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ECOLOGICAL INTERACTIONS AMONG PREDATORS IN EXPERIMENTAL STREAM COMMUNITIES¹

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Abstract. Field observations on the effect of brook trout on an assemblage (sometimes described as a guild) of predatory salamanders suggest that the interactions among predators in small, headwater streams may be important in determining the structure of this assemblage of predators and thereby, the predation pressure felt by species at lower trophic levels. The interactions among predators and the potential role of those interactions in headwater stream communities was examined in 16 replicated experimental streams. I examined the ecological interactions among four species of co-occurring predators, adult *Salvelinus fontinalis* (98–122 mm standard length [SL]), larval *Gyrinophilus porphyriticus* (36–58 mm snout–vent length [SVL]), larval *Eurycea bislineata* (13–21 mm SVL), and *Cambarus bartonii* (6–17 mm carapace length [CL]), in an experiment that began in mid-June and ran for 3 mo. Brook trout affected both survival and growth of the larger salamander species, *Gyrinophilus*, and *Salvelinus* and *Gyrinophilus* affected the growth of the smaller salamander *Eurycea* and the crayfish *Cambarus*. The presence of *Gyrinophilus* had no effect on relative condition or fecundity of *Salvelinus*. Larger predators caused *Cambarus* and *Eurycea* to alter their activity levels and habitat, but *Gyrinophilus* made no adjustments to the presence of *Salvelinus*. Results demonstrate that *Gyrinophilus* is vulnerable to predation/aggression from brook trout, but that *Eurycea* and *Cambarus* are able to behaviorally avoid predation by both large predators at a significant cost to growth. The effect of brook trout on the two species of salamander in the experimental streams parallels the observed differences between salamanders in trout and trout-free waters in the field. Thus, interactions among predators in headwater streams directly and indirectly influence population dynamics of the interacting species by affecting survival, growth, behavior, and habitat use. The interactions among these predators can determine, in part, the predation environment experienced by individuals at lower trophic levels.

Key words: biotic interactions; *Cambarus*; complex interactions; *Eurycea*; experimental streams; *Gyrinophilus*; habitat use; headwater stream communities; lotic ecosystems; predation; predator avoidance; *Salvelinus*.

INTRODUCTION

The role of predators in aquatic communities has been documented in marine habitats such as the rocky intertidal (Connell 1961, Paine 1966) and a broad range of freshwater systems from phytotelmata (Maguire et al. 1968, Addicott 1974) and temporary ponds (Wilbur 1972, Morin 1983, Wilbur 1987), to large lakes (Hrbáček 1962, Brooks and Dodson 1965, Carpenter et al. 1987) and streams (Peckarsky and Dodson 1980a, b, Power et al. 1985). The direct and indirect effects of predators can be a dominant force affecting the distribution and abundance of species in these communities (Paine 1980, Vanni 1986). Predation can reduce populations of prey species (Connell 1961, Addicott 1974) and can change the outcome of competitive interactions (Paine 1966, Morin 1983). Predators may influence patterns of prey habitat use (Fraser and Cerri 1982, Werner et al. 1983, Power et al. 1985, Schlosser

1987), activity levels (Stein and Magnuson 1976, Peckarsky 1980, Sih 1982), and distribution of prey species (Peckarsky and Dodson 1980, Petranks 1983). Demographic features such as prey colonization, growth rate, length of larval period, size at metamorphosis, and age at first reproduction can be affected by predators and, along with direct predation, can influence prey population dynamics (Wilbur 1987, 1988, Resetarits and Wilbur 1989).

If prey may be simultaneously affected by more than one predator, the interactions among those predators may have important consequences for prey populations (Fauth and Resetarits 1991). Predator–predator interactions may affect the distribution and population dynamics of the interacting predators and thereby affect the intensity and profile of the predation pressure felt by populations at lower trophic levels.

Field observations on the effect of brook trout on an assemblage (sometimes described as a guild) of predatory salamanders (W. J. Resetarits, Jr., unpublished data) suggested that the interactions among predators in small, headwater streams may be important in determining the structure of this assemblage of predators.

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A small (1 m high), deeply undercut waterfall on the West Upper Fork of Little Stony Creek near Mountain Lake, Virginia, has served as a barrier to brook trout since the early 1940s (Burton and Odum 1945, W. J. Resetaitis, Jr., *personal observation*). The presence of trout in the section below the waterfall appears to have a marked effect on the abundance of salamanders in and along the stream (Fig. 1). A difference in body size between salamanders from the area containing trout and from the trout-free plot was also observed for one species (*Gyrinophilus*), and a difference in the abundance of crayfish (*Cambarus bartonii*) was also noted between trout and trout-free sections. The effects on salamander species were either positive or negative, depending on the species. A positive effect in this system would likely be the result of indirect effects (via direct effects on a competing species). These data suggest that this assemblage of predators changes in a complex way with the addition of brook trout.

The purpose of this study was to determine how the interactions among four species of sympatric predators affect the abundance and size distribution of each predator, and thus, the structure of this assemblage (guild) of predators. The four predators are the larvae of the plethodontid salamanders *Gyrinophilus porphyriticus* and *Eurycea bislineata*, the brook trout *Salvelinus fontinalis*, and the crayfish *Cambarus bartonii*. These species were chosen because they comprised the obligately aquatic portion of this assemblage and because the preliminary data suggested strong interactions among these species.

The a priori expectations for the outcome of these interactions were based on aspects of the life history of the four species. I expected larval *Gyrinophilus* and small adult *Salvelinus* to compete because of similar gape sizes and generalist prey habits. The expected result of competition would be reduced growth with the outcome favoring *Salvelinus*. I expected no effect on the survival of either species because of the similarities in size. The two large predators were each expected to reduce the survival of *Eurycea* and *Cambarus* via predation. Brook trout forage from the water's surface to the substrate, while *Gyrinophilus* forage from the surface of the substrate downward, including under cover objects and in the gravel and sand matrix. *Eurycea* and *Cambarus* forage on the surface of the substrate and in the stream matrix. I expected greater than additive effects based on the prediction that the presence of both predators would leave no safe refuge; avoidance of either predator would involve increased exposure to predation from the other.

