

Effects of snails and fish on benthic invertebrate assemblages in a headwater stream

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Abstract. At natural densities in enclosures in an eastern Tennessee headwater stream, snails (*Elimia clavaeformis*) and juvenile creek chubs (*Semotilus atromaculatus*) affected benthic invertebrate assemblages. *Elimia* reduced the total number of invertebrates without affecting total invertebrate biomass. Conversely, creek chubs reduced the total biomass, but not the total number of invertebrates. No interaction was detected between snail and fish effects on either total invertebrate biomass or abundance. Both taxa appeared to affect the benthos by direct and indirect trophic pathways. *Elimia* reduced the abundance of non-tanypodine chironomids, apparently by interference. *Elimia* also appeared to reduce the abundances of some predators of benthic insects (salamanders [*Desmognathus fuscus*], dragonfly nymphs [*Lanthus* sp.], and young-of-the-year creek chubs). Juvenile creek chubs (55–70 mm total length [TL]) excluded young-of-the-year chubs (15–25 mm TL) from the enclosures and appeared to reduce the abundance of dragonfly nymphs. These changes may have increased the abundances of herbivorous/detritivorous insects such as the stonefly *Leuctra*. Multiple regression analyses indicated that snail and fish mass were more important than light in determining the total biomass and numbers of invertebrates in the channels.

Key words: snails, fish, predation, benthos, stream, food webs, interference.

Animal populations are often influenced simultaneously by a variety of biotic interactions, including those that involve multiple trophic levels or other indirect pathways. Studies showing that predators can maintain prey diversity by consuming competitively dominant prey species provide familiar examples of these kinds of interactions (cf. Paine 1974, 1980, Morin 1983, Duran and Castilla 1989). However, predation may not mediate competition if the dominant competitor is not consumed by the predator. For example, predation by fishes in headwater streams may have little effect on competitive interactions between herbivorous snails and aquatic insects unless the snails are consumed by the fish.

Interactive effects of fishes and snails on stream benthos have not been examined, nor is there a consensus on the direct effects of these two common taxa on the benthos. In some studies, fish predation has been shown to have, at most, weak effects on the abundances of benthic stream invertebrates (Allan 1982, Reice 1983, Flecker and Allan 1984, Culp 1986, Reice and Edwards 1986). Other studies, in contrast, have shown significant effects of fishes on inverte-

brate abundances (Flecker 1984, Gilliam et al. 1989, Schlosser and Ebel 1989, Power 1990). These studies have identified a wide variety of factors that may influence the outcome of interactions between fish and invertebrates, including species of fish present, taxonomic composition of the benthos, and substrate type. Cooper et al. (1990) recently illustrated that prey immigration/emigration rates strongly influence the outcome of predator/prey experiments in streams.

Studies of snail grazing in streams and other freshwater habitats have frequently focused on the effects of snails on algal biomass, productivity, and assemblage structure (e.g., Sumner and McIntire 1982, Steinman et al. 1987, McCormick and Stevenson 1989, Lamberti et al. 1989). The effects of snails on other invertebrates have received less attention (Hawkins and Furnish 1987, Cuker 1983). However, some evidence exists that herbivorous snails can reduce abundances of other grazing invertebrates, particularly small sedentary species. In Oregon streams, for example, the abundance of the snail *Juga silicula* is inversely correlated with the abundances of some invertebrate taxa. Additionally, experimental reduction of *Juga* density in one stream channel resulted in an increase in abundance of other invertebrates,

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particularly chironomids (Hawkins and Furnish 1987). The grazing snail *Lymnaea* reduced the abundances of more sedentary invertebrates in cages in an arctic lake (Cuker 1983).

