

## FACTORS AFFECTING STAGE-SPECIFIC DISTRIBUTION IN THE STREAM SALAMANDER *GYRINOPHILUS PORPHYRITICUS*

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**ABSTRACT:** In streams, reach-scale physical habitat (i.e., pool, run, riffle, cascade; hereafter mesohabitat) is viewed as an important control on the distribution of organisms. However, there is limited understanding of stage-specific mesohabitat associations in species with complex life histories and of associated causes and population-level implications of these distribution patterns. In intensive field surveys, I found that larvae and adults of the stream salamander *Gyrinophilus porphyriticus* (Plethodontidae) displayed similar associations with pools and riffles. However, larvae were negatively associated with cascades and adults were negatively associated with runs. Adults had no effect on the survival, growth, or activity of larvae in a controlled experiment, suggesting that stage-specific negative associations were not a function of intraspecific interactions. These negative mesohabitat associations may be related to the size-distribution of interstitial spaces in cascades and runs, which were biased against larval and adult body sizes, respectively. My results indicate that incorporating reach-scale habitat structure in sampling programs is critical for accurate assessments of stream amphibian populations, and that perturbations altering reach-scale habitat structure may differentially affect life history stages of *G. porphyriticus*.

**Key words:** Adults; *Gyrinophilus porphyriticus*; Habitat; Headwaters; Larvae; Life history; Plethodontidae; Salamanders; Streams

UNDERSTANDING what controls species distribution is a basic goal of ecology (Begon et al., 1990; Hanski and Gilpin, 1997; MacArthur, 1972). The relative importance of biotic and abiotic factors is a central question in this area of research (Andrewartha and Birch, 1954; Barbour et al., 1987; Power et al., 1988). The physical complexity of the stream environment has resulted in extensive investigation of abiotic factors that influence species distribution (Hauer and Lamberti, 1996; Statzner et al., 1988; Vannote et al., 1980). Reach-scale physical habitat (hereafter mesohabitat) receives considerable attention in this context, largely due to the correlation between mesohabitat types (i.e., pool, run, riffle, cascade) and a range of abiotic conditions (Frissell et al., 1986; Gordon et al., 1992; Hawkins et al., 1993; Montgomery and Buffington, 1997). Of these conditions, consistent differences among mesohabitat types in substrate composition and flow may be particularly important in influencing species occurrence and abundance (Allan, 1995; Hankin, 1984; Schlosser, 1991; Statzner et al., 1988; Vogel, 1994). Biotic interactions are also clearly important in structuring species

distribution in streams, but investigations of these factors tend to be limited to experimental enclosures or localized field surveys (i.e., within reaches < 100 m in length), leading to uncertainty regarding their contribution to among-reach variation in species occurrence and abundance (Folt et al., 1999; Peckarsky et al., 1997; Power and Dietrich, 2002; Ward, 1997).

There is a strong foundation of research examining the role of species interactions in determining the composition of stream amphibian communities (e.g., Hairston, 1987; Petranka, 1983; Resetarits, 1991). These studies have identified individual size as a key determinant of the outcome of both inter- and intraspecific interactions and, therefore, a strong predictor of the occurrence of stream amphibian species and size-classes within a reach (Beachy, 1991; Formanowicz and Brodie, 1993; Gustafson, 1994; Resetarits, 1995). There also has been increased attention to the influence of physical habitat on the distribution of stream amphibians, both in the context of anthropogenic perturbation of habitat structure (Corn and Bury, 1989; Lowe and Bolger, 2002; Welsh and Ollivier, 1998) and natural variability in this structure (Barr and Babbitt, 2002; Bruce, 2003; Smith and Grossman, 2003; Welsh and Lind, 1996). While these studies

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suggest that mesohabitat and correlated physical conditions may influence stream amphibian distribution, their conclusions are based on data for a single life-history stage (i.e., size class) or for multiple stages combined into one measure of species occurrence. As a result, contributions to observed mesohabitat associations of (a) stage-specific patterns of habitat use and (b) size-structured intraspecific interactions are not well understood.

The spring salamander, *Gyrinophilus porphyriticus* (Plethodontidae), is found in small, cool, well-oxygenated streams along the Appalachian uplift, from central Alabama to southern Quebec (Petranka, 1998). Larvae are strictly aquatic and the larval period has been estimated to be 3–5 years, with a modal period of 4 years (Bruce, 1980). Adults are highly aquatic, but forage terrestrially at night (Deban and Marks, 2002; DeGraaf and Rudis, 1990). For simplicity, I use the term “adult” to refer to transformed individuals, but I do not mean to imply sexual maturity. During the day, larvae and adults are found in interstitial spaces among the larger substrate particles of the streambed (Bruce, 2003). In the northern Appalachians, larval size range is 26–80 mm snout–vent length (SVL) and adults can reach 120 mm SVL (Lowe, 2003; Lowe et al., 2004). In this part of the species’ range, both stages feed primarily on aquatic and terrestrial invertebrates (Burton, 1976). Prior research has shown that the total abundance of *G. porphyriticus* (i.e., larvae and adults combined) in New Hampshire headwater streams is negatively related to the concentration of fine sediment in the streambed (Lowe and Bolger, 2002), and that adults are especially sensitive to reduction in interstitial habitat caused by sedimentation (Lowe et al., 2004). However, little is known about which variables structure the within-stream distribution of this species, including the influence of mesohabitat structure on both species-level and stage-specific patterns of distribution. Likewise, although *G. porphyriticus* larvae and adults have been shown to reduce the growth and survival of smaller species of salamanders in experimental enclosures (Beachy, 1994; Formanowicz and Brodie, 1993; Gustafson, 1993, 1994; Resetarits, 1991), interactions between *G. porphyriticus* larvae and adults have not been examined.

The objective of this research was to better understand the relative importance of physical conditions and intraspecific interactions in structuring the within-stream distribution of *G. porphyriticus* larvae and adults. To meet this objective, I used intensive field surveys of a fishless stream (i.e., where adults of *G. porphyriticus* were top predators) to assess mesohabitat associations in larvae and adults of *G. porphyriticus*, and to determine if mesohabitat associations were related to differences in the body condition of *G. porphyriticus* individuals. I used a controlled experiment to investigate interactions between the two life history stages. Based on existing evidence for the importance of size in structuring stream amphibian communities and for the effectiveness of *G. porphyriticus* as a salamander predator (Wright and Haber, 1922), I predicted that negative effects of *G. porphyriticus* adults on conspecific larvae would lead to differential mesohabitat associations in the two stages. In the fishless study stream, variation in mesohabitat association without evidence of negative intraspecific interactions would suggest that the stages have different mesohabitat preferences, or that they are passively sorted into different mesohabitat types by processes unrelated to habitat preferences (Bond et al., 2000; Fonseca and Hart, 2001; Tyler and Gilliam, 1995).

## MATERIALS AND METHODS

### *Study Site*

I assessed mesohabitat associations of *G. porphyriticus* larvae and adults in Merrill Brook, a fishless stream in Dartmouth College’s Second College Grant, Coos County, New Hampshire, USA. Merrill Brook is a first-order stream (i.e., it begins where water running overland first converges to form a discernable channel) and flows into the much-larger Dead Diamond River. A wetland at the confluence serves as a barrier to brook trout that might enter Merrill Brook from the river. Consequently, *G. porphyriticus* is the top predator in Merrill Brook. I focused this study on a 1000-m long section of Merrill Brook starting at the confluence with the wetland and encompassing the entire perennial portion of the stream. Typical of headwater streams in the northeastern USA, the width

and depth of the channel were highly variable throughout the study section, resulting in no consistent longitudinal trend in these variables