STUDY AREA AND SPECIES

Mountain Lake headwater streams

The study was conducted at Mountain Lake Biological Station (MLBS), Giles County, Virginia. The streams in the vicinity of MLBS are principally first-

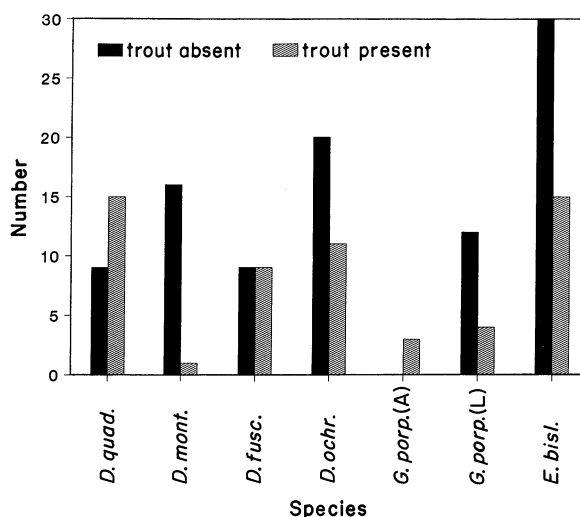


FIG. 1. Number of salamander individuals by species in field plots containing trout (*Salvelinus fontinalis*) and in trout-free plots on West Little Stony Creek. Species are *Desmognathus quadramaculatus*, *D. monticola*, *D. fuscus*, *D. ochraceus*, *Gyrinophilus porphyriticus* adults and larvae, and *Eurycea bislineata*.

and second-order mountain brooks with clear, cool water, running over rubble, gravel, sand, and bedrock, with silt and detritus accumulations in the pools. These mountain brooks occur over elevations from 1200 to ≈ 450 m. The vertebrate fauna increases in diversity as the streams grow larger with lower elevation (Burton and Odum 1945). Uppermost reaches of these streams support diverse salamander assemblages (Organ 1961) containing up to seven species. Most are present from the highest elevation to where the streams enter the low elevation valley floors. Larvae of *Gyrinophilus porphyriticus* and *Eurycea bislineata* are the most common salamanders encountered in the streams at higher elevations. Brook trout, *Salvelinus fontinalis*, are the only fish species present at the highest elevations; additional fish species are added with decreasing elevation (Burton and Odum 1945). The crayfish *Cambarus bartonii* is the most common large invertebrate and the only crayfish in the higher elevation streams.

The species

The brook trout, *Salvelinus fontinalis*, is a dominant fish in clear, cool, headwater streams in the southern Appalachians (Burton and Odum 1945). The species feeds on a wide range of prey items, from zooplankton to fish and frogs; however, terrestrial and aquatic insects, and other aquatic invertebrates make up the bulk of prey taken in most populations (Carlander 1969). The brook trout is the largest predator in most streams it inhabits and can reach sizes of over 200 mm standard length (SL) even at the upstream limit of its distribution in high-elevation, first-order streams.

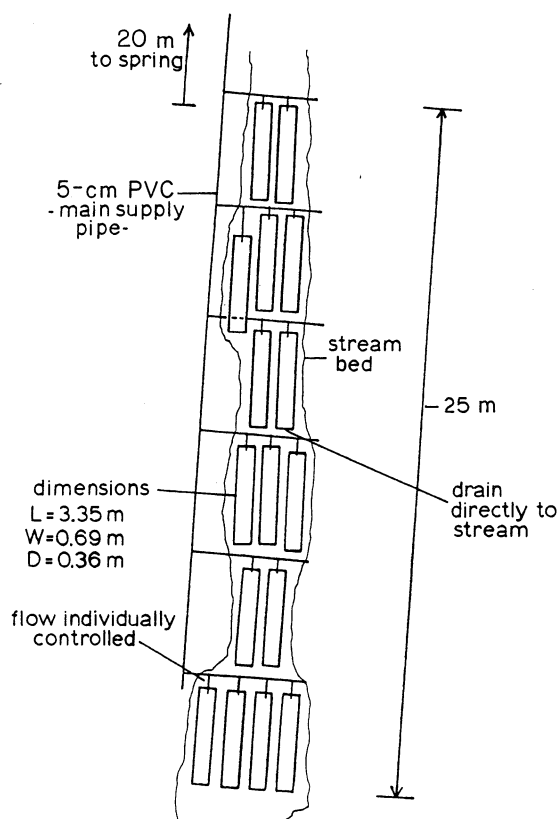


FIG. 2. Schematic diagram of stream array below Sartain Spring, Mountain Lake Biological Station.

The spring salamander, *Gyrinophilus porphyriticus*, is a large semiaquatic salamander common in the Appalachians (Dunn 1926). Larvae attain large (up to 60 mm snout-vent length [SVL]) sizes (Bruce 1980) and may spend up to 4 yr in the aquatic larval stage (Bruce 1980). *G. porphyriticus* larvae are benthic, generalized predators that generally seek shelter under rocks and in the gravel matrix during the day and emerge to forage at night (W. J. Resetarits, Jr., *personal observation*). *Gyrinophilus* larvae reach densities of $\approx 5\text{--}10/\text{m}^2$ in streams near MLBS (W. J. Resetarits, Jr., *personal observation*).

The two-lined salamander, *Eurycea bislineata*, is a small (22–48 mm SVL, postmetamorphic) salamander that lives in and along streams ranging from tiny seeps to large trout streams. Larvae hatch at 8–10 mm SVL and grow to 15–20 mm SVL by fall of the 1st yr (Duellman and Wood 1954, Bruce 1982b). Larvae live in the stream for 1–3 yr before metamorphosing at 18–32 mm SVL (Duellman and Wood 1954, Bruce 1982a, b). Adults are abundant, and the larvae are the most abundant urodele larvae in streams near MLBS. Adults of *E. bislineata* feed on aquatic and terrestrial arthropods (Hamilton 1932, Burton 1976). Larvae feed primarily on immature aquatic insects (Caldwell and Houtcooper 1973, Burton 1976).

Cambarus bartonii is the only species of crayfish native to Salt Pond Mountain and is the only species found in the headwaters of Little Stony Creek (Hobbs and Walton 1966). In these headwaters, *C. bartonii* occurs in all habitats and is extremely abundant (Hobbs and Walton 1966, W. J. Resetarits, Jr., *personal observation*). They may reach large size (>30 mm carapace length [CL]) even in very small streams, though the average individual is much smaller. *C. bartonii* is both a benthic predator and scavenger, feeding on anything it can catch and subdue.

All animals used in this experiment were collected from first- and second-order tributaries of Little Stony Creek, a tributary of the New River, on Salt Pond Mountain, Giles County, Virginia. *Salvelinus fontinalis* were collected from Pond Drain Branch, a second-order tributary containing no other fish, at an elevation of 970 m. *Gyrinophilus*, *Eurycea*, and *Cambarus* were collected in Hunter's Branch, a first-order, fishless tributary of Pond Drain, at an elevation of 1160 m. Individuals of these three species came from above the limit of brook trout in the Pond Drain-Hunter's Branch system, but the populations from which they were drawn are potentially continuous across the trout/no-trout interface.