In the southeastern United States, creek chub (*Semotilus atromaculatus*) and snail grazers in the genus *Elimia* frequently dominate the biomass of vertebrate and invertebrate faunas in headwater streams. Adult creek chubs are omnivorous cyprinids; juveniles of this species feed largely on benthic invertebrates during summer (Keast 1966, Barber and Minckley 1971). Although Gilliam et al. (1989) and Schlosser and Ebel (1989) showed that creek chubs can reduce abundances of benthic invertebrates in experimental stream channels, field studies have not been conducted to examine the effect of *Elimia* on other invertebrates. In this study, we used field enclosures to examine the effects of creek chubs and *Elimia clavaeformis* on benthic assemblages in a shaded Tennessee headwater stream, using an experimental design that allowed us to detect interactions between the effects of these two common animals. We also compared the effects of fish and snails on the benthos with that of natural variation in light using multiple regression.

Study Area

The study was conducted in Ish Creek, a second-order stream on the U.S. Department of Energy's Oak Ridge Reservation in eastern Tennessee (35°54'N, 84°22'W). Base flow of Ish Creek during summer is ~3 L/s, whereas thunderstorm-induced spates may increase discharge to >200 L/s. The stream is extensively shaded by riparian vegetation; incident photosynthetically active radiation (PAR) averaged less than 3.4 E m⁻² s⁻¹ over 24 h for the enclosures used in this study. In summer, the stream is composed of a series of small pools (commonly 1–2.5 m wide and 2–8 m long, and 15–50 cm deep). These pools are separated by short, shallow riffles largely uninhabitable by fishes; the gradient in the study reach is ~1.5%. Creek chubs and blacknose dace (*Rhinichthys atratulus*) dominate the fish fauna (50 and 35%, respectively, by numbers of individuals).

Methods

We manipulated the densities of creek chubs and *Elimia* within Plexiglas channels oriented

parallel to the flow of water. The channels were constructed in side-by-side pairs; each member of a pair was 30 cm wide × 1.2 m long with walls 40 cm high. The ends of the channels were covered with 6-mm mesh plastic screen. Ten pairs of channels were placed in pools at sites with similar water depths and velocities. Water velocity inside and outside the channels in these pools was 0–2 cm/s; water depth in the channels ranged from 15 to 18 cm at base flow. Gravel from the streambed was placed in each channel to a depth of 4 cm, and cobbles were added at natural densities.

The experiment used a split-plot design, with each pair of channels serving as a whole plot. Creek chubs were manipulated on the whole-plot scale: both channels of a given pair contained either creek chubs at natural density (two fish per channel) or no fish. Snails were the subplot factor: within each pair of channels, one channel contained *Elimia* at natural density (144 snails per channel), and the other channel lacked *Elimia*. Compared with a complete block design, the design we used provides a relatively powerful test of the snail and snail × fish interaction factors, but it provides a weaker test of the fish effect (Kirk 1982). Plots were limited to a pair of channels by the size of the stream.

The natural density of creek chubs was determined by electrofishing. The natural density of *Elimia* was estimated by counting snails within a quadrat (0.05 m²) tossed into the stream at 44 locations throughout the study reach. Snails and fish were added to appropriate channels on 15 June 1988 and 21 June 1988, respectively. The snails used in the channels were collected from Ish Creek; individuals too large to fit through the mesh at the ends of the channels were selected. We obtained juvenile creek chubs (55–70 mm total length [TL]) from Ish Creek by electrofishing. These fish were held in the laboratory for 3–5 d; each fish was weighed before being used in the experiment.

Every 1 to 2 d during the 50-d experiment, we removed small *Elimia* that immigrated into the channels and any debris that accumulated on the screens. Small snails capable of passing through the plastic screens were easily distinguished by their size from the snails we had added. Immediately after each of two spates (13 and 26 July), fine sediment was gently swept from surfaces within each channel to a level approximating the sediment of the surrounding streambed.

Before sampling the benthos at the end of the experiment (11 August), we collected snails and fish that were added to the channels and counted salamanders (*Desmognathus fuscus*) and young-of-the-year creek chubs that colonized the channels. Juvenile creek chubs were returned to the laboratory for weighing.

We sampled the benthos in each channel in two steps. First, all cobbles within a channel were gently removed and washed by hand in a water-filled bucket. This water was then poured through a 0.3-mm sieve. Second, the channel was closed at each end with plexiglass panels fitted with foam rubber borders, and the contents of the channel were thoroughly stirred by hand. We then poured 40 L of water from the channel through the 0.3-mm sieve. Samples were stored in 70% ethanol. Invertebrates were enumerated under a dissecting microscope and weighed. The total weights of invertebrates from the 20 preserved samples were measured on the same date.

