Differences in an ensemble of streamside salamanders (Plethodontidae) above and below a barrier to brook trout

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Abstract. I examined the species composition, relative abundances, and size distributions of an ensemble of streamside salamanders in two contiguous sections of an Appalachian headwater stream: one containing brook trout and one that was trout free. The two stream sections were separated by a natural waterfall that formed a permanent barrier to the upstream movement of fish. The two stream sections differed in the overall abundance of salamanders, the relative abundance of the six species present, and the size-distribution of the salamander ensemble. These results suggest that brook trout have an effect on the structure of co-occurring ensembles of salamanders, and that the continued coexistence of stream salamanders with brook trout does not indicate lack of strong ecological interactions.

Introduction

Predatory fish play an important role in the distribution and abundance of the aquatic stages of amphibians. Predation by fish on the eggs, larvae and adults of amphibians is well documented (e.g., Macan, 1966; Heyer et al., 1975; Formanowicz and Brodie, 1982; Petranka, 1983; Sexton and Phillips, 1986), but in spite of its presumed importance few studies have examined the impact of fish on amphibian assemblages that typically co-occur with fish (see Efford and Mathias, 1969; Neish, 1971). Fish affect the distribution (Semlitsch, 1988), behavior (Stangel and Semlitsch, 1987), and performance (Semlitsch, 1987) of larval *Ambystoma* in pond habitats, and the distribution (Petranka, 1983), behavior (Kats et al., 1988), and oviposition sites (Kats and Sih, 1992) of *Ambystoma barbouri* in stream habitats. However, little is known of the effect of fish on the ensembles (*sensu* Fauth et al., 1996) of "streamside" plethodontid salamanders that commonly co-occur with fish across the southern Appalachians Mountains of the eastern United States (Hairston, 1987). The co-occurrence of these salamanders with fish has long provided a puzzling contrast to the "conventional wisdom" on fish-amphibian interactions (Hairston, 1987), and contrasts sharply with the typically allotopic distributions of stream dwelling salamanders and fish in Europe (e.g., Thiesmeier and Schuhmacher, 1990; Thiesmeier, 1994; Sound and Veith, 1994).

In this study I took advantage of a natural barrier (waterfall) to upstream movement of brook trout to examine the composition of the streamside salamander ensembles in contiguous streamsections with and without brook trout. Brook trout had not penetrated above the falls on the West Upper Fork of Little Stony Creek (New River Drainage), Giles County, Virginia, USA, since at least 1941 (Burton and Odum, 1945); thus, the existence of this discrete barrier provided the opportunity to examine the differences between a section with trout and one that was trout-free without the confounding effects of stream size or elevation that commonly parallel trout and trout-free stream reaches. Unfortunately, no other similar barriers were found that could serve as replicates, so the inferences from this study are limited to the specific stream studied. Nonetheless, these are the only data of their kind and provide baseline information and comparative data for future studies of similar sites.

"Streamside" salamander ensembles of the southern Appalachian Mountains are comprised of both aquatic and semiaquatic salamanders and their aquatic larvae (Hairston, 1949; Organ, 1961a). In the vicinity of Mountain Lake Biological Station (MLBS) in western Virginia, the ensemble consists primarily of six species in the family Plethodontidae. The two largest species are *Gyrinophilus porphyriticus*, which in the study area is a habitat generalist, and *Desmognathus quadramaculatus*, the largest and most aquatic of the four *Desmognathus* present. *Desmognathus monticola* is a somewhat smaller, stream edge species, *D. ochrophaeus* is the smallest and most terrestrial, and *D. fuscus* is intermediate in size and habitat use between *D. monticola* and *D. ochrophaeus* (Hairston, 1949, 1986; Organ, 1961a). The sixth species, *Eurycea wilderae*, is a small, slender species whose adults may occur anywhere from mid-stream out onto the forest floor. Larvae of *E. wilderae* are the most abundant urodeles in the streams in this area. Larvae of the six species spend varying lengths of time in an aquatic stage, ranging from as little as two to eight months in *D. ochrophaeus* (Tilley, 1973) to two to four years in *D. quadramaculatus* (Organ, 1961a; Bruce, 1988) and four to six years in *G. porphyriticus* (Bruce, 1980; WJR unpublished data). Larval *G. porphyriticus* and *D. quadramaculatus* reach large size before metamorphosing (Organ, 1961b; Bruce, 1980, 1988).