MATERIALS AND METHODS

Experimental stream system

The experiment was conducted in 16 experimental streams located immediately below a permanent spring at an elevation of 1220 m. Streams were constructed from steel and polyethylene cattle feed bunks 3.35 m long, 0.69 m wide, and 0.36 m deep. The stream array was built in the bed of Sartain Creek, which originates at the spring. The array occupies 25 m of the stream bed and consists of six rows of experimental units packed as closely as possible to reduce uncontrolled variation in experimental conditions (Fig. 2). The canopy of vegetation over the stream array (primarily *Rhododendron maximum*) was left intact to preserve natural stream conditions. Streams were placed directly on the stream bed and leveled to provide a gradient of 3.3–4.5 cm/m, resulting in a shallow upstream end and a deep downstream end.

Water was supplied by a series of interconnected holding tanks (2300 L total capacity) fed directly by spring flow. Each stream was provided with an inflow pipe and an individual valve to control flow rate and drained through a rotating standpipe. The design eliminated any possibility of communication between units, thus assuring their statistical independence. Standpipes were provided with a hood of fiberglass window screening over a frame of plastic gutterguard mesh to prevent the escape of animals. The experimental streams have a 5.5-cm lip along each side, and the ends of the tank were coated with petroleum jelly to prevent escapes. The streams were completely open to the environment

to allow aerial colonization by insects and natural input of terrestrial drift organisms and litter.

The experimental streams were designed to provide adequate cover and to represent the habitat heterogeneity present within natural stream pools (e.g., in such factors as water depth, substrate depth, substrate type, and amount of light). Each stream received 40 L of unwashed commercial sand, 30 L of commercial river gravel, 4 L of packed leaf litter raked from the forest floor near the stream, 1 large spillway rock, 12 flat rocks of varying size, and a 40-cm section of black corrugated plastic drain pipe (Fig. 3). Each ingredient was thoroughly mixed (where appropriate), and aliquots were randomly assigned to individual units.

The flow regime in the experimental streams mimicked the flow regime in the nearby headwater streams on Salt Pond Mountain. The spring output, and therefore the flow regime in the experimental streams, varied with rainfall in much the same manner as local stream flow. Flow rate into the experimental streams varied from a high of 13.5 L/min at the start of the experiment in mid-June to intermittent flow during a severe drought in August and September when nearby natural streams were extremely low and often broken up into isolated pools.

Water temperature varied as a result of both ambient temperatures and flow rate. Water temperatures were between 10° and 18°C for most of the experiment.

Experimental design

The experiment was a randomized complete block design using two species at two densities (0 and X) in a full factorial experiment with four replicates each for a total of 16 experimental units ($2 \times 2 \times 4 = 16$). Blocks were comprised of the closest possible packing of four experimental units, contingent on the limitations of the stream bed (Fig. 2). Treatments were assigned randomly within each block. Treatments consisted of zero or five *Gyrinophilus* or zero or one *Salvelinus* per pool (Table 1). Trout were paired by size and pairs assigned randomly to the four blocks. Individuals within pairs were then assigned randomly to treatments within blocks. Trout ranged in size from 98 to 122 mm SL. *Gyrinophilus* larvae were divided into two size classes and then randomly assigned to each experimental unit by size class; each stream received two individuals from the large size class and three from the small size class. Larvae ranged from 36 to 58 mm SVL.

All streams received 13 larvae of the salamander *Eurycea bislineata*, ranging in size from 13 to 21 mm SVL. *Eurycea* larvae were ranked by size, divided into groups of 17 on that basis and randomly assigned, one per stream, from each size group. One of the 17 randomized groups of larvae was then preserved as a reference sample. Fourteen crayfish (*Cambarus bartonii*) ranging from 6 to 17 mm CL (15–40 mm total length

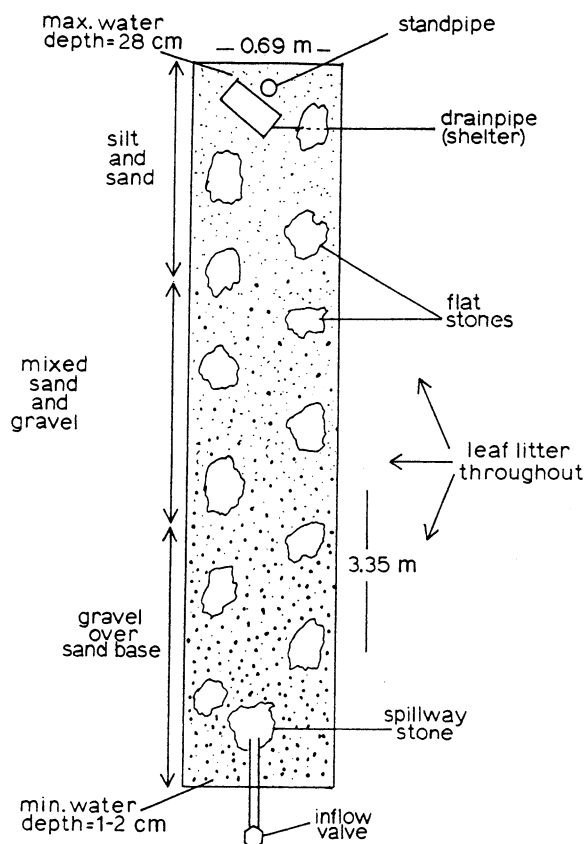


FIG. 3. Schematic diagram of individual experimental streams.

[TL]), were assigned in a like manner to each of the 16 streams, with one group preserved for reference.

Species were added once sufficient numbers of individuals were collected; *Gyrinophilus* on 14 June 1987, *Eurycea* on 18 June, *Salvelinus* on 19 June, and *Cambarus* on 28 June. The experiment was terminated on 24–25 September 1987 with the removal of *Salvelinus* and *Gyrinophilus*. Beginning on 25 September each stream was searched once, leaf litter removed, then searched three more times during which all rocks and the corrugated pipe were removed. Each search involved intensively searching the entire surface area of the stream, including lifting all remaining cover objects. The streams were then treated with 1.5 mL of Rotenone to bring any animals that remained in the gravel and sand to the surface. Streams were then searched twice more. All introduced animals were removed by 28 September.

