 mm length) and chironomid larvae ($>90\%$ Tribe Chironomini, mainly *Micropsectra* and *Chironomus*) showed no significant treatment effects. Large (7–26 mm length) *Sialis* nymphs (family Sialidae) formed most of the volume in a few samples, but were rare numerically (see below).

Invertebrate density by number showed fish effects

TABLE 1. Invertebrate abundances as $\bar{X} \pm SE$ volume (mm^3) per 42 cm^2 core. *P* values refer to orthogonal contrast comparing 0-fish vs. 2- plus 6-fish treatments. No significant differences (NS) were detected between the 2- and 6-fish treatments.

	0 fish	2 fish	6 fish	<i>P</i>	Collecting pool
11 September					
All invertebrates	552.8 ± 145.7	84.8 ± 26.4	122.5 ± 28.8	<.05	18.5 ± 3.7
Oligochaeta	446.1 ± 145.0	43.7 ± 11.1	43.6 ± 21.5	<.05	5.8 ± 1.5
Isopoda	58.6 ± 19.2	3.6 ± 1.7	12.5 ± 12.0	<.05	0.5 ± 0.4
Bivalvia	36.4 ± 13.0	12.0 ± 4.4	18.6 ± 7.8	NS	6.4 ± 1.9
Chironomidae	7.4 ± 2.7	6.3 ± 3.9	16.3 ± 9.0	NS	4.0 ± 1.2
Sialidae	0.0	18.7 ± 18.7	28.4 ± 13.6	NS	0.0
Other*	4.4 ± 2.3	0.7 ± 0.6	3.2 ± 1.7	NS	1.8 ± 0.6
Evenness (<i>J'</i>)	0.42 ± 0.06	0.58 ± 0.09	0.64 ± 0.05	<.05	0.73 ± 0.05
12 November					
All invertebrates	714.3 ± 180.5	232.3 ± 47.6	215.9 ± 48.3	<.05	
Oligochaeta	402.3 ± 206.9	83.0 ± 16.5	85.5 ± 24.6	<.05	
Isopoda	189.9 ± 116.7	35.9 ± 28.2	23.1 ± 16.0	NS	
Bivalvia	44.4 ± 13.7	23.9 ± 9.8	17.0 ± 3.2	NS	
Chironomidae	44.9 ± 16.3	21.8 ± 7.7	18.4 ± 5.0	NS	
Sialidae	7.9 ± 7.9	48.2 ± 48.2	56.1 ± 39.9	NS	
Other*	24.9 ± 11.3	19.6 ± 8.6	16.0 ± 8.6	NS	
Evenness (<i>J'</i>)	0.48 ± 0.09	0.61 ± 0.04	0.61 ± 0.05	NS	

* The "other" category includes, in descending order in the 0-fish treatment, Gastropoda, Tipulidae, Ostracoda, Coleoptera, Hirudinea, and Ceratopogonidae.

similar to those revealed by analysis of volumes (Table 2). The total number of individuals was sharply reduced by fish (reductions of 55–61%), and reflected strong reductions in the two major taxa (oligochaetes and isopods). Densities by number in the two- and six-fish treatments were remarkably similar.

The experimental compartments contained the same major taxa as the natural collecting pool (Tables 1 and 2). Oligochaetes and isopods would appear to be less abundant in the collecting pool (which was subject to long-term exploitation by the entire natural fish community) than in the zero-fish treatment which excluded fish, but we make no statistical comparisons between replicated experimental treatments and subsamples from the single natural pool (see Methods).

Evenness of invertebrate taxa

Evenness, *J'*, of the invertebrate taxa increased in the presence of fish in September ($P < .05$), but showed

no significant treatment effect in November ($P = .10$; Table 1). Increased evenness reflected marked reductions in oligochaetes and isopods, while other taxa were more constant among treatments. In September, oligochaetes and isopods formed only 50% of the invertebrate volume in the compartments containing fish, vs. 91% in the zero-fish compartments. Similarly, in November these two taxa formed 51% of the volume in fish-containing compartments, vs. 83% in the zero-fish compartments. The increase in evenness ($J' = H' / \ln S$) reflected an increase in diversity, H' ($P < .05$), and not a change in richness, S ($P > .50$). These results were unchanged if sporadically occurring *Sialis* were excluded.