The brook trout, *Salvelinus fontinalis*, is the dominant predator in clear, cool, headwater streams of the southern Appalachians, where it usually has few fish associates (Burton and Odum, 1945). It takes a wide range of prey, from zooplankton to fish and frogs; however, terrestrial and aquatic insects and aquatic invertebrates make up the bulk of prey taken in most populations (Carlander, 1969). Brook trout reach over 200 mm standard length (SL) even at their upstream limit in high elevation, first-order streams (personal observation).

Materials and methods

The study was carried out on the West Upper Fork of Little Stony Creek, near MLBS. West Upper Fork is a small (1.5-2.0 m wide, < 20 cm average depth), first-order mountain brook with clear, cold water, and a substrate of rubble, gravel, sand and bedrock, with silt and detritus accumulations in the pools. Flow is relatively constant and flooding is infrequent. Brook trout are the only fish that occur in the Upper Forks of Little Stony Creek. The fauna is otherwise dominated by invertebrates, principally crayfish (*Cambarus bartonii*) and stoneflies (Plecoptera), and the adults and larvae of salamanders (Plethodontidae).

In streams near MLBS the upstream mobility of brook trout is limited primarily by the severity of stream gradients and the size of the stream, however, only on the West Upper Fork of Little Stony is that limit discrete and temporally stable. The upper limit of brook trout at the study site is a 1.5 m high, deeply undercut waterfall at ~ 1090 m elevation that forms a barrier to upstream movement. It has marked the maximum extent of brook trout penetration into the West Upper Fork since at least 1941 (Burton and Odum, 1945). The contiguous sections of stream above and below the falls which comprise the study site are virtually indistinguishable; there is no change in gradient, vegetation, or substrate, and no tributaries, springs or seeps provide input along the study section.

The sampling design consisted of 6 pairs of five-meter-long subplots arranged linearly along the stream, one of each pair with trout and one without trout. Paired subplots were numbered from the waterfall outward (for convenience) and both members of a numbered pair were sampled on the same day and night to control for temporal variation. Total linear distance across the site was 60 m and the change in elevation over the site was less than 10 m. Sampling involved intensive daytime and nighttime searches of both the terrestrial and aquatic habitat within each subplot. The entire surface area was searched from bank to bank, including a 1 m buffer strip of forest floor along the edge, and all manageable cover objects > 25 cm^2 lifted, checked for salamanders (larval and adult), then replaced; $> 95\%$ of individuals observed were successfully captured (for each species). Day and night samples (12 each) for both members of a pair of subplots were done on the same day. Each subplot sample (24 total) required ~ 3 h of hands and knees searching/subplot. All samples were completed in August 1986. Daytime samples resulted in such low numbers of salamanders that day and night samples were pooled for analysis. Two dimensional (surface) sampling captures only those individuals of each species which are at the surface on a given night. This subset has been estimated as a small proportion of the total animals present (Hairston, 1986), yet allows estimates of relative abundance suitable for comparison between sites if sampled on the same night (same environmental conditions). All salamanders observed were collected, killed by over-anaesthetization in chloretone, patted dry, weighed to the nearest 0.01 g, measured (snout-vent length, SVL, and total length, TL) to the nearest 1.0 mm, and preserved in 10% formalin. Larval, juvenile and adult streamside salamanders can be very difficult to identify; these specimens were preserved to assure accurate identification and to serve as a reference collection for future work at MLBS.

Data analysis

Data were analyzed to test the hypothesis that the two plots, one above the waterfall and one below, differed with regard to their respective salamander ensembles. The primary difference of interest between the two plots was the presence and absence of brook trout, but clearly this study does not constitute a rigorous test of the effect of trout on salamanders. Because this study is, by necessity, unreplicated, the description and conclusions apply only to this particular pair of plots. Nonetheless, just as the comparisons between two adjacent ponds or lakes that primarily differ in one obvious factor are instructive with regard to the potential affects of that factor (e.g., Carpenter et al., 1987), these data provide valuable insights into the potential effects of brook trout and generate hypotheses to be tested by manipulative experiments (e.g., Resetarits, 1991, 1995; see also Werner, in press).