Habitat use

In order to measure activity levels and habitat use in the experimental streams behavioral observations were made on two dates, 29 July and 26 August. The observations were done at night, between 2000 and

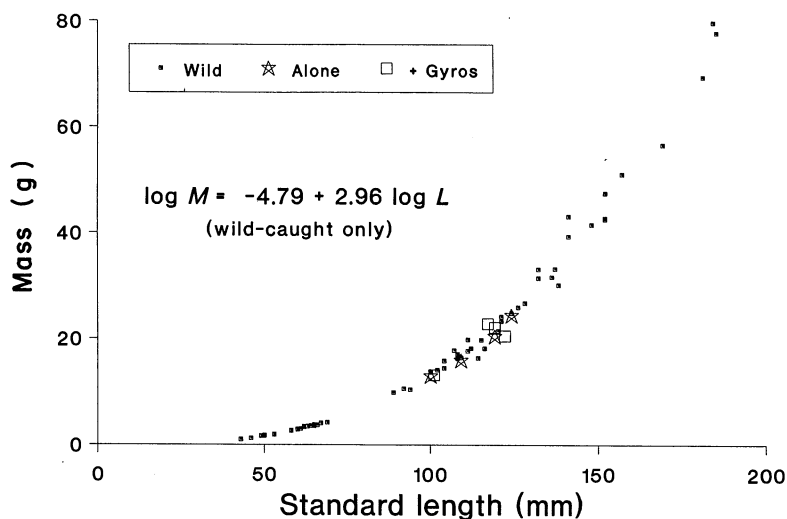
Salvelinus length-mass regression

FIG. 4. Regression of mass on standard length (SL) for 66 wild-caught brook trout from Pond Drain Creek (solid squares). Superimposed are eight experimental animals originally taken at the same locality. Experimental animals spent 100 d in experimental streams, in the presence or absence of *Gyrinophilus*.

2330, and consisted of visual searches of each stream using a headlamp. Streams were not physically disturbed during the searches. The streams were divided into four zones of equal length. Zone 1 was the deep end of the stream and Zone 4 was the shallow end (Fig. 3). Searches were conducted in the same direction on all streams searched on a given night. Individuals were identified to species and their location among the four zones was noted. Use of the headlamp only mildly disturbed animals, and only when they were directly in the beam. The frequency of observations (cover objects were not moved) of the four species was a measure of species-specific activity levels. Location among the zones measured relative habitat use along a natural habitat gradient from pool center (equivalent to Zone 1) to stream edge (equivalent to Zone 4). In the experimental streams this corresponds to a depth gradient of deep to shallow and a substrate gradient of silt-sand-leaf litter to gravel (Fig. 3).

Data analysis

Response variables were survival and growth (change in mass) for *Gyrinophilus*, and survival and body size (mass) for *Eurycea* and *Cambarus*. Response variables for *Salvelinus* were survival, a relative condition factor (K_N), and fecundity. Growth in length was negligible during the experiment, and trout were not weighed at introduction. The condition factor was determined by measuring the deviation from the predicted mass at a given SL based on the regression of log mass on log standard length for a sample of 66 wild-caught brook trout (Fig. 4). These trout were taken in two samples, one on 19 August and one on 24 August 1987, from the same locality that provided the original experimental animals. Relative fecundity (number of ova per millimetre SL) was used to graphically represent the effects of treatments on fecundity; analysis of covariance (ANCOVA) was used to analyze the raw data

TABLE 1. Data summary by species and treatment showing appropriate response variables for each species. KEY: number of individuals introduced in each stream (n), mean percent survival (%), mean growth (G), mean relative condition (K_N), mean relative fecundity (RF), and mean body size (snout-vent length [SVL] or carapace length [CL]).

Variable	<i>Gyrinophilus</i>			<i>Salvelinus</i>			<i>Eurycea</i>			<i>Cambarus</i>		
	n	%	G	n	K_N	RF	n	%	SVL	n	%	CL
Control	0	0	13	27	.37	14	14	14.4
GYRO	5	60	.95	0	13	29	.27	14	25	12.1
SALV	0	1	.95	.66	13	40	.32	14	34	12.6
GYRO + SALV	5	25	.33	1	.98	.66	13	25	.23	14	30	11.7

while factoring out body size. By chance, 7 of the 8 *Salvelinus* were females. Response measures for *Salvelinus* and *Gyrinophilus* were based on responses of individuals. *Gyrinophilus* were individually identified within each stream by drawing (under a microscope) the pattern of lateral line pores on the dorsal surface near the hind legs. These patterns are sufficiently unique and persistent to allow unambiguous identification of individuals in captive populations.

Growth, body size, relative condition, and fecundity were analyzed using analysis of variance (ANOVA) of the complete design for *Eurycea* and *Cambarus* (16 cells), and of a subset of the full design for *Gyrinophilus* and *Salvelinus* (8 cells each). Tukey's hsd was used to test for differences between more than two treatment means. Survival was analyzed using contingency table analysis. Hypothesis testing for survival used Fisher's exact test for 2×2 tables (*Gyrinophilus* and *Salvelinus*) and the chi-square statistic for 2×4 tables (*Eurycea* and *Cambarus*).

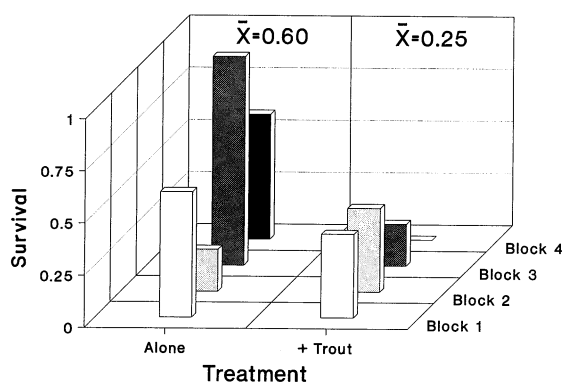
A single replicate of the *Gyrinophilus* + *Salvelinus* treatment had no surviving *Gyrinophilus*. Yates' method was used to estimate the missing value for growth rate in the ANOVA and Yates' bias estimate was used to adjust the resulting ANOVA sums of squares (Steel and Torrie 1980). This estimate does not provide additional information but simply facilitates the analysis of variance (Steel and Torrie 1980).

Activity levels (number of individuals observed) were corrected for number of survivors in each stream. The data were then square root transformed (square-root [$X + 0.5$]) and analyzed using analysis of variance. Tukey's hsd was used to compare individual treatment means. Because block effects were not close to significance for any analyses performed, the nonsignificant block and error sums of squares were pooled for testing the effects of treatments.