Total biomass and total abundance of invertebrates were analyzed by ANOVA. Effects with $p < 0.05$ were considered significant for these planned contrasts. Individual taxa found in all four treatment combinations and with average abundances of at least three per channel (14 of 28 taxa found) in any one treatment combination were analyzed individually. A type I error rate of 0.05 was divided equally among the 14 taxa ($p < 0.0036$ for significance). Abundance data were logarithmically transformed if Bartlett's test indicated heterogenous variances among treatment combinations. We also examined, but did not analyze statistically, abundance data for two relatively large-bodied taxa of interest (gomphid nymphs and young-of-the-year creek chubs) which were not found in each treatment combination.

We examined the influence of fish, snails, and incident light levels on total invertebrate biomass and total invertebrate numbers by multiple regression. This analysis was motivated by the fact that total primary productivity in the channels was highly correlated with incident light (Hill and Harvey 1990). Dependent variables in this analysis were wet mass of juvenile creek chubs, ash free dry mass of snails (shell removed), and photosynthetically active radiation. PAR was measured with three Ozalid paper light meters positioned above each channel and exposed for a 24-h period during the experiment (Friend 1961).

We also compared the rank abundances of invertebrate taxa within the channels with their abundances on natural substrates. We used pooled data from the five +fish/+snail channels for this comparison. Rank abundances on natural substrates were determined by pooling data from ten samples (Hess sampler, 0.363-mm mesh) taken adjacent to the ten pairs of channels at the end of the experiment. The two sets of ranks were compared with Spearman's rank correlation coefficient.

Results

Invertebrate assemblages that developed in channels containing natural densities of both fish and snails were similar to those sampled outside the channels. Rank correlation of the abundances of taxa in the +fish/+snail treatments with those in samples from natural substrates was 0.94 for the ten most abundant taxa in the channels ($p < 0.001$) and 0.81 for the 20 most abundant taxa ($p < 0.001$). The average weight change for juvenile creek chubs in the channels did not differ from zero over the 50-d experiment (t -test, $p = 0.12$).

Snails reduced the total numbers of invertebrates by 33% ($p = 0.04$, Fig. 1). This effect resulted largely from the strong effect of snails on non-tanypodine chironomids ($p < 0.01$), which were the most abundant taxon in the benthos (Table 1). Salamanders were also less abundant in the channels that contained snails (Table 1). The analysis also suggested negative effects of snails on leptophlebiid mayflies ($p = 0.07$) and young-of-the-year creek chubs (Table 1). Snails did not affect total invertebrate biomass ($p = 0.73$, Fig. 1).

In contrast to snails, juvenile creek chubs did not significantly reduce the total numbers of invertebrates ($p = 0.22$, Fig. 1) nor the abundances of any individual invertebrate taxon (Table 1). However, fish did reduce total invertebrate biomass by 42% ($p = 0.01$, Fig. 1). Juvenile creek chubs also excluded young-of-the-year creek chubs (15–25 mm TL) from channels (Table 1). However, the abundance of the stonefly *Leuctra* was greater in channels containing juvenile fish (Table 1).

The effects of fish and snails tended to be additive (i.e., no interaction), including their effects on total invertebrate numbers and biomass (fish \times snail interaction, $p = 0.99$ and 0.42, respectively). Abundances of gomphid nymphs

