Nordic Society Oikos

Competitive asymmetry and coexistence in size-structured populations of brook trout and spring salamanders

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Resetarits, W. J. Jr. 1995. Competitive asymmetry and coexistence in size-structured populations of brook trout and spring salamanders. – Oikos 73: 188–198.

The question of coexistence of competing species has generated much of the basic theory of community ecology. The question becomes more complex when competition occurs between size-structured populations of predators in which the nature of the interaction extends beyond exploitative competition. I conducted a field experiment examining the interactions between fingerling brook trout, *Salvelinus fontinalis* (total length 78–101 mm), and larval spring salamanders, *Gyrinophilus porphyriticus* (snout-vent length 35.7–62.4 mm), in an array of replicate experimental streams. Brook trout affected both the growth and survival of larval spring salamanders, reducing survival by 50% and growth by > 90% for mass and 44% for SVL. Brook trout also altered the habitat use of larval *G. porphyriticus*. *G. porphyriticus* had no effect on any of the responses of fingerling *S. fontinalis*. These results parallel those found in an earlier experiment on interactions between small adult brook trout and larval spring salamanders.

Interactions between size-structured populations of *G. porphyriticus* and *S. fontinalis* are characterized by strong asymmetry in favor of *S. fontinalis* across a wide range of relative body sizes. This calls into question the mechanisms allowing continued coexistence of *G. porphyriticus* and *S. fontinalis*, and in general, the persistence of stream salamanders with predatory fish. Persistence is likely a complex function of the interactions between the life history and local demography of both *G. porphyriticus* and *S. fontinalis*, coupled with characteristics of the local environment, rather than the result of classic mechanisms of species coexistence such as niche divergence or alpha selection. Such complex mechanisms of species coexistence are likely more common in situations involving competition between size-structured populations than single factor explanations based on models of exploitative competition between competitors of fixed body sizes and life stages.

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The general concept of competitive exclusion has occupied a central role in ecology and evolution since Darwin (1859) first suggested that closely related species "generally come into the severest competition with each other". The question of the coexistence of competing species was elaborated by Grinnell (1904, 1917), formed the central theme of the Lotka-Volterra competition equations (Volterra 1926, Lotka 1932) and the experimental tests of those equations by Gause (1934), and has been raised to a central principal of ecology (Gause 1934, Hardin 1960, MacArthur and Levins 1967, Vandermeer 1972). However, the principle of competitive exclusion has also been widely criticized as being overly simplistic, untestable or circular (e.g., Miller 1967, Grant 1972, Connell 1980). In spite of such criticism, the idea of competitive exclusion and species coexistence remains logically compelling,

has a large body of supporting evidence, and has continued to drive much of the empirical and theoretical research on competition (Aarssen 1983).

Set within the framework of competitive exclusion and the concept of limiting similarity (MacArthur and Levins 1967), theoretical and empirical study of competition focused, until recently, on closely related species, because it is here that theory predicts strong competition and the potential for competitive exclusion (MacArthur and Levins 1967, Abrams 1983). Closely related species have the greatest likelihood of sharing the same fundamental niche (Hutchinson 1957) and therefore having, in essence, a joint carrying capacity in a given habitat. Yet, this very concept, coupled with the realization that species of very different morphologies, phylogenies, life histories etc. compete in natural systems (e.g., Brown and Davidson 1977, Eadie and Keast 1982, Polis and McCormick 1986, Morin et al. 1988, Fauth et al. 1990) has led to alternative proposals for competitive exclusion.

Two critical conditions must be met for competitive exclusion to occur: 1) interspecific competition must be stronger than intraspecific competition (Volterra 1926, Lotka 1932, Gause 1934), and 2) interspecific competition must be consistently asymmetric. The latter is an unstated corollary of the competitive exclusion principle (Aarssen 1983). Consideration of both of these factors has led to one alternative view of competition and competitive exclusion (Aarssen 1983, Ågren and Fagerström 1984, elaborated in Keddy 1989). This theory proposes that dissimilar species are more likely to experience competitive exclusion because 1) the likelihood that intra- and interspecific competition are of near-equal intensity should increase with increasing similarity (Aarssen 1983, Ågren and Fagerström 1984), 2) dissimilar species are more likely to demonstrate strong competitive asymmetry as a result of different morphologies, body sizes, or life histories (Keddy 1989). Thus, the long standing reliance on limiting similarity as a mechanism for determining likely competitors (and candidates for possible competitive exclusion)(Hutchinson 1959, MacArthur and Levins 1967, see Abrams 1983 for a review) is called into question (Fauth et al. 1990, Resetarits unpubl.).

When competition occurs between species of very different morphologies, the nature of the potential interactions becomes more complex. Broad sense interspecific competition (population level -/-), includes the reciprocal negative effects of two competing populations as a result of exploitative and interference modes of competition as well as intra-guild predation (Polis and McCormick 1987, Polis et al. 1989) over the entire range of body sizes (and life stages) (Polis 1984, 1988, Werner and Gilliam 1984, Werner 1986). How species impact one another has seldom been addressed in size-structured populations of large, mobile organisms (but see Persson 1988, Polis 1988). Likewise, most instances where competitive symmetry or asymmetry have been quantified involve specific size-classes (or life stages) of species pairs (i.e. Morin and Johnson 1988, Fauth et al. 1990, see reviews in

Lawton and Hassell 1981, Connell 1983, Schoener 1983), rather than entire size- or stage-structured populations. Steps toward assessing the net asymmetry between competing natural populations are critical to determine the importance of competition in natural communities, and to understand the mechanisms of species coexistence. Under conditions where effects are manifested in strong impacts on survival, growth rate and correlated fitness measures, persistence of inferior competitors demands explanation, and the explanation may be broadly instructive regarding the distribution and abundance of species in natural systems.