Invertebrate size distributions

Oligochaetes and isopods, whose abundance reflected a significant fish effect, also showed shifts in size distributions in the presence of fish. The body width

TABLE 2. Invertebrate abundances by number of individuals. Otherwise same as Table 1.

	0 fish	2 fish	6 fish	<i>P</i>	Collecting pool
11 September					
All invertebrates	278.4 ± 74.9	107.8 ± 23.8	118.0 ± 44.1	<.05	18.5 ± 4.0
Oligochaeta	227.6 ± 73.9	87.5 ± 22.3	87.3 ± 43.1	<.05	5.3 ± 1.7
Isopoda	27.8 ± 5.0	4.7 ± 2.2	8.8 ± 7.7	<.05	0.7 ± 0.5
Bivalvia	14.8 ± 6.1	8.5 ± 3.8	6.7 ± 1.5	NS	4.3 ± 1.4
Chironomidae	7.0 ± 2.3	6.2 ± 2.7	13.0 ± 2.5	NS	5.3 ± 1.3
Sialidae	0.0	0.2 ± 0.2	0.7 ± 0.3	NS	0.0
Other	1.2 ± 0.6	0.8 ± 0.3	1.5 ± 0.6	NS	3.7 ± 1.7
12 November					
All invertebrates	172.8 ± 48.3	77.6 ± 14.7	76.7 ± 11.1	<.05	
Oligochaeta	102.1 ± 52.5	33.1 ± 6.6	34.1 ± 9.8	<.05	
Isopoda	16.8 ± 9.3	5.2 ± 3.1	2.0 ± 1.2	<.05	
Bivalvia	9.3 ± 3.2	3.8 ± 1.4	6.7 ± 3.1	NS	
Chironomidae	28.5 ± 8.9	24.5 ± 4.9	26.0 ± 5.8	NS	
Sialidae	0.2 ± 0.2	0.5 ± 0.5	0.7 ± 0.4	NS	
Other	15.8 ± 6.3	10.5 ± 4.8	7.3 ± 2.5	NS	

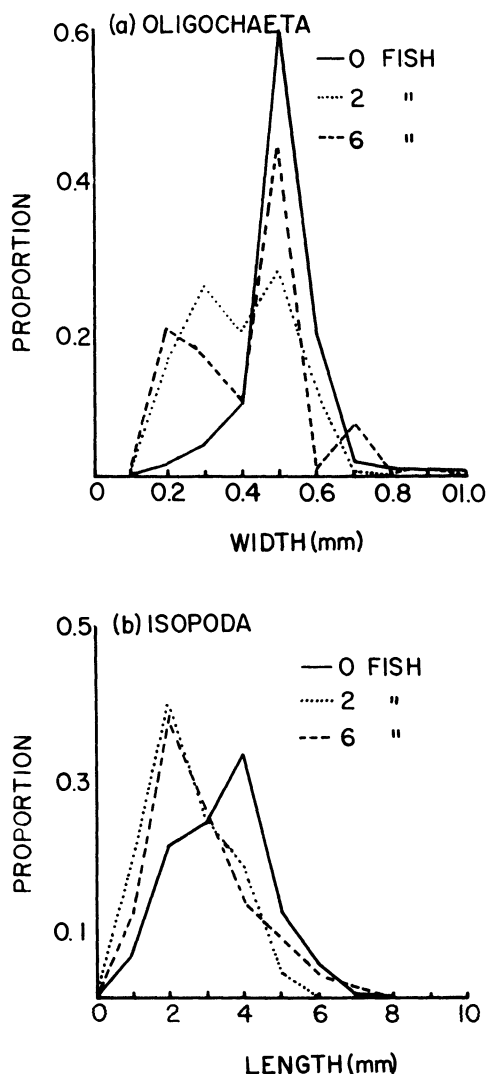


FIG. 1. Shifts in the size-distributions of the two major taxa (oligochaetes and isopods) in the presence of fish.

distribution of oligochaetes (Fig. 1) showed a shift towards smaller size classes in the presence of fish (the distribution is the proportion of total volume in each width class, because fragmentation precluded exact counts of individuals, but the distributions are based on at least several hundred individuals). This pattern held in both September and November.

Size distributions of isopods also showed a shift towards smaller sizes when fish were present (Fig. 1). Size distributions in the absence and presence of fish were significantly different (distribution by number; Kolmogorov-Smirnov two-sample test, $P < .05$ in September and in November).