Distributions of individuals among species on the two plots were compared using contingency table analysis, testing the hypothesis that relative abundances were the same on the two plots. Larvae and adults of a given species were not separated in this analysis. Absolute abundances of salamanders on the two plots were compared using a paired t-test on log transformed count data (log Y +1: Steele and Torrie, 1980); samples taken on the same night on a pair of subplots were treated as independent estimates of the number of salamanders on the respective plots. This does not constitute pseudoreplication with respect to the specific hypothesis being tested (see above). Potential differences in body size (SVL) on the two plots was explored using ANOVA (see table 2 for details) for all salamanders and t-tests for each species individually. Body size distributions for all salamanders, larvae only, and adults only, were examined using the Kolmogorov-Smirnov two-sample test (Steele and Torrie, 1980).

Results

Relative abundances of the six species of salamander differed between the plot containing trout and the trout-free plot, as did the total number of salamanders (table 1; fig. 1). An analysis of the distribution of individuals among species showed a highly significant difference between the plots ($\chi^2_5 = 15.21$, $P < 0.01$). The majority of that difference resulted from the deviations of the numbers of *D. monticola* and *D. quadramaculatus* from expected values. The two species show opposing patterns, with densities of *D. monticola* reduced in the presence of brook trout and densities of *D. quadramaculatus* reduced in the absence of brook trout. *Desmognathus fuscus* was also more abundant with trout than expected. The remaining differences, the reductions in *D. ochrophaeus* and larvae of *E. wilderae* and *G. porphyriticus* (fig. 1), parallel the 40% reduction in

Table 1. Data summary from field plots. Data are total number of individuals per species in trout-present and trout-free plots, mean SVL ± 1 standard error, and mean mass ± 1 standard error.

	Trout-free			Trout		
	Total no.	Mean SVL (mm)	Mean mass (g)	Total no.	Mean SVL (mm)	Mean mass (g)
D. fuscus	9	38.7 ± 3.5	1.27 ± 0.28	9	40.7 ± 2.8	1.47 ± 0.27
D. monticola	16	35.1 ± 4.3	1.83 ± 0.62	1	35.0	1.16
D. ochrophaeus	20	28.2 ± 2.8	0.63[a] ± 0.12	11	25.3 ± 4.2	0.58 ± 0.25
D. quadramaculatus						
adults	7	59.6 ± 2.6	4.58 ± 0.50	15	60.0 ± 3.0	5.42 ± 0.81
larvae	2	31.5 ± 0.5	0.77 ± 0.04	0	–	–
E. wilderae						
larvae	30	15.0 ± 0.8	0.10 ± 0.01	15	16.5 ± 1.2	0.11 ± 0.02
G. porphyriticus						
adults	0	–	–	3	85.7 ± 7.3	9.08 ± 2.18
larvae	12	51.3 ± 2.7	2.90 ± 0.47	4	39.8 ± 6.9	1.75 ± 0.70
Totals	96	38.7 ± 2.9	1.31[a] ± 0.18	58	31.4 ± 1.8	2.38 ± 0.42

[a] excludes 1 *D. ochrophaeus* for which mass was not measured.

Table 2. a) ANOVA for the differences in body size (SVL) between the trout-present and trout-free plots showing significant effect of plot. b) ANOVA for body size including species as a factor. Larvae and adults are considered separate species for this analysis. Inclusion of species removes the effect of plot, indicating that difference between the plots in body size is driven by the difference in relative abundance of species.

a)

Source	df	SS	MS	F	Prob (> F)
Plot	1	1887	1887	4.97	0.027
Error	152	57744	379.9		
Total (corr)	153	59632			

b)