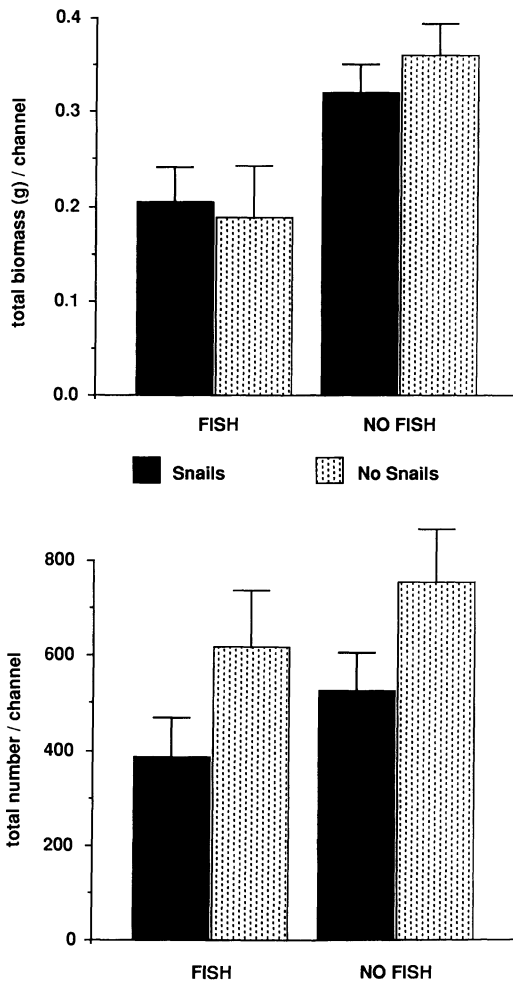


FIG. 1. Effects of juvenile creek chubs and *Elimia* on the total biomass and numbers of invertebrates in instream channels in Ish Creek, Tennessee. Vertical bars = 1 SE.

suggested an interaction: nymphs were absent from +fish/+snail channels, and relatively rare in +fish/-snail channels compared with -fish/-snail and -fish/+snail channels (Table 1).

Multiple regressions of total invertebrate numbers and biomass versus fish mass, snail mass, and light (PAR) corroborated the ANOVAs for those two dependent variables. Snail mass was the only significant factor in the multiple regression with total number of invertebrates as the dependent variable (Table 2). Likewise, fish mass provided the only significant partial regression coefficient for total invertebrate biomass (Table 2).

Discussion

At least three mechanisms could explain the negative effect of snails on herbivorous invertebrates evident in this study: (1) resource alteration, (2) interference, and (3) habitat alteration. In this experiment, snails increased the productivity of the tightly attached layer of periphyton but did not alter its biomass; snails also prevented the accumulation of upper, more loosely attached layers of periphyton (Hill and Harvey 1990). Thus, exploitative effects of snails on other invertebrate grazers are likely to depend on the specific food preferences of the latter. "Bulldozing" interference by snails is probably most important for smaller taxa such as chironomids, which have relatively low mobility (Cuker 1983). This hypothesis is supported by our present study and that of Hawkins and Furnish (1987). Measurements of snail activity indicate that at their natural density in Ish Creek, snails will pass over a given point on the substrate >3 times per day (A. J. Stewart, Oak Ridge National Laboratory, unpublished data). Finally, snails reduced the accumulation of silt throughout the channels they occupied. Animals with preferences for fine sediment, such as gomphids, may thus be affected negatively by snails.

If snails reduce the numbers of some insect taxa (particularly small chironomids), they may have negative indirect effects on predators of these taxa (Hawkins and Furnish 1987). For examples, this hypothesis could explain the low density of salamanders in +snail treatments, as well as the apparent effects of snails on gomphid nymphs and young-of-the-year creek chubs. Chironomids and small taxa in general are abundant in the diets of immature *Desmognathus fuscus* (Wilder 1913, Burton 1976, Krzysik 1979). The diet of gomphids in a North Carolina stream (the same gomphid genus as that found in Ish Creek) consisted of ~20% chironomids (Wallace et al. 1987). Chironomids also dominate the diet of chubs <30 mm TL in Ish Creek (B. Harvey, unpublished data). An indirect trophic pathway of this type, however, did not link *Elimia* to the growth of juvenile creek chubs; weight change of juvenile chubs was not affected by the snails. The small chironomids negatively affected by snails are probably not a major component of the diet of chubs 55–70 mm TL.