Fish growth

Results for invertebrate abundances and size distributions revealed strong effects of the presence of fish, but also a conspicuous absence of strong effects be-

TABLE 3. Density-dependent growth by creek chubs ($\bar{X} \pm SE$).

	Treatment		P
	2 fish	6 fish	
Change in length (mm)			
11 August to 11 September	4.8 ± 0.4	3.0 ± 0.5	<.01
11 September to 12 November	3.0 ± 0.5	1.1 ± 0.3	<.01

tween the two- and six-fish treatments. However, growth of the creek chubs was dependent on fish density (Table 3, two-tailed t tests, $n_1 = n_2 = 6$ compartments, $P < .01$). Growth was greater over the 11 August–11 September interval than the longer 11 September–12 November interval, presumably reflecting consumption of initially abundant resources, and/or the influence of higher summer temperatures. Variances of the final length distributions did not differ between the two- and six-fish treatments (pooling replicates, $\bar{X} = 49.64$, $s^2 = 3.53$, $n = 12$ for the two-fish density, and $\bar{X} = 45.20$, $s^2 = 3.79$, $n = 36$ for the six-fish density; F test on variances, two-tailed, $P > .50$).

Oligochaete activity

Activity of oligochaetes was reduced in the presence of fish, and the decline was greater in the six-fish treatment than the two-fish treatment (Table 4). Thus, although oligochaete abundance in the cores did not differ between the two- and six-fish treatments (Tables 1 and 2), availability of the oligochaetes to fish apparently differed between these treatments.

DISCUSSION

Our results support the hypothesis that stream fish can significantly influence benthic invertebrate communities. Notably, in years that are favorable for recruitment, warm-water streams can have high densities of young minnows (family Cyprinidae), 20–45 mm in length (Mendelson 1975, Fraser and Sise 1980), which typically form loose aggregations in every pool and backwater (Mendelson 1975). In such areas the impact of fish on the invertebrate fauna should be substantial. This conclusion strongly contrasts with findings of recent experimental work with salmonid fish in streams (Allan 1982, Culp 1986, Reice and Edwards 1986). Thorp (1986) concluded that fish rarely affect the struc-

TABLE 4. Activity of oligochaetes (proportion protruding above sediment) at the three fish densities.

Fish density (no./compartment)	Activity		P
	Mean	95% CI	
0	.819	.742–.900	<.05
2	.278	.178–.398	
6	.014	.0004–.075	

ture of benthic invertebrate communities in either lentic or lotic waters. However, Healey (1984), reviewing a similar but slightly earlier literature, reached the opposite conclusion for lentic waters, and although he acknowledged that a fish effect in lotic waters had not been found, he predicted that "... some significant consequences of fish predation to stream-dwelling insects will soon be demonstrated." Indeed, Flecker (1984) studied a stream invertebrate community in which $\approx 85\%$ of the individuals were chironomids. He did not find a significant reduction in chironomids across a gradient of sculpin (*Cottus* spp.) densities in cages, but he did find greater numbers of chironomids and a stonefly (*Leuctra*) in cages that excluded fish, compared to cages that were open to fish, chiefly blacknose dace, *Rhinichthys atratulus* (family Cyprinidae), and sculpins, *Cottus bairdi* and *C. giardi* (family Cottidae). However, Flecker de-emphasized the effect by concluding that strong fish effects are likely only in taxa which are not replenished rapidly by drift from upstream (e.g., chironomids and *Leuctra*), or in slow-flowing waters. Nine other insect categories were unaffected by fish in Flecker's (1984) study. Flecker and Allan (1984), in a study in the same stream, found no effect of closed vs. open cages on the abundance of *Leuctra* or other insects, but chironomids were not counted. Similarly, Reice (1983) found no difference in invertebrates between fish enclosures and plots open to a community of several fish species, mainly cyprinids and centrarchids. Allan (1983) and Flecker and Allan (1984) reviewed other literature, and discussed several hypotheses for the lack of fish effects in stream experiments.