RESULTS

Gyrinophilus.—The presence of *Salvelinus* had a significant effect on both the growth and survival of *Gyrinophilus*. Effects on survival were independent of *Gyrinophilus* body size. Survival was 60% (12/20) for *Gyrinophilus* alone and 25% (5/20) for *Gyrinophilus* in the presence of brook trout (Fisher's exact test, $P = .027$, one-tailed test; Fig. 5a). Survival in individual streams ranged from 40 to 100% for *Gyrinophilus* alone and from 0 to 40% for *Gyrinophilus* in the presence of *Salvelinus*. Individual growth of *Gyrinophilus* was reduced in the presence of trout to 35% of the growth in *Gyrinophilus*-only tanks ($F_{1,5} = 9.93$, $R^2 = 0.67$, $P = .026$; Fig. 5b). Growth of individual *Gyrinophilus* ranged from 0.61 to 1.81 g for trout-free streams and from 0.04 to 0.5 g for streams containing *Salvelinus*. Frequency of tail and limb damage was low and no greater in the *Gyrinophilus*-*Salvelinus* treatment than for *Gyrinophilus* alone. A single mutilated *Gyrinophilus* carcass was found in a *Gyrinophilus* + *Salvelinus* stream when

a) *Gyrinophilus* survival



b) *Gyrinophilus* growth

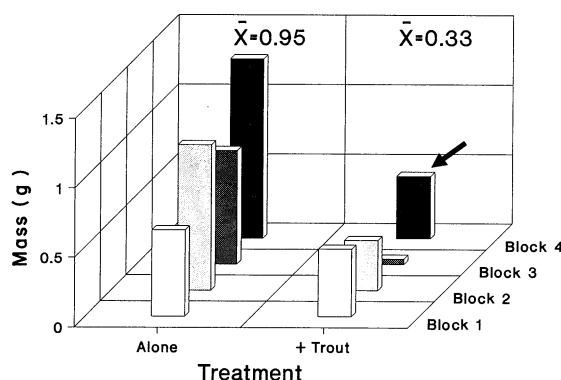


FIG. 5. (a) Survival and (b) growth of *Gyrinophilus* in the experimental streams. Numbers in each column represent treatment means.

the experiment was taken down. The carcass was found under a rock and was missing the entire caudal area including the cloaca, one hind limb, and both front limbs. The caudal damage was sufficient to cause death and could only have been inflicted on a live *Gyrinophilus* by the trout.

Salvelinus.—The presence of *Gyrinophilus* had no detectable effect on survival, relative condition, or measures of reproductive parameters of *Salvelinus*. Only one trout died (*Gyrinophilus*-*Salvelinus* stream) during the experiment, so that measures of survival are of little value. The final relative condition of all the experimental trout was within the range exhibited by wild-caught trout from the same population (Fig. 4), indicating that *Salvelinus* in the experimental streams experienced conditions for growth comparable to those in natural streams. The regression lines for experimental and wild-caught trout were not significantly different. Relative condition did not differ between animals from the *Salvelinus* alone treatment ($\bar{X} = 0.95 \pm 0.046$) and *Gyrinophilus*-*Salvelinus* treatment ($\bar{X} =$

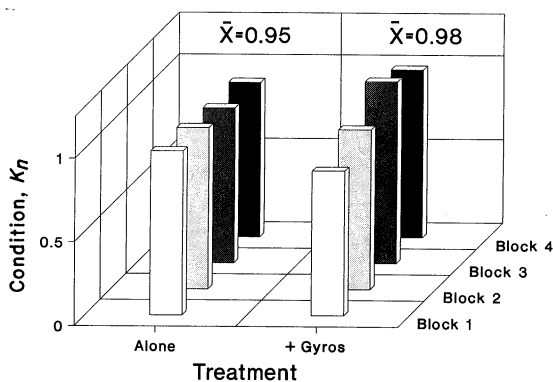
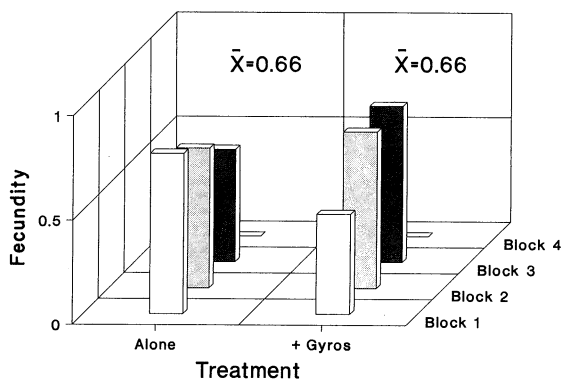
a) *Salvelinus* relative conditionb) *Salvelinus* relative fecundity

FIG. 6. (a) Relative condition and (b) relative fecundity of *Salvelinus* in the experimental streams. Numbers in each column represent treatment means. The fourth block (5b) contained a male and a female and was excluded from the analysis.

0.98 ± 0.014 ; $F_{1,6} = 0.35$, $R^2 = 0.06$, $P = .58$; Fig. 6a). Absolute fecundity showed no differences between the *Gyrinophilus-Salvelinus* treatment ($\bar{X} = 74.0 \pm 8.7$) and the *Salvelinus* alone treatment ($\bar{X} = 75.7 \pm 10.2$; Fig. 6b; Table 2) for the three pairs of females. There was no consistent trend in egg size between treatments.

Eurycea.—Treatments had no significant effect on survival of *Eurycea* larvae ($\chi^2 = 3.53$, $df = 3$, $P = .317$; Fig. 7a). Overall survival for the experiment was 30%. The highest survival was in the *Salvelinus* treatment

($\bar{X} = 0.404 \pm 0.066$) and the lowest in the *Salvelinus-Gyrinophilus* treatment ($\bar{X} = 0.250 \pm 0.058$). Treatments had a highly significant effect on the mean size of surviving larvae ($F_{3,12} = 9.011$, $R^2 = 0.68$, $P = .0045$; Fig. 7b). All three treatment means were lower than the control mean ($\bar{X} = 0.365$ g): both the *Gyrinophilus* ($\bar{X} = 0.268$), and the *Gyrinophilus-Salvelinus* ($\bar{X} = 0.233$) treatments showed a significant difference from the control mean using multiple comparisons (Fig. 7b). The mean for the *Salvelinus* treatment ($\bar{X} = 0.322$) was not significantly different from the controls.

The effect of both predators in concert was additive, meaning that the net effect of the two predators on final size was the sum of the effects of each predator alone, rather than the result of a more complex interaction. The predicted value of the combined predator effect based on a linear additive model underestimated the actual effect by only 6.1% (predicted = 0.225 g; observed = 0.233 g). The estimated value falls within one standard error of the observed *Gyrinophilus-Salvelinus* treatment mean.