TABLE 1. Abundances of taxa as mean (and SE) number per channel under different treatment combinations. p values are derived from ANOVA. $p(\text{fish})$, $p(\text{snail})$, and $p(f \times s)$ are the probability values for the fish main effect, the snail main effect, and the fish \times snail interaction, respectively.

	–fish/–snail	–fish/+snail	+fish/–snail	+fish/+snail	$p(\text{fish})$	$p(\text{snail})$	$p(f \times s)$
Chironomidae							
Non-Tanypodinae	411.2 (53.3)	234.8 (37.1)	292.0 (56.2)	155.8 (41.5)	0.11	*	0.61
Tanypodinae	86.6 (19.3)	83.0 (24.0)	82.4 (25.1)	61.8 (21.9)	0.64	0.53	0.66
Psephenidae							
<i>Psephenus</i> ^a	50.0 (27.2)	28.4 (11.0)	15.0 (6.0)	16.0 (8.5)	0.47	0.78	0.49
Leptophlebiidae							
<i>Habrophlebiodes</i>	48.6 (17.4)	24.2 (6.1)	34.2 (5.9)	29.0 (6.2)	0.71	0.07	0.21
Cyclopoida	41.6 (11.1)	34.6 (16.0)	52.8 (23.7)	21.8 (6.2)	0.97	0.16	0.35
Heptageniidae							
<i>Stenacron</i>	30.8 (7.0)	34.4 (16.5)	28.0 (9.9)	21.4 (7.3)	0.46	0.90	0.67
Oligochaeta	27.6 (6.3)	27.2 (5.8)	41.6 (8.9)	38.6 (6.2)	0.12	0.80	0.84
Ceratopogonidae	19.4 (4.5)	16.4 (4.5)	23.4 (7.9)	9.4 (2.6)	0.79	0.12	0.30
Epemerellidae							
<i>Ephemerella</i> ^a	9.0 (4.8)	12.0 (5.1)	3.4 (1.5)	3.2 (1.5)	0.21	0.54	0.49
Baetidae							
<i>Baetis</i> ^a	6.0 (3.0)	0.8 (0.8)	1.8 (1.1)	0.4 (0.3)	0.24	0.15	0.58
Sialidae							
<i>Sialis</i>	5.8 (1.4)	5.2 (2.0)	5.8 (1.1)	4.0 (1.1)	0.70	0.42	0.69
Plethodontidae							
<i>Desmognathus</i>	3.4 (0.9)	2.0 (0.5)	2.6 (0.4)	0.6 (0.4)	0.18	*	0.40
Elmidae	1.2 (1.0)	2.2 (0.9)	3.8 (1.5)	1.6 (0.9)	0.22	0.67	0.27
Leuctridae							
<i>Leuctra</i> ^a	0.8 (0.5)	4.0 (1.9)	12.4 (4.7)	9.6 (3.2)	*	0.71	0.35
Gomphidae							
<i>Lanthus</i> ^b	2.8 (1.2)	3.0 (2.7)	1.0 (0.3)	0			
Cyprinidae							
young-of-the-year							
<i>Semotilus</i> ^b	2.2 (0.2)	1.4 (0.2)	0	0			

^a Log-transformed before analysis.

^b No ANOVA because of 0 treatment means.

* $p < 0.0036$.

Although juvenile creek chubs reduced the total biomass of invertebrates, they had no effect on the total numbers of invertebrates. The juvenile chubs' reduction of invertebrate biomass appears to be the result of effects on large taxa such as gomphids, and the overall tendency for invertebrate taxa to be less abundant (but not significantly so) in +fish treatments. Where fishes tend to select larger prey, reductions in the numbers of prey by fishes will be difficult to detect, in part because larger taxa are also generally rare. However, large rare taxa often account for a substantial proportion of total invertebrate biomass.