The strongly asymmetric competition between larval spring salamanders *Gyrinophilus porphyriticus* (Green) and small adult brook trout *Salvelinus fontinalis* (Mitchill) reported previously (Resetarits 1991) could be expected to change with the relative sizes of the two species (Werner and Gilliam 1984), possibly moving towards symmetry at similar sizes, reversing the direction of the asymmetry, or reducing the intensity of competition (Polis 1988). Variation in the strength of competition (or its degree or direction of asymmetry) with changes in life stages is one potential mechanism promoting coexistence. Persistence of strong asymmetry across a range of size-classes would suggest that *G. porphyriticus* is at risk of competitive exclusion. Examining the interactions between several size-classes of co-occurring predators is an important step toward understanding how these populations interact, and is critical to determining the net effects of interspecific competition across the entire life cycle of each species (Polis 1984, 1988, Werner and Gilliam 1984, Wilbur 1984, 1988, Werner 1986).

I conducted a field experiment assaying the interactions between the larval/juvenile stages of these two important aquatic predators to examine changes in the interaction with changing body size. The results of this and a previous experiment (Resetarits 1991) provide insights on the nature of interactions between competing size-structured populations and have important implications for the coexistence of these two species in small Appalachian streams.

Study area and species
Mountain Lake headwater streams

The study was conducted at Mountain Lake Biological Station (MLBS), Giles County, Virginia, USA. Streams near MLBS are first-and second-order mountain streams with clear, cool water running over rubble, gravel, sand and bedrock, with silt and detritus accumulations in the pools. These streams occupy elevations from ca 450 to 1200 m. Vertebrate diversity increases as the streams grow larger with decreasing elevation, primarily from addition of fish species (Burton and Odum 1945). The uppermost reaches support diverse salamander assemblages of up to seven species (Organ 1961, Resetarits

1991). Most of these species occur from the highest elevations to where streams enter the low elevation valleys. Larvae of *G. porphyriticus* and *Eurycea bislineata* are the most common stream-dwelling salamanders at high elevations. Brook trout, *S. fontinalis*, are the only fish present at the highest elevations (Burton and Odum 1945, pers. obs.).

The species

S. fontinalis is the dominant native fish in clear, cool, headwater streams in the southern Appalachians (Burton and Odum 1945). It takes a wide range of prey, from zooplankton to fish and frogs; however, terrestrial and aquatic insects, and other aquatic invertebrates make up the majority of prey in most populations (Carlander 1969). Brook trout are primarily drift feeders, taking suspended organisms from the water column and the surface. They are the largest predators in most streams they inhabit and reach sizes of over 200 mm standard length (SL), even at the upstream limit of their range (pers. obs.). High elevation streams near MLBS contain healthy (unsupplemented) populations of native brook trout. Though abundant in these streams, their reproductive success is highly variable, both within and among streams. Following good years, fingerling brook trout densities can be high in individual streams; following bad years, they may be completely absent from those same streams, resulting in spatial and temporal variation in the densities of juvenile size (age) classes (Resetarits and E. A. Marschall pers. obs.). The causes of this local variation are unknown. Similarly, adult brook trout exhibit a mosaic pattern of presence/absence in small headwater streams as a result of variation in stream morphology (Flebbe 1994, Resetarits and Marschall pers. obs.)(note: fishing pressure is virtually zero in these small, high elevation streams).

G. porphyriticus is a large semi-aquatic salamander common in the Appalachians (Dunn 1926). Larvae reach > 60 mm snout-vent length (SVL) and may spend up to six yr in the aquatic larval stage at MLBS (Resetarits unpubl.). Larvae are benthic, generalist predators that hide under rocks and in the gravel matrix during the day and emerge to forage at night on and in the stream substrate (pers. obs.). Larvae commonly reach local densities of ca 5–10/m² in streams near MLBS, excluding the smallest size-class (young of the year) which live deep in the gravel matrix and rarely occur in field samples (Resetarits unpubl., M. Gustafson pers. comm.). Larval G. porphyriticus are the most abundant large, aquatic predator above the upstream limits of brook trout. Densities may fall by > 50% in sections containing brook trout (Resetarits 1988). Larval densities remain high in MLBS streams, except in (and, perhaps, following) extreme drought years (Resetarits unpubl., M. Gustafson pers. comm.).

Brook trout and larval spring salamanders are the most abundant large predators in high elevation headwater streams of the Allegheny Mountains of western Virginia. The two species occur at a wide range of sizes (at least two orders of magnitude) and utilize similar microhabitats, from the open water of pools to beneath boulders and cobbles at the stream edge (Resetarits and Marschall pers. obs.). Species diversity is relatively low and the range of available habitats is restricted, creating the potential for strong interactions between several size classes of these species. The interaction between larval *G. porphyriticus* and small adult *S. fontinalis* is highly asymmetric; adult *S. fontinalis* exert a strong negative effect on survival and growth of larval *G. porphyriticus*, with no reciprocal effect on *S. fontinalis* (Resetarits 1991). The effects on both growth and survival of *G. porphyriticus* suggest that either attempted predation or interference competition may be the mechanism of interaction, rather than simple exploitative competition (Resetarits 1991). Interference competition and intraguild predation are most likely in relatively restricted habitats, such as in these small streams, where resources can be effectively monopolized (Polis 1988).

Materials and methods
Experimental stream system

The experiment was conducted in nine experimental streams located below a permanent spring (elevation ~1220 m) at MLBS. Streams were constructed from steel and polyethylene cattle feed bunks 3.35 m long, 0.69 m wide and 0.36 m deep, in the bed of Sartain Branch, which originates at the spring. The canopy over the stream array (primarily *Rhododendron maximum*) was left intact to preserve natural conditions. Bunks were placed directly on the stream bed and leveled to a gradient of 3.3–4.5 cm/m, resulting in a shallow upstream and a deep downstream end. Each had a separate inflow pipe and valve to control flow rate, and drained directly into the stream bed via a rotating standpipe. Standpipes were covered with fiberglass window screening over a frame of plastic gutterguard mesh. The bunks have a 5.5 cm lip along the sides and the ends were coated with petroleum jelly to prevent escape. The streams were otherwise open to the environment to allow aerial colonization by insects and natural input of terrestrial drift organisms and litter (see Resetarits 1991 for additional details). Aquatic drift was limited to organisms inhabiting the spring, as it is for the upper reaches of many spring-fed streams. The design eliminated any communication between units, assuring biological and statistical independence.

The experimental streams approximated the habitat heterogeneity of natural stream pools (e.g. variable water depth, substrate depth, substrate type, and amount of light), providing habitats from open water to shallow, rocky edge. Each stream received 40 l of unwashed com-

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mercial sand, 30 l of commercial river gravel, 4 l of packed leaf litter, 1 large spillway rock, and 12 flat cover rocks of varying size (see Fig. 2 in Resetarits 1991 for additional detail). Each ingredient was thoroughly mixed (where appropriate) and aliquots randomly assigned to individual streams. Spring output varied directly with rainfall, thus, the flow regime in the experimental streams mimicked the natural streams.

Experimental design

I used a randomized complete block design partially crossing two species at two densities (0 and X; 0 × 0 treatment excluded). Each treatment was replicated three times for a total of 9 units. Treatments consisted of zero or eight larval *G. porphyriticus* or zero or six fingerling *S. fontinalis* per stream. Experimental densities were based on field densities (by size class) in streams near MLBS. Treatments were assigned randomly within each block. Larvae and fingerlings were randomly assigned to size-stratified samples and samples then randomly assigned to experimental streams. Larval *G. porphyriticus* ranged from 35.7–62.4 mm snout-vent length (SVL) (mean ± 1 SD, 48.7 ± 7.4 mm) and from 1.1 – 4.85 g mass (2.7 ± 1.2 g). This size range included larvae in their third through sixth year (Resetarits unpubl.); younger (smaller) larvae were not included. Fingerling *S. fontinalis* ranged from 78–105 mm total length (TL) (93.0 ± 7.9 mm) and from 4.55–10.4 g mass (7.6 ± 1.8 g). Trout were approximately 18 months from hatching.

The experiment began 5 May 1990 with the addition of *G. porphyriticus* and *S. fontinalis*, and ended 9 July 1990 with the removal of all survivors (65 d). Termination protocol is described in a previous paper (Resetarits 1991). All animals were collected from first- and second-order tributaries of the New River, on Salt Pond Mountain, Giles County, Virginia. *S. fontinalis* came from Pond Drain and White Rocks Branch. *G. porphyriticus* were collected in Hunter's Branch, a first-order, fishless tributary of Pond Drain. Use of animals from fishless waters eliminates the possible effects of prior experience with brook trout. Because of the effects of drift (Bruce 1985, 1986, Cooper et al. 1990), however, it is unlikely that genetic differentiation has occurred between upstream (trout-free) and downstream sections.

Habitat use

Behavioral observations were conducted on three dates (1, 5 and 6 July 1990) to assay activity and habitat use by both species. Diurnal habitat use for *S. fontinalis* was not quantified because they were impossible to observe without disturbance. Observations were therefore done at night, between 2000 h and 0030 h, and consisted of searching each experimental stream with a headlamp, without physical disturbance. Streams were divided into

four zones of equal length. Zone 1 was the shallow and Zone 4 was the deep end. Searches were conducted in the same direction on all streams on a given night. Individuals were identified to species and their location noted. Larval *G. porphyriticus* are primarily nocturnal, so the number observed was a measure of species-specific activity; for *S. fontinalis*, it was simply a measure of their preference for nocturnal resting sites, thus limiting the value of the *S. fontinalis* data. Location among the zones measured habitat use along a natural gradient from stream edge (equivalent to Zone 1) to pool center (equivalent to Zone 4), with a corresponding depth gradient of shallow to deep water and a substrate gradient of gravel to silt-sand-leaf litter.

Data analysis

Response variables were survival and growth (change in SVL [ΔSVL] for *G. porphyriticus* or change in total length [Δ TL] for *S. fontinalis*, and change in mass [Δ mass]). Mean growth per stream formed the unit of statistical analysis and was based on the responses of uniquely identified animals. *G. porphyriticus* were individually identified within each stream by the pattern of lateral line pores on the dorsal surface near the hind legs (Resetarits 1991). Fingerling *S. fontinalis* were individually photographed at introduction and subsequently identified by juvenile parr marks.

Growth was analyzed by multivariate analysis of variance (MANOVA) on the multivariate vector of Δlength and Δmass. Survival was analyzed using contingency table analysis with Fisher's exact test for 2 × 2 tables.

Activity levels (cumulative number of individuals observed) were square-root transformed and the values were corrected for number of survivors in each stream by using the angularly transformed survival values as a covariate in an analysis of covariance (ANCOVA). Distributions within streams were tested using the χ^2 tests for goodness of fit.

Because block effects were not close to significant for any responses, block and error sums of squares were pooled to test treatment effects. Statistical analyses were performed using the PROC GLM procedure of PC-SAS (version 6.03, SAS Institute 1988) and the Statgraphics system (version 3.0, Statistical Graphics Corporation 1988).

Results

Responses of larval G. porphyriticus

Mean survival was 50% for *G. porphyriticus* alone and 25% in the presence of fingerling *S. fontinalis*, but the difference was not significant (Fisher's exact test, P = 0.068, one-tailed test, Fig. 1a). Mean initial size of non-survivors in the *G. porphyriticus* alone treatment (49.01 ±

Table 1. MANOVA of growth and individual ANOVAs for Δ SVL and Δ mass for larval *Gyrinophilus porphyriticus*.

MANOVA (Δ SVL, Δ Mass)

Source of Variation	df	Wilks' λ	F	P
Treatment	2,3	0.0333	43.58	0.006

ANOVA of Δ SVL

Source of variation	df	SS	MS	F	P
Treatment	1	3.8400	3.8400	8.35	0.045
Error	4	1.8392	0.4598		
Total	5	5.6792			

ANOVA of Δ mass

Source of variation	df	SS	MS	F	P
Treatment	1	0.7004	0.7004	95.08	0.0006
Error	4	0.0295	0.0074		
Total	5	0.7299			

8.03, Fig. 2) was not significantly different from mean initial size of non-survivors with *S. fontinalis* (51.97 ± 6.20, t = 1.10, df = 28, P < 0.30, two-tailed test, Fig. 2).

Table 2. Analysis of covariance for *Gyrinophilus* activity using survival as the covariate.

Source of variation	df	SS	MS	F	P
Survival (Covariate)	1	2.974	2.974	26.39	0.0143
Treatment	1	0.670	0.670	5.94	0.0927
Error	3	0.338	0.113		
Total	5	3.982			

Thus, mortality due to brook trout was not obviously skewed by size, though the smallest size class is not represented among survivors in the *S. fontinalis* treatment.

S. fontinalis had a significant effect on ΔSVL, reducing it from a mean of 3.66 mm for *G. porphyriticus* alone to a mean of 2.06 mm ($F_{1,4} = 8.35$, P = 0.045, Table 1, Fig. 1c). Change in mass was highly significantly less with *S. fontinalis*: a mean increase of 0.73 g for *G. porphyriticus* alone vs 0.05 g with *S. fontinalis* ($F_{1,4} = 95.08$, P = 0.0006, Table 1, Fig. 1d). The MANOVA on growth demonstrated a highly significant effect of *S. fontinalis* on *G. porphyriticus* ($F_{2,3} = 43.58$, Wilk's λ = 0.0333, P = 0.006, Table 1). Thus, *S. fontinalis* is implicated in re-
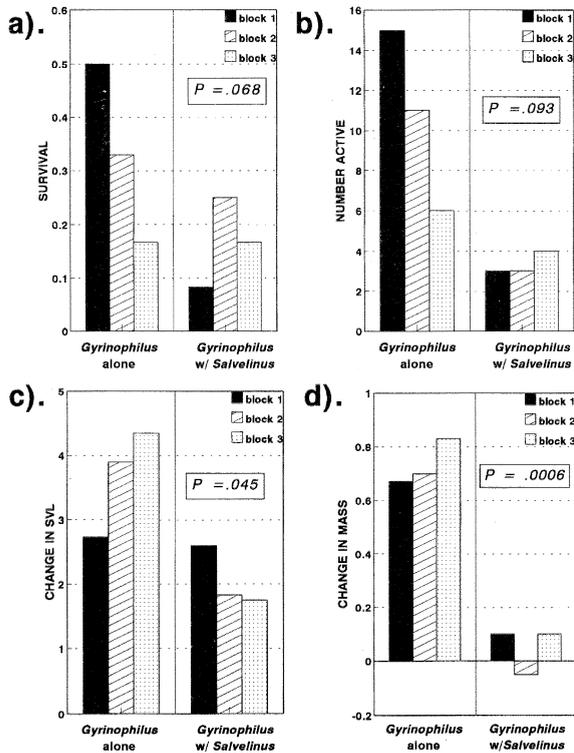

Fig. 1. Responses of larval *G. porphyriticus* by treatment and block for (a) survival, (b) activity, (c) change in SVL, and d) change in mass.
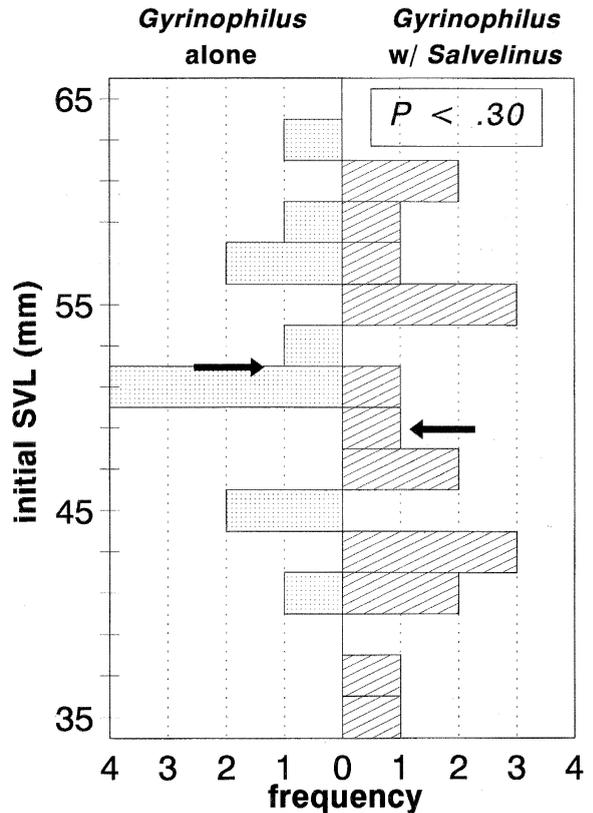

Fig. 2. Initial size-frequency distributions of non-survivors of *G. porphyriticus* in treatments with and without brook trout. Arrows indicate location of means.
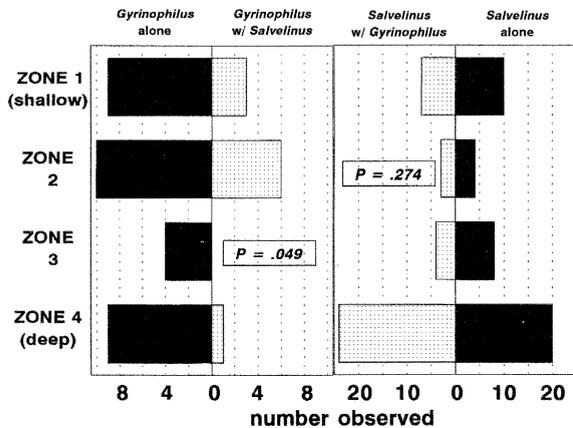
Fig. 3. Distribution of activity within zones of the artificial streams by species and treatment showing the habitat shift by *G. porphyriticus*. Zone 1 is the shallow end of each stream, Zone 4 the deep end.

Fig. 4. Responses of fingerling *S. fontinalis* by treatment and block for (a) survival, (b) activity, (c) change in TL, and d) change in mass.

duced survival of larval *G. porphyriticus* in the experimental streams and clearly affected growth in terms of both length and mass. The average length increment lost over the 65 d due to *S. fontinalis* (1.6 mm) is equivalent to 20% of the average annual growth (7.97 mm/yr) for *G. porphyriticus* from trout-free streams at MLBS (Resetarits unpubl.).

Variation in survival explained 75% of the observed variation in *G. porphyriticus* activity among streams ($F_{1,5}$ = 26.39, R^2 = 0.747, P = 0.014, Table 2, Fig. 1b). Activity was not significantly different between streams with *G. porphyriticus* alone and those also containing *S. fontinalis*, after removing the sums of squares due to the covariate survival ($F_{1,5}$ = 5.94, R^2 = 0.168, P = 0.093, Table 2, Fig. 1b). Distribution within the streams was also examined. Because of the low number of observations of *G. porphyriticus* in streams containing *S. fontinalis*, observations were combined into two classes, (from the original four) shallow (Zones 1 and 2) and deep (Zones 3 and 4), for analysis. Distribution of activity (night) between shallow and deep halves of the stream was not significantly different from uniform for *G. porphyriticus* alone (χ^2 = 1.125, df = 1, P = 0.289, Fig. 3), but was significantly different from uniform for *G. porphyriticus* with *S. fontinalis* (χ^2 = 6.4, df = 1, P = 0.011, Fig. 3). The distribution of *G. porphyriticus* with *S. fontinalis* was significantly skewed (toward the shallow half of the stream) compared to predicted distributions based on streams containing only *G. porphyriticus* (χ^2 = 3.883, df = 1, P = 0.049, Fig. 3). Thus, activity levels in *G. porphyriticus* were not significantly affected by *S. fontinalis*, but the distribution of activity within the streams was significantly affected.
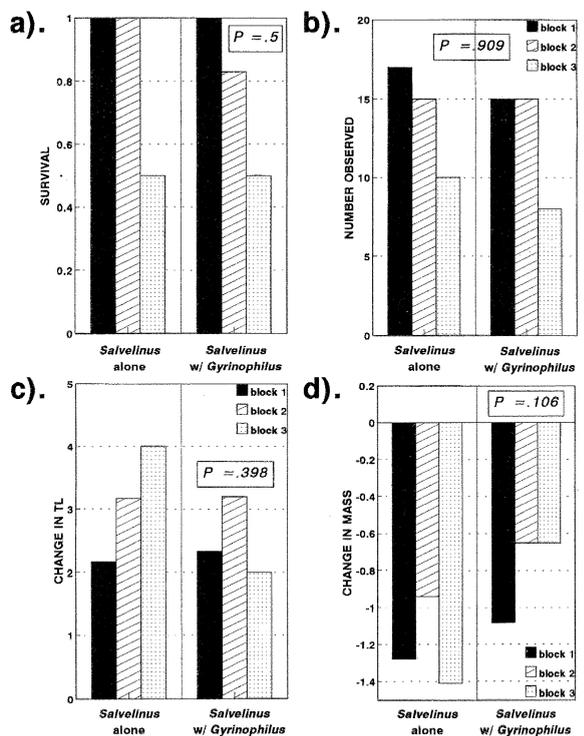
Table 3. MANOVA of growth and individual ANOVAs for Δ TL and Δ mass for fingerling *Salvelinus fontinalis*.

MANOVA (Δ TL, Δ Mass)

Source of Variation	df	Wilks' λ	F	P
Treatment	2,3	0.4385	1.92	0.290

ANOVA of Δ TL

Source of variation	df	SS	MS	F	P
Treatment	1	0.5460	0.5460	0.89	0.398
Error	4	2.4479	0.6120		
Total	5	2.9939			

ANOVA of Δ mass

Source of variation	df	SS	MS	F	P
Treatment	1	0.2604	0.2604	4.32	0.106
Error	4	0.2411	0.0603		
Total	5	0.5015			

Table 4. Analysis of covariance for *Salvelinus* activity using survival as the covariate.

Source of variation	df	SS	MS	F	P
Survival (covariate)	1	1.027	1.027	12.19	0.0397
Treatment	1	0.001	0.001	0.02	0.9087
Error	3	0.253	0.084		
Total	5	1.281			

Responses of fingerling S. fontinalis

All trout used lost weight during the experiment, suggesting that densities were high relative to food availability in the experimental streams. Very low or negative increase in mass was also observed for fingerling brook trout raised at ambient densities in large field enclosures in MLBS streams (Marschall 1991), suggesting that seasonal loss of mass to maintenance and increasing length may not be an artifact of the experimental streams.

Larval *G. porphyriticus* had no effect on the survival of fingerling *S. fontinalis* (Fisher's exact test, P = 0.5, one-tailed test, Fig. 4a). Mean survival was 83% for *S. fontinalis* alone and 77% with *G. porphyriticus*. There was no effect of larval *G. porphyriticus* on either ΔTL (Table 3, Fig. 4c), Δmass (Table 3, Fig. 4d) of *S. fontinalis*, or on the MANOVA of growth (Table 3). Larval *G. porphyriticus* had no effect on the survival or growth of fingerling *S. fontinalis* in the experimental streams.

An analysis of covariance was performed on the total number of individuals observed in the three nocturnal surveys. As expected most of the surviving *S. fontinalis* were readily observed in resting positions in each stream. The ANCOVA revealed that *G. porphyriticus* had no effect on the number of *S. fontinalis* observed ($F_{1,5} = 0.02$, $R^2 = 0.001$, $P = 0.909$, Table 4, Fig. 4b) and that the covariate survival (angularly transformed) explained 80% of the variance in the number of *S. fontinalis* observed in the streams ($F_{1,5} = 12.19$, $R^2 = 0.802$, $P = 0.040$, Table 4, Fig. 4b). *S. fontinalis* were non-uniformly distributed in both the *S. fontinalis* alone streams ($\chi^2 = 13.24$, df = 3, P = 0.004, Fig. 3) and the *S. fontinalis* with *G. porphyriticus* streams ($\chi^2 = 30.42$, df = 3, P = 0.000001, Fig. 3) with distributions skewed toward both the shallowest section (Zone 1) and the deepest section (Zone 4). Distributions of *S. fontinalis* in the presence of *G. porphyriticus* were not significantly different from those predicted from the distributions of *S. fontinalis* alone ($\chi^2 = 3.89$, df = 3, P = 0.274, Fig. 3). *G. porphyriticus* had no effect on the nocturnal distribution of trout, and, thus, presumably, on their habitat use in general (any effect of *G. porphyriticus* on trout behavior, e.g., as a result of interspecific aggression, should manifest itself at night).

Discussion

This experiment demonstrated strongly asymmetric interactions between specific size classes of *G. porphyriticus* and *S. fontinalis*. Fingerling *S. fontinalis* reduced survival and growth, and altered the habitat use of larval *G. porphyriticus* in experimental stream communities. There were no reciprocal effects of larval *G. porphyriticus* on fingerling *S. fontinalis*. These results are strikingly similar to those reported for interactions between small adult *S. fontinalis* and larval *G. porphyriticus* (Resetarits 1991) (see Fig. 5). In both cases *G. porphyriticus* survival was reduced; 58% by adult *S. fontinalis* (Resetarits 1991) and 50% by fingerling *S. fontinalis*. The non-significance of the latter effect was probably the result of low statistical power; the similarity of the effects of the two size-classes suggests that the decrease in survival with either size-class of trout is real. Mean growth (in mass) was reduced 65% by adult *S. fontinalis* and > 90% by fingerling *S. fontinalis*. Mean growth in length was not affected by adult *S. fontinalis*, but was reduced 44% by fingerling *S. fontinalis*. Fingerling *S. fontinalis* caused *G. porphyriticus* to shift habitat use from a uniform distribution to one favoring shallower water (Fig. 3). No clear habitat shift occurred with adult *S. fontinalis*; larvae preferred shallow water under all conditions.

The outcome of interactions between these two species
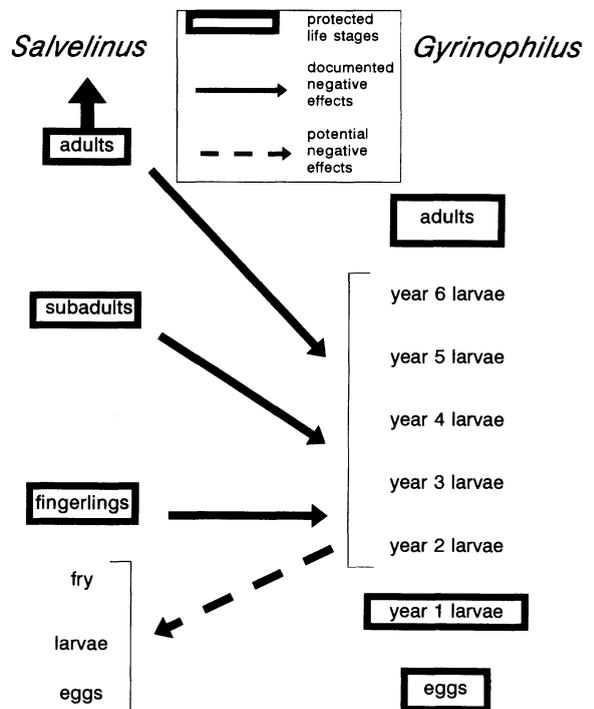

Fig. 5. Summary of asymmetric interspecific interactions between life stages (size classes) of *S. fontinalis* and *G. porphyriticus*. The vertical axis is body size. The vertical arrow indicates the potentially much larger terminal sizes achieved by adult brook trout. See text for additional details.

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is insensitive to variation in the size of *S. fontinalis* across the considerable size range encompassed by these two experiments (see Fig. 5 for a summary). *S. fontinalis* have a strong negative effect on larval *G. porphyriticus* and the net strength of that effect would remain relatively constant as a result of the relative abundance of brook trout size classes in natural streams (Marschall 1991); many small fish have an effect similar to one large fish. I suggest that the nature of this interspecific interaction extends beyond simple exploitative competition to severe interference competition (Resetarits 1991), since larval salamanders should not die of starvation given the water temperatures and the duration of either experiment (65 and 100 d). Salmonids, including brook trout, are known for being highly aggressive towards potential competitors (Fausch and White 1981, 1986). The rather low survival of *G. porphyriticus* when alone in both experiments suggests that aggression, in this case intraspecific aggression, may be responsible for reduction in survival in the *G. porphyriticus* only streams. Lower survival (50%, present experiment vs 65%, Resetarits 1991) corresponds to higher densities (8/stream vs 5/stream).

The variables affected in larval *G. porphyriticus* have strong potential effects on fitness. Mortality has obvious fitness consequences and the level of growth reduction in both experiments could delay metamorphosis a year or more (if size at metamorphosis is fixed) or produce significantly smaller size at metamorphosis, size at first reproduction, and concomitant reduction in brood size (Smith 1987, Semlitsch et al. 1988). Smaller size at metamorphosis may also be important for *G. porphyriticus* because, unlike the larvae which are prey generalists, adults specialize on salamanders (Bruce 1979, 1980, Hairston 1987); reduced adult body size could severely limit the size of salamander prey available, thus limiting adult growth rate.

The persistent asymmetry (and severity) of the interaction between larval *G. porphyriticus* and *S. fontinalis* raises the question of the coexistence of these two species. Competitive exclusion theory predicts that, under these conditions, *G. porphyriticus* should be excluded from stream sections occupied by brook trout (Gause 1934). Though Pielou (1974) points out that the conditions for competitive exclusion are seldom met in natural systems, it is important to determine whether violation of these conditions is simply fortuitous, or whether violation, in itself, is a precondition for coexistence or may even constitute an important evolutionary strategy for coexistence. In this system the traditional mechanisms of coexistence are probably not sufficient; niche divergence (or character displacement) seems unlikely to overcome the strong effects of competition because of the broad distribution, size-structured populations, and the generalized trophic morphology, food habits and habitat use of these two predators, and because the interaction extends beyond simple exploitative competition. The alternative, the evolution of competitive ability (alpha selection, Gill 1972), or competitive combining ability (Aarssen 1983)

is unlikely due to the disparity in the capabilities of the two species and the degree of asymmetry of the interaction.

The strong effects seen in these experiments and the general negative correlation between the success of aquatic breeding salamanders and the presence of predatory fish (Petranka 1983, Hairston 1987, Thiesmeier and Schuhmacher 1990) lead us to the general question of: What mechanisms allow the coexistence of palatable (vulnerable) species of salamanders with predatory fish? This is especially problematic in cases where the full range of negative effects of "broad-sense competition" (exploitation, interference and intraguild predation) are realized. Fish-salamander competitive (narrow sense) interactions are typified by strong asymmetries favoring fish, as illustrated for larval *G. porphyriticus* and *S. fontinalis* (Resetarits 1991, this paper), adult newts, *Notophthalmus viridescens*, and adult banded sunfish, *Enneacanthus obesus* (Bristow 1991), and juvenile *Siren intermedia* and adult black-banded sunfish, *Enneacanthus chaetodon* (Resetarits unpubl.). These examples involve species that co-occur naturally to varying degrees. Anecdotal examples of the exclusion of salamanders from lentic waters by fish abound, and the negative correlation between the presence of predatory fish and that of most pond-breeding salamanders is an established truism (Hairston 1987).

Little is known of the interactions between fish and stream breeding salamanders. Several species of obligately paedomorphic salamanders, such as *Cryptobranchus allegeniensis* and several species of *Necturus*, co-occur with fish at all life-stages, but almost nothing is known of the role of fish in their ecology. Among metamorphosing species with stream-dwelling larvae, *Salamandra salamandra terrestris* in central Europe breed and the larvae develop in small stream habitats, but larvae are completely excluded from the downstream sections where predatory fish occur (Thiesmeier and Schuhmacher 1990). Several species of *Dicamptodon* coexist with predatory fish in Pacific Coast streams of the US (Antonelli et al. 1972, D. Wake and M. Power pers. comm.), as do many plethodontids in the eastern US, but, again, little is known of the dynamics of these interactions (except for *G. porphyriticus*). *Ambystoma barbouri* (Kraus and Petranka 1989) provides an interesting, well-studied example of the almost total exclusion of the larvae of a stream-breeding salamander from waters containing predatory fish (green sunfish, *Lepomis cyanellus*) (Petranka 1983, Kats et al. 1988, Sih et al. 1988, 1992). *Ambystoma barbouri* belongs to a family of pond-breeding salamanders (Ambystomatidae) typically excluded from ponds by fish, and which have very different breeding habits from more typical stream-dwelling (in the broad sense) salamanders in the family Plethodontidae (Dunn 1926), such as *G. porphyriticus*. *A. barbouri* lay clusters of eggs in relatively accessible areas in stream pools, avoiding pools containing fish whenever possible, and the relatively conspicuous young occupy the open

water benthic habitat of these pools. The larvae grow fast, completing metamorphosis within a single season (approx. two months post-hatching [Sih et al. 1992] in contrast to approx. three to six yr in larval *G. porphyriticus* [Bruce 1980, Resetarits unpubl.]). Relatively accessible and conspicuous eggs and young, and the relatively simple physical structure of the stream pools contribute to their elimination from pools with fish (Petranka 1983, Kats et al. 1988, Sih et al. 1988, 1992). However, their relatively rapid growth and development, combined with the mosaic pattern of fish distribution in stream pools, allows many individuals and even entire cohorts to complete metamorphosis without ever encountering fish; the strongest selection may be on females to select fish-free oviposition sites rather than on larvae to evolve mechanisms of persisting with fish.

Differences in the outcome of the interaction with fish (i.e., virtual exclusion of *A. barbouri* versus broad coexistence for *G. porphyriticus*) parallel these differences in life history, habitats, population structure, as well as evolutionary history, and support the view that a complex set of factors mediate coexistence of *G. porphyriticus* with brook trout in eastern North America.

Natural coexistence of *G. porphyriticus* and *S. fontinalis* (really a question of the persistence of *G. porphyriticus*) is probably dependent on characteristics of the life history and demography of both species, combined with characteristics of the local environment. Identification of factors that contribute to coexistence in this system may be instructive in terms of other persistent species associations characterized by extreme asymmetry.

(1) Upstream (trout-free) and downstream populations of *G. porphyriticus* may share a source-sink relationship (Pulliam 1988) and comprise an extensive metapopulation (Gill 1978, Gotelli 1991). Downstream populations would be maintained or supplemented by colonists from more successful upstream populations. Downstream drift has been identified as an important factor in the population dynamics of *S. s. terrestris* in central European streams (Thiesmeier and Schuhmacher 1990). Bruce (1985, 1986) suggested that downstream populations of stream-dwelling salamanders in western North Carolina were supplemented by drift of larvae from the upstream sections and small feeder streams, and that downstream drift in these streams could best be interpreted under the production hypothesis of Waters (1965) as a density dependent response to elevated densities in upstream sections. Many such upstream source areas near MLBS are trout-free and support high densities of larval *G. porphyriticus* (Resetarits 1991, unpubl.), providing considerable potential for drift colonization, replenishment, or supplementation of downstream areas (Cooper et al. 1990). Densities of larval *G. porphyriticus* in West Little Stony Creek (near MLBS) are three times higher in stream sections lacking trout (Resetarits 1991).

(2) Specific life stages of *G. porphyriticus* are protected from the impact of brook trout. Post-metamorphic individuals shift from the aquatic larval habitat to a semi-

terrestrial (semi-aquatic) stream edge habitat. This ontogenetic niche/habitat shift removes adult *G. porphyriticus* from potential interaction with brook trout, e.g. aggression; the adult population provides a protected source for new recruits to the larval population. Protected nest sites likewise shelter the eggs from brook trout predation. Eggs are deposited overhanging the water in flooded subterranean cavities, thus reducing or eliminating the risk of trout predation. After hatching, larvae spend at least the first year in the interstices of the stream matrix and in small feeder creeks (pers. obs.), where they are protected both from brook trout and from larger *G. porphyriticus* larvae, which are cannibalistic (pers. obs.). Young of the year are rarely encountered near MLBS, typically representing less than 5% of samples (Resetarits unpubl., M. Gustafson pers. comm.).

Chesson (1986) demonstrated theoretically that variation in recruitment can promote coexistence if fluctuations are not positively correlated between species. Coexistence required that favorable conditions for recruitment occur when each species was at low density, and that generations overlap. This ties in with the life history of *G. porphyriticus*, in which both the long lived adults and the protected early life stages serve as storage (sensu Warner and Chesson 1985) for the frequent periods when local recruitment of *S. fontinalis* is poor. *G. porphyriticus* reproduction is much less variable than that of *S. fontinalis* in streams near MLBS. Populations in trout-free sections were reduced in only one year out of six, as a result of an unusually severe drought (pers. obs., M. Gustafson pers. comm.). In contrast, brook trout reproduction and resultant population densities are highly variable, both temporally and spatially, as a result of undetermined environmental factors (Resetarits and E. A. Marschall, pers. obs.).

(3) Spatial and temporal variation in the reproductive success of brook trout may contribute to the persistence of *G. porphyriticus* by providing a spatial and temporal mosaic of brook trout size/age distributions and densities. A poor recruitment year for brook trout may translate into several good years of reduced pressure for *G. porphyriticus* populations, especially if interactions with juvenile *S. fontinalis* are more frequent, more consistent, or more severe than with adults, as suggested by experimental results (see above). The longitudinal variability in these small streams may also provide localized, trout-free (or reduced density) reaches (Flebbe 1994, Resetarits and Marschall pers. obs.) that function as local refuges for *G. porphyriticus*.

(4) Behavioral avoidance, i.e., the use of cover objects as refuges, or microhabitat shifts within the stream itself (especially into extremely shallow areas [see Fig. 3]), may reduce local effects of brook trout on *G. porphyriticus* larvae. In structurally complex habitats, the effects of *S. fontinalis* on *G. porphyriticus*, although still severe, may be insufficient to drive local larval populations extinct. Larval populations may persist, albeit at reduced densities and growth rates. Population parameters may

therefore differ between trout and trout-free sections, but survival to metamorphosis may be sufficient to maintain adult population densities at sustainable levels in this long-lived species.

In summary, all of the above factors likely contribute to maintaining *G. porphyriticus* populations in streams inhabited by brook trout, and suggest mechanisms by which other stream-dwelling salamanders, such as species of *Desmognathus*, *Eurycea*, and *Leurognathus marmoratus*, may coexist with predatory fish.

Negative interspecific interactions between size-structured populations of predators can be broadly characterized as interspecific competition; the outcome being the net effect of one population on a competing population (population level -/-, or, as in this case, 0/-) across all sizes/ages/lifestages. The potential interactions between such populations include exploitation, interference, and intraguild predation (Polis 1988). Complex interactions of this type are probably common between species that simultaneously occupy a range of body sizes and life stages (Werner and Gilliam 1984), and likely do not obey many rules of competition laid down in theory. Coexistence between competing populations of species with dissimilar morphologies and capabilities does not depend on a single response, such as niche divergence (Gause 1934), alpha selection (Gill 1972), or competitive combining ability (Aarssen 1983) but on complex suites of characteristics which either periodically shift the balance of competition, reverse the sign of the interaction at different life stages, negate local competitive effects, provide temporal or spatial refuges, foster metapopulation dynamics (Gill 1978), or simply allow an inferior competitor to absorb the costs of competition over the long haul. Interactions of this type are probably far more common between size-structured populations of mobile species than competitive interactions that fit the classic parameters and invoke classic explanations for species coexistence.

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