Our stream differed from those in previous experiments in several ways, and it is not yet clear what properties of streams will predict the strength of fish effects. Our experiment is the first to treat soft sediments, and coarser substrata in stony streams may represent more effective refugia than burrows in sediments. This may not be true for chironomids, which showed no significant fish effect in our study, but did in Flecker's (1984) study. The density of fish in our natural stream also appears to exceed those in the other studies, especially studies of salmonids. Notably, in his seminal study, Allan (1982) estimated that there were 647 trout in his 1220-m experimental section, and this corresponded to a density of 0.125 fish/m². By comparison, the mean density of fish ≥ 20 mm in pools in our natural stream was at least 5.6 fish/m². However, Reice and Edwards (1986) stocked a brook trout (*Salvelinus fontinalis*) fry into each of their 600-cm² enclosures, for a density of 17 fish/m², and they reported natural densities similar to ours. Our experiment may also differ from others in the potential for immigration by invertebrates to obscure fish effects. Flecker (1984), Culp (1986), and Reice and Edwards (1986) all emphasize that immigration by mobile forms can mask any local fish effects, especially at high flow rates, and

they suggest that immigration was probably important in their studies. By contrast, our major taxa do not appear frequently in the drift (e.g., Mendelson 1975), and our flow rates were lower than those reported in the other studies. With few exceptions (Thorp and Bergey 1981, Hanson and Leggett 1986), studies done in the littoral zone of ponds, which lack flowing water, have documented fish effects on both total invertebrate abundances and/or population size structure (Crowder and Cooper 1982, Gilinsky 1984, Morin 1984, Mittelbach 1988, and references therein). Further, recent experiments on trout in pools of slow-moving streams show fish effects on the abundance of some taxa (S. Cooper and N. Hemphill, *personal communication*; see also Hemphill and Cooper 1984). Because the obscuring effect of migration is likely to depend on the area/perimeter ratio of fish cages, experiments comparing entire pools (S. Cooper and N. Hemphill, *personal communication*) or larger sections of streams (the design of Allan 1982) may be more powerful than experiments with small cages in streams.

The presence of fish caused strong effects in our experiment, but the data fail to reveal significant differences between the volumes and numbers of invertebrates in the two- and six-fish treatments (4 and 12 chubs/m²), suggesting that resources were sensitive to fish density over some interval between 0 and 4 chubs/m², but insensitive at higher densities. We are hesitant to conclude, however, that increases in density beyond 4 fish/m² would not produce changes in invertebrate abundances in a longer term experiment. All compartments were fishless and developed a dense invertebrate community over the 8-mo colonization period prior to the introduction of fish, and we feel it is likely that the full effect of the fish was not realized over the subsequent 3-mo period. By November, volumes of isopods, bivalves, chironomids, and the "other" category suggested a greater effect in the six-fish treatment (but the volumes of oligochaetes did not). In addition, the densities of at least oligochaetes and isopods were clearly lower in the collecting pool, which contained a normal fish community and was not subjected to a fishless period; however, the differences cannot be unambiguously assigned to fish effects. The collecting pool was subject to normal flooding, while the experimental chambers were protected from strong flood currents and washouts.

Given that the resource levels in the two- and six-fish treatments were similar, the density-dependent growth of the creek chubs may be surprising. We feel this result probably reflects the lower activity of the oligochaetes at the higher fish density, and thus an effect of resource depression (*sensu* Charnov et al. 1976) rather than depletion. Density-dependent growth on identical resource levels as measured in core samples would also be expected if some fraction of the standing crop becomes "available" at some identical rate in each treatment, but that "available" fraction is simply di-

vided among more fish at higher densities. Increased interference competition at the higher density could also explain density dependence, but the fact that variances in final body sizes were similar in the two treatments fails to provide positive evidence for this hypothesis.

Our main conclusion is that fish can alter the abundance and size structure of major invertebrate taxa in soft-bottom slow streams. This means that factors which alter fish density in different areas of a stream will tend to indirectly structure the local invertebrate community. Predation hazard is known to structure fish density on at least three spatial scales: shifts in depth within pools (Power 1987, Gilliam and Fraser 1988), shifts between pools and riffles (Schlosser 1987), and shifts between pools with and without predators (Fraser et al. 1987). Fish should tend to structure stream invertebrate communities across these same spatial scales, and spatial variation in physical factors to which fish respond, such as water velocity, should have analogous effects. Recolonization of depleted areas would tend to counteract patterns of fish-induced patchiness, and other processes, such as periodic scouring from floods (Fisher 1983), would tend to counteract or possibly reinforce these patterns. The relative strengths and time scales of these various factors will determine the strength of correlations between the feeding activities of fish and spatial structure of invertebrates.

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