Like snails, creek chubs appeared to have both direct and indirect effects on the benthos. For example, in contrast to the results of Flecker

(1984), we found that the stonefly *Leuctra* was more abundant in +fish channels. Possibly, *Leuctra* benefitted from lower predation pressure by invertebrate predators such as gomphid nymphs in +fish channels. Barber and Minckley (1971) noted that dragonfly nymphs made up ~10% of the diet of 41–60-mm creek chubs from the headwaters of the Mississippi River. Wallace et al. (1987) found that stoneflies were the taxon consumed most frequently by gomphid nymphs in a North Carolina headwater stream. An indirect positive effect of insectivorous fishes on *Leuctra* was unlikely in the stream studied by Flecker (1984), where invertebrate predators were scarce (Flecker and Allan 1984). Exclusion of young-of-the-year creek chubs by juvenile creek chubs from channels provides

TABLE 2. Multiple regressions of total biomass and number of invertebrates (excluding snails) versus fish mass, snail mass, and photosynthetically active radiation (PAR).

Dependent variable	Independent variable	Regression coefficient	p	Partial r^2
Total invert. biomass	Fish mass	-0.08	<0.01	0.44
	Snail mass	<0.01	0.73	<0.01
	PAR	<0.01	0.94	<0.01
Total number invertebrates	Snail mass	-0.3	0.02	0.20
	PAR	64.6	0.21	0.14
	Fish mass	-69.8	0.24	0.06

another possible pathway for positive indirect effects of juvenile creek chubs on the benthos. Because young-of-the-year creek chubs consume primarily small chironomids, abundance of the latter may be indirectly enhanced by the presence of juvenile chubs. Power (1990) found that juvenile fishes enhanced the abundance of chironomid larvae in algal mats in a California river, apparently by reducing abundances of young-of-the-year fishes and invertebrate predators. For individual insect taxa, the relative importance of negative direct effects and positive indirect effects of insectivorous fishes will clearly depend on the diet of the fish and the significance of invertebrate predators. As suggested by Power's study, positive indirect effects may predominate for small herbivorous insects that have a refuge from fish predation because of their size or microhabitat.

Cooper et al. (1990) provided evidence that prey exchange rates can strongly influence the outcome of predator/prey experiments in streams. Strong effects of fishes on the benthos have been found where immigration rates of prey were probably low, in part because of low water velocity (Gilliam et al. 1989, Power 1990, this study). However, two spates during our experiment no doubt strongly affected local distributions and abundances of invertebrates by altering immigration and emigration rates. The immigration rates of benthic invertebrates in experimental settings are also influenced by the characteristics of the experimental units used, particularly mesh size; the 6-mm mesh we used was relatively coarse compared with other studies that have shown significant fish effects (Cooper et al. 1990).

One difficulty with any study using enclosures is that certain treatments are "islands" within natural regions with very different biotic conditions. In our study, channels without fish or snails were very different from the surrounding natural conditions, which may have had important effects on immigration or emigration rates in those channels.

Our study provided virtually no evidence for interactions between creek chubs and *Elimia* effects on the benthos. The fact that creek chubs do not feed on snails reduces the likelihood that fish will alter the effects of snails on other invertebrates. Also, juvenile creek chubs and snails appear to have direct effects on different size components of the benthos (fish, large; snails, small).

Although no indirect food web connection between fish and snails was apparent, both taxa appeared to have indirect effects on benthic insects. However, these indirect pathways were very different. The indirect effects of creek chubs suggested by this study followed the "trophic cascade" pattern and thus appeared positive for some herbivorous insects. The indirect effects of snails suggested by this study are negative; that is, snails may reduce resources for predators of small benthic insects. Indirect effects in food webs are evident in a variety of aquatic systems (e.g., Kerfoot and Sih 1987) and appear to be important for stream benthos as well.

Finally, multiple regression analyses suggested that creek chubs and *Elimia* had stronger effects on the benthos than light did. In contrast, Hill and Harvey (1990) found that light provided control of total primary production in the same system. These two results suggest that "top-down" effects of predation are decoupled from primary production in Ish Creek. Consumption of bacteria and fungi by benthic invertebrates that are also herbivorous (Rounick and Winterbourn 1983) may partially explain this pattern. These results parallel the model of trophic interactions suggested by McQueen et al. (1989) for freshwater pelagic ecosystems: bottom-up control appears strong at the bottom of the food web (primary producers), whereas top-down controls are stronger at higher trophic levels.

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