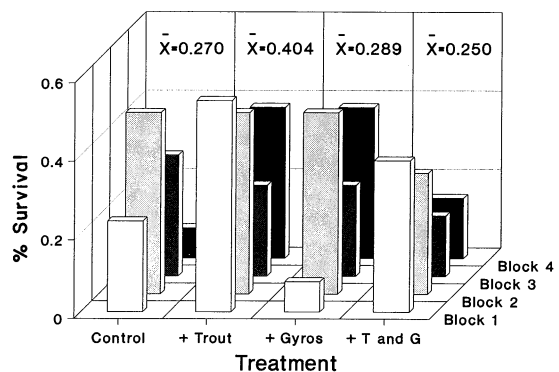
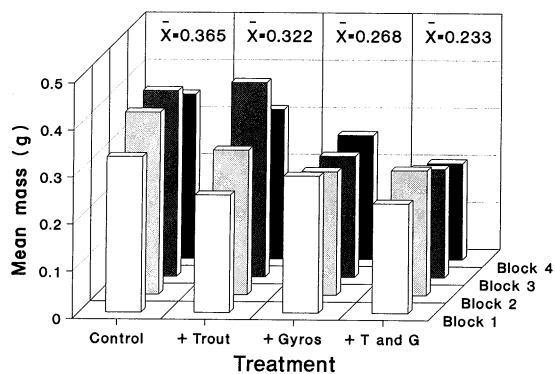
a) *Eurycea* survivalb) *Eurycea* growth

FIG. 7. (a) Survival and (b) body size as a measure of growth for *Eurycea* in the experimental streams. Numbers in each column represent treatment means.

TABLE 2. Summary of ANCOVA for fecundity in *Salvelinus*. SL = standard length.

Source	df	ss	MS	F	P
Covariate (SL)	1	43.70	43.70	0.126	.75
Treat	1	2.90	2.90	0.008	.93
Error	3	1038.23	346.08		
Total	5	1084.83			

Cambarus. — The effect of treatments on crayfish survival was not significant ($\chi^2 = 6.42$, $df = 3$, $P = .093$; Fig. 8a). The mean survival for the controls (0.14) was lower than that for all other treatments (Fig. 8a) and well below the overall mean (0.26). The effect of treatments on size was suggestive ($F_{3,12} = 3.079$, $R^2 = 0.44$, $P = .068$; Fig. 8b) though not significant, and multiple comparisons revealed no significant differences between treatments.

The pattern of mean body size among treatments followed the same pattern for *Cambarus* as that observed in *Eurycea*. Treatment means were ranked in the same order (control, *Salvelinus*, *Gyrinophilus*, *Gyrinophilus-Salvelinus*), but the effect of two predators in concert was less than additive. The predicted effect is 54% greater than the observed magnitude of the combined predator effect.

Habitat use

Observations focused on two aspects of behavior, overall activity level (time spent out of refuge) and microhabitat use. Nocturnal habitat data for *Salvelinus* reflect the location of their refuges (Fig. 9a). *Salvelinus* were found in all areas of the streams during the day, but their activity did center in the deep half of the streams. *Gyrinophilus* activity centered in the shallow half when alone and in the shallowest quarter in the presence of brook trout (Fig. 9a). The limited data precluded statistical analysis of habitat use. There was no significant difference in the level of *Gyrinophilus* activity between the treatments ($F_{1,6} = 0.169$, $R^2 = 0.03$, $P = .699$). The difference in the number of observations between the *Gyrinophilus* alone treatment and the *Gyrinophilus-Salvelinus* treatment is almost completely explained by the difference in the number of survivors (Fig. 5a).

Eurycea showed a reduction in activity in the presence of both *Salvelinus* (36% of control) and *Gyrinophilus* (64% of control; Fig. 9b); however, this reduction was not significant for treatments in general ($F_{3,15} = 1.432$, $R^2 = 0.26$, $P = .282$), or for individual comparisons of means. The lack of significance likely results from the small number of observations and the large number of zero cells in the ANOVA. Activity in the *Salvelinus* treatment was significantly shifted towards shallow water relative to the controls ($\chi^2 = 21.27$, $df = 1$, $P < .0001$). Seventy-five percent of the *Eurycea* observed in the *Salvelinus* treatment were the shallow half (all in Zone 4) compared to 9% in the controls (all in Zone 3). Reduction in activity in the *Gyrinophilus* treatment showed no comparable shift in pattern ($\chi^2 = 3.19$, $df = 2$, $P = .20$). Reduction in activity within the zones was primarily a reflection of the overall reduction in activity. Activity in the *Salvelinus-Gyrinophilus* treatment was reduced to only 9% of the control value. Predicted activity using an additive model of predator effects predicts that 0% would be active in

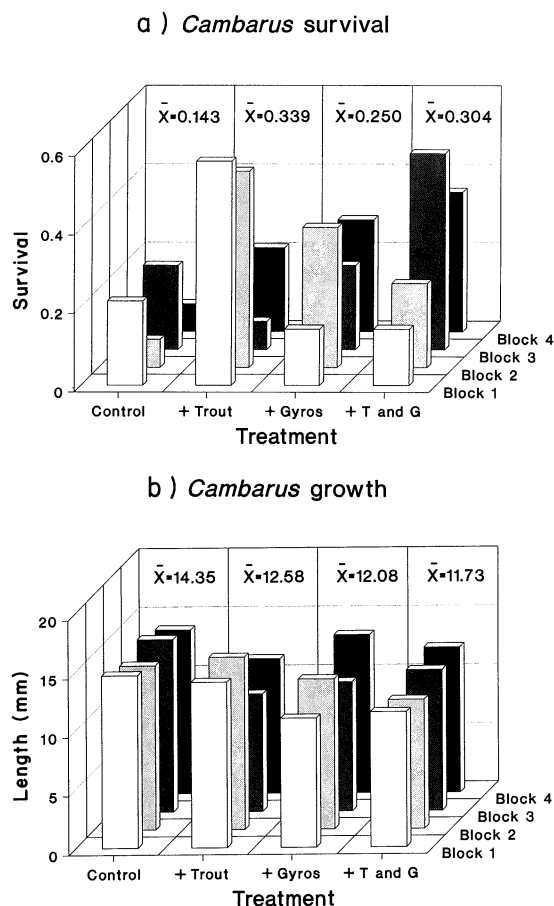


FIG. 8. (a) Survival and (b) body size (carapace length) as a measure of growth for *Cambarus* in the experimental streams. Numbers in each column represent treatment means.

the *Salvelinus-Gyrinophilus* treatments, a close fit to the 9% observed value.

Activity in *Cambarus* (Fig. 9c) showed a similar pattern to that seen in *Eurycea*. Treatment had a highly significant effect on activity in *Cambarus* ($F_{3,15} = 11.79$, $R^2 = 0.75$, $P = .0007$). *Cambarus* activity was reduced to 34% of control values in the presence of *Salvelinus*. The presence of *Gyrinophilus* reduced activity to 48% of the control value. Pairwise comparison of means showed a significant difference between the controls and each of the three different predator treatments. *Cambarus* showed a slight, nonsignificant shift in activity towards the shallowest part of the streams in the presence of *Salvelinus* ($\chi^2 = 4.54$, $df = 3$, $P = .21$). Fifty percent of the activity occurred in the shallowest section (Zone 4) compared to only 28% in the controls. The reverse of this trend, a significant shift toward deeper water, was seen in the presence of *Gyrinophilus* ($\chi^2 = 32.95$, $df = 2$, $P < .0001$). Seventy-nine percent of the activity was seen in the deeper water of Zones 1 and 2 compared to 31% in the controls. Both patterns for *Cambarus* show the expected results based on the

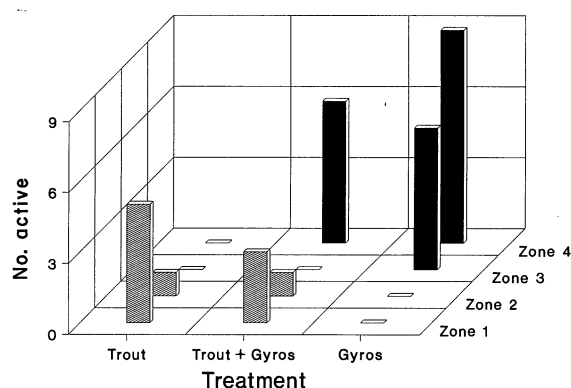
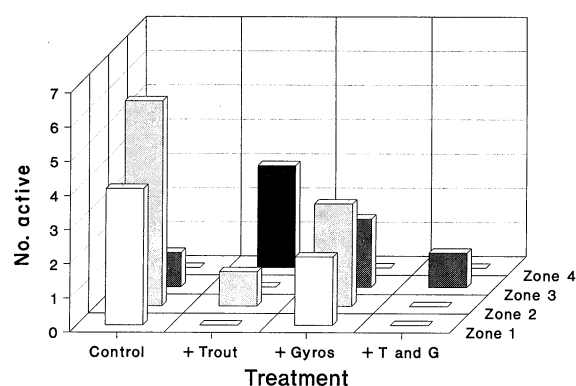
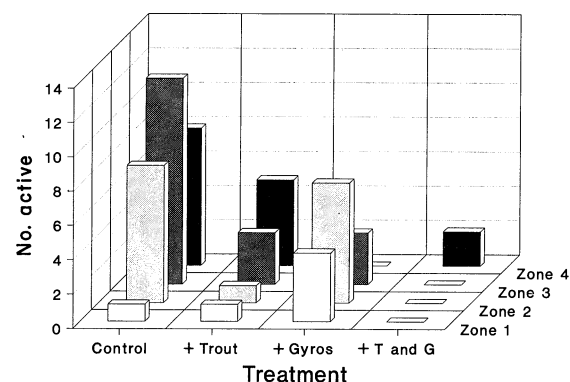
a) *Salvelinus* and *Gyrinophilus* activityb) *Eurycea* activityc) *Cambarus* activity

FIG. 9. (a) Distribution of activity for *Gyrinophilus* and *Salvelinus*, (b) *Eurycea*, and (c) *Cambarus* in the experimental streams. Zone 1 represents the deep end of the streams, Zone 4 the shallow end (see Fig. 3).

habitat use of *Salvelinus* and *Gyrinophilus*. Activity in the *Salvelinus*-*Gyrinophilus* streams was reduced to 7% of the level observed in the control streams. The only activity observed was two individuals active in the shallowest zone. The additive model based on individual predator treatments predicts no activity in the joint treatment (–17%) compared to the actual value of 7%).

DISCUSSION

Ecologists have typically viewed the effects of predation, in terms of an individual prey or a prey population, from the perspective of predator-induced mortality. While this is the most extreme negative effect a predator can have on an individual, it is not necessarily the most important or the only effect on a population. Predators may affect their prey in more subtle ways than by directly inducing mortality (see Peckarsky 1980, Werner et al. 1983, Power 1984, Morin 1985, Werner 1986, Wilbur 1987, Resetarits and Wilbur 1989). In streams, predatory fish have been shown to affect the depth distributions of armored catfish (Power 1984), to reduce or eliminate grazing minnows (Power et al. 1985) and salamanders (Petranka 1983) from stream pools, and to elicit behavioral avoidance in dace (Fraser and Cerri 1982), chubs (Gilliam and Fraser 1987, Schlosser 1987), salamanders (Petranka 1983, Petranka et al. 1987), notonectid (Sih 1982) and gerrid (Cooper 1984) insects, and crayfish (Stein and Magnuson 1976). Predatory salamanders may have similar effects on their smaller salamander prey (Southerland 1986a, b). Nonlethal effects of predators, such as reduced growth rates, altered behavior, and changes in patterns of habitat use, can affect the population dynamics of prey species by altering demographic characteristics of populations. Changes in activity levels and habitat use may intensify interactions with certain species and may force species into new sets of interactions. In this study I observed both lethal and nonlethal effects of predators.

This experiment focused on the interaction between two large predators (*Gyrinophilus* and *Salvelinus*), which are common in the headwater streams near MLBS, and the effects of these two large predators on two smaller predators (*Eurycea* and *Cambarus*) common in the same streams. The interaction between the two large predators was strongly asymmetric, favoring *Salvelinus*. Brook trout were unaffected by *Gyrinophilus*, but significantly reduced both the survival and growth of *Gyrinophilus*. The exact mechanism of either effect is unknown, but amphibian larvae rarely die of starvation, except during prolonged periods of severe food deprivation, so the induced mortality was likely the result of attacks by the trout on the *Gyrinophilus* larvae. Most of the *Gyrinophilus* were too large to be eaten by the trout used in the experiment, so the two possible mechanisms for the reduction in *Gyrinophilus* survival are predation (or attempted predation) and interference

competition. Aggressive, territorial feeding interactions are common among salmonids, including brook trout (Fausch and White 1981, 1986), and the data here suggest that this aggression extends to other predators as well.

It is also uncertain whether the reduction in growth seen in *Gyrinophilus* was the result of competition with *Salvelinus* or avoidance of *Salvelinus* as a predator. The overall result for *Gyrinophilus* is the same: a reduction in growth in a long-lived, slow-growing species such as *Gyrinophilus* may affect the demography of *Gyrinophilus* populations that overlap with brook trout. The magnitude of the reduction in growth, projected over the several years it takes to reach metamorphosis (Bruce 1980, 1985) may mean an extra full year to reach metamorphosis, or it may translate to a smaller size at metamorphosis, both of which can affect fitness and population dynamics by delaying age at first reproduction and reducing age-specific fecundity (Smith 1987, Semlitsch et al. 1988).

The effects of *Salvelinus* on *Eurycea* and *Cambarus* are very similar, but differ from expectations. Trout had no effect on survival in either species, though all individuals of *Eurycea* and $\approx 90\%$ of the *Cambarus* were small enough to be eaten by the trout. Both *Eurycea* and *Cambarus* were shown to be capable of behaviorally avoiding trout predation in these complex experimental mesocosms, but at the cost of reduced growth. Stein and Magnuson (1976) have shown behavioral avoidance of smallmouth bass by crayfish, *Orconectes propinquus* via decreased activity and choice of substrate, both of which were strategies available in my experimental streams. Larvae of *Eurycea bislineata* behaviorally avoid water that has been conditioned with the presence of a predatory fish, *Lepomis cyanellus* (Petranka et al. 1987). This is similar to the results obtained for bluegill sunfish (*Lepomis macrochirus*) in the presence of large predatory bass (*Micropterus salmoides*) (Werner et al. 1983). The size class of bluegill that were at risk of predation shifted from their preferred habitat to a habitat with lower predation risk and lower resource levels, resulting in a significant reduction in growth.

The reduction in growth and activity is even greater for *Eurycea* and *Cambarus* faced with *Gyrinophilus*, though the mechanisms for avoiding predation are equally effective. The greater response to *Gyrinophilus* may result from the shared benthic microhabitat and refugia. Avoidance of *Gyrinophilus* may involve far more disruption of normal activities than the avoidance of *Salvelinus*. The presence of large predators greatly reduces activity and can result in habitat shifts away from the preferred habitat of the predator, which may also be the preferred habitat of the prey (Werner et al. 1983, Schlosser 1987). The effect of the two different predators with distinct habits is to reduce observable activity to near zero. The two small species are constrained to be less active in the presence of the

large predators, thus affecting their ability to forage and, in the case of habitat shifts, affecting the range of habitats (or simply the overall area) available for foraging (Werner et al. 1983). Power et al. (1985), Fraser and Cerri (1982), and Schlosser (1987) have observed similar predator-mediated habitat and activity changes in stream fishes and Petranka (1983), Hairston (1986), Southerland (1986a,b), and Roudebush and Taylor (1987) have reported habitat shifts in response to predators in stream-associated salamanders.

The effect of the two large predators together was additive for *Eurycea* and less than additive for *Cambarus*. The less than expected combined effects, however, may result from the reduction of *Gyrinophilus* densities by *Salvelinus*. Brook trout may partially reduce the impact of their own presence on prey species by reducing the densities of other large predators. Interference competition or intraguild predation (Polis and McCormick 1987) between predators is one possible mechanism for reducing the net effect of multiple predators on prey species.

The ability to survive in spite of the risk of predation depended on avoidance of predators, but avoidance had a cost of reduced growth (Werner et al. 1983). The species (*Gyrinophilus*) that did not reduce its activity and alter its habitat use in the presence of a larger predator (*Salvelinus*) suffered both reduced growth and reduced survival. Species such as *Eurycea bislineata* and *Cambarus bartonii* that remain common in streams containing brook trout and *Gyrinophilus* may do so because of their ability to behaviorally reduce the risk of predation. The measure of the effect of a predator on potential prey is not simply whether the prey can continue to coexist with the predator, but whether the predator alters the conditions of that existence. Continued coexistence with a predator does not signify lack of interaction. Thus, the effect of predators on coexisting species manifests itself in more subtle ways than by directly inducing mortality.

Reduction in growth in *Eurycea* and *Cambarus* may affect their fitness and population dynamics, as was discussed for *Gyrinophilus*. *Eurycea* may take up to 3 yr to reach metamorphosis (Bruce 1982a, b) and have a broad range of potential sizes at metamorphosis. Thus, the effects of predators on *Eurycea* may include prolonging the larval period and reducing size at metamorphosis, which may translate into changes in age and size at first reproduction, and age-specific fecundity (Smith 1987, Semlitsch et al. 1988). With respect to *Cambarus bartonii*, fecundity has been shown to be positively correlated with body size in congeners (Penn 1943, Smart 1962) and therefore age-specific fecundity may be affected by a reduction in growth.

This experiment demonstrates significant interactions among predators that result in effects on ecologically meaningful variables in 3 of the 4 species in the experiments. The changes observed in survival, growth, activity, and habitat use have the potential to influence

population dynamics of these species, which may ultimately result in changes in the structure of the stream community (Werner et al. 1983). This is especially true because of the high trophic position of all the species in the experiment.

The results of this experiment relate directly to results of intensive field sampling on the West Upper Fork of Little Stony Creek (W. J. Resetarits, Jr., unpublished data, and Fig. 1). The 58% mean reduction in *Gyrinophilus* survival in this experiment compares with the 66% mean reduction of *Gyrinophilus* on field plots containing *Salvelinus* compared to trout-free plots. Field data on growth were not available, but mean body size on the field plots was significantly smaller for *Gyrinophilus* in the presence of brook trout. *Eurycea* show a marked reduction in number on plots with *Salvelinus*, but show no differences in body size. The results of my experiment suggest that the reduction in *Gyrinophilus* number and size in the field reflect actual changes in the *Gyrinophilus* population resulting from the presence of *Salvelinus*. The experimental data on *Eurycea* suggest that the reduced numbers observed on field plots containing *Salvelinus* reflect changes in the behavior of *Eurycea*, the *Eurycea* being less active in the presence of brook trout and therefore less likely to be observed, even under intensive sampling.

The results of this experiment underscore the potential importance of biotic interactions in lotic ecosystems (Peckarsky 1983). The lethal and nonlethal effects induced by predators in this experiment affect components of life history both directly and indirectly related to population dynamics in the interacting species. Thus, the structure of an assemblage (guild) of generalist predators can be affected by the interactions among the members of the assemblage. The net effect of an assemblage of predators on lower trophic levels may depend on the outcome of such predator-predator interactions.

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