Source	df	SS	MS	F	Prob (> F)
Species	7	40863	5838	50.1	0.0001
Plot	1	3.501	3.5	0.03	0.8644
Error	145	16882	116.4		
Total (corr)	153	59632			

total salamander numbers with trout. Though the difference in the mean total number of salamanders falls just short of significance (paired t-test on log transformed (log Y+1) count data (Steele and Torrie, 1980), one-tailed alternative, $t_5 = 1.97$, $P = 0.053$; fig. 1), the consistency of the pattern suggests that there is a real difference, even though the absolute increase in *D. quadramaculatus* and the relative increase in *D. fus-*

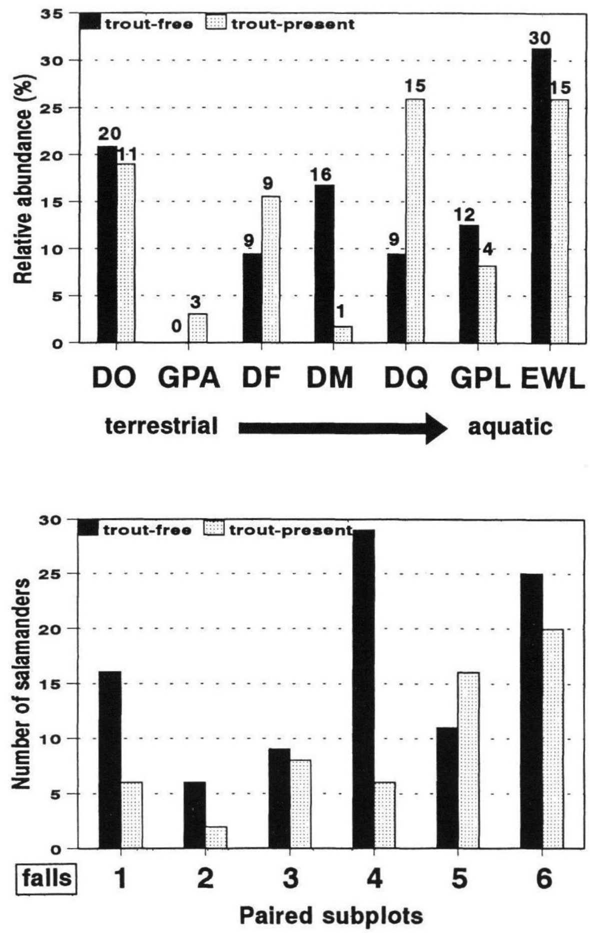

Figure 1. (top) Relative abundances of six species of salamanders on the trout-present and trout-free plots on the West Upper Fork of Little Stony Creek, arranged to illustrate the typical distribution along the terrestrial to aquatic gradient (personal observation). Numbers above bars are the actual numbers for each species (n = 96 for trout-free plot; n = 58 for trout-present plot). Larvae and adults of *Gyrinophilus porphyriticus* are displayed separately reflecting the difference in habitat use; two larval *D. quadramaculatus* taken on the trout-free plots are included with the adults, but are obligately aquatic like larvae of *G. porphyriticus* and *E. wilderae.* The distributions of individuals among species in trout-present and trout-free plots are significantly different. (bottom) Number of individuals collected on each pair of subplots.

cus in the trout plot partially offset the strong decreases in *D. monticola* and larvae of *E. wilderae* and *G. porphyriticus.* Regressions of log body mass on log SVL for all salamanders showed no differences in slope or intercept between trout-present and trout-free plots (trout-free, r = 0.98, log mass = 2.76 × log length − 9.92; trout-present, r = 0.99, log mass = 2.83 × log length − 10.14) in spite of changes in relative species abundances.

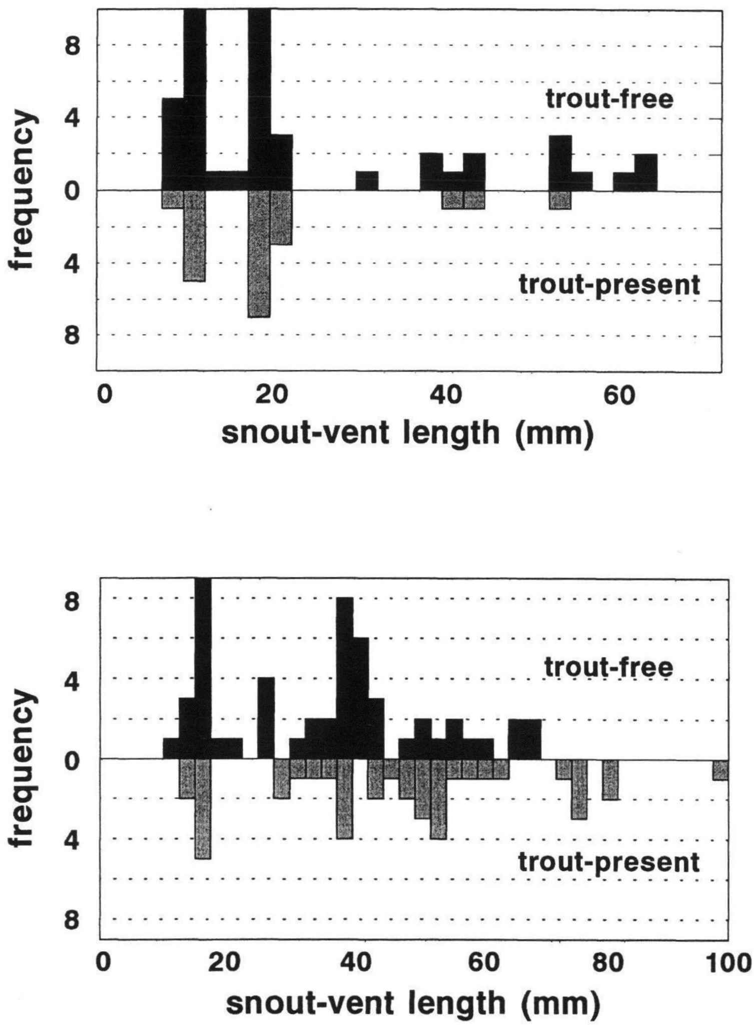

Figure 2. Size-frequency distributions for larval (top) and adult (bottom) salamanders in the trout-free (dark bars) and trout-present (light bars) plots.

An ANOVA on body size (SVL) revealed a significant effect of trout presence; salamanders with trout were significantly larger (table 2). However, adding species as a factor in the ANOVA shows that the difference in body size was driven by the differences in species composition (tables 1, 2).

Considering size independent of species is another important way (besides relative abundance) of examining changes in an ensemble of generalist predators (Hairston, 1987); predator size distribution may be as important to prey species as the species composition. The size-frequency distributions for all species pooled do not differ significantly between trout-present and trout-free plots (Kolmogorov-Smirnov test, $D = 0.195$, $P = 0.128$). Partitioning the data into postmetamorphic and larval individuals revealed no difference in mean size ($t_{62} = 0.931$, $P = 0.356$; table 1) or size-frequency distribution (Kolmogorov-Smirnov, $D = 0.267$, $P = 0.305$; fig. 2) for larval salamanders, while postmetamorphic individuals showed a highly significant difference in mean size ($t_{90} = 2.762$, $P = 0.007$; table 1) and can be shown to be sampled from different size-frequency distributions (Kolmogorov-Smirnov, $D = 0.338$, $P = 0.012$; fig. 2). This results primarily from a shift toward larger individuals (larger species) in the section containing trout. Comparison of body size by species between trout-present and trout-free plots was significant only for larval *G. porphyriticus* ($t_{14} = 1.89$, $P = 0.04$: table 1).

Discussion

The range of fish effects on amphibian populations is not well understood, and few studies have clearly documented changes in amphibian assemblages that can be ascribed to the presence of predatory fish (but see Sexton and Phillips, 1986; Semlitsch, 1988; Werner and McPeek, 1994). In particular, little information exists on the effect of fish on the diverse ensembles of plethodontid salamanders that co-occur with fish over thousands of kilometers of streams in the southern Appalachians. The tacit assumption has been that because these species regularly co-occur with fish, fish have little impact on their ecology. The discovery of the trout barrier and its known history provided a unique opportunity to examine whether total abundance, size distributions and species composition of salamanders differ between sections with and without brook trout.

There are differences between the trout-present and trout-free sections of the study stream in both the absolute and relative abundances of several species of salamanders. The result is a qualitatively different salamander ensemble in terms of relative abundances of species, and a quantitatively different ensemble in terms of numbers and size distributions. Differences in the numbers of larval *E. wilderae* and *G. porphyriticus*, and the mean size of larval *G. porphyriticus*, parallel differences seen in experimental streams in which the two species occurred with and without brook trout (Resetarits, 1991). In that experiment, the presence of *S. fontinalis* caused a reduction in activity of *E. wilderae* of the same magnitude as the reduction in the number observed on the stream plots, while for *G. porphyriticus* the actual number of surviving larvae with and without trout reflected the numbers observed on the stream plots. The difference in body size on the stream plots with trout was paralleled by a reduction in growth in the experimental streams containing trout. This suggests that brook trout may affect fully aquatic salamanders in at least two ways; by reducing populations, as suggested for *G. porphyriticus* (Resetarits, 1991, 1995), and by reducing activity or changing habitat use (Resetarits, 1991), as suggested for *E. wilderae* and perhaps *D. quadramaculatus*.

Observed differences among adults revolve around the three species of *Desmognathus* that occur closest to the stream, *D. quadramaculatus, D. monticola*, and *D. fuscus*.

Desmognathus monticola is intermediate in body size and habitat use (Hairston, 1986, 1987; Southerland, 1986b) and is negatively affected by *D. quadramaculatus* in terms of both abundance (Hairston, 1986, 1987) and habitat use (Southerland, 1986a, b; Roudebush and Taylor, 1987). Similarly, *D. monticola* has been shown to affect aspects of habitat use by *D. fuscus* (Keen, 1982). Thus, the observations from my stream plots are consistent with the relationships among these three species seen in previous studies. One potential scenario is that the decrease in the abundance of *D. monticola* on the plot with trout releases both *D. quadramaculatus* and *D. fuscus* from competition/predation, precipitating their increases. Alternatively, brook trout may positively affect the abundance of *D. quadramaculatus*, producing both a decrease in the abundance of *D. monticola* and an increase in the relative abundance of *D. fuscus*. Thus, the indirect effects of trout on adults in this ensemble may be as important as the direct effects. Numbers of *D. ochrophaeus*, the most terrestrial species, did not differ between the two plots. Adults of *G. porphyriticus* were seen only on the trout-present plot.

Salamanders and fish are important components of Appalachian stream communities. Interactions between the two may affect the distribution and population dynamics of species in each taxon, and exert a strong influence on the structure of the stream community as a whole (Resetarits, 1991, 1995). In this study, the total abundance of salamanders, the relative abundances of species, and the resulting size distributions of the salamander ensemble of a high altitude headwater stream differed between contiguous plots with and without brook trout. Differences were apparent in both the aquatic and the streamside components of the salamander ensemble, suggesting that effects may cascade outward from the stream to affect more terrestrial/stream edge species. While not conclusive because of the lack of replicate streams, my observations suggest that the effects of brook trout on this ensemble are strong and potentially complex; the complexity arising from the interactions of the direct effects of brook trout on individual species with the direct effects of competition and predation among the salamanders themselves (Hairston, 1987).

In contrast to stream-dwelling salamanders derived from primarily pond-dwelling families, such as *Ambystoma barbouri* (Kraus and Petranka, 1987) and many European stream dwellers (e.g., species/subspecies of *Salamandra, Chioglossa*, and *Euproctus*), the family Plethodontidae had its evolutionary origin in streams, specifically streams in the southern Appalachian region, and has had an unbroken history of occupation in those streams (Wilder and Dunn, 1920; Wake, 1966; Beachy and Bruce, 1992). As a result, stream dwelling plethodontids may show a more complete suite of adaptations to the stream habitat than their European counterparts (Wilder and Dunn, 1920; Wake, 1966; Beachy and Bruce, 1992; Thiesmeier, 1994), including the ability to persist, at some level, with predatory fish. However, persistence does not mean lack of strong ecological interactions. My data suggest that brook trout may strongly affect stream salamanders and that the effect is not uniform among species. The apparent result, in West Upper Fork, is a qualitatively and quantitatively different salamander ensemble above and below the barrier to brook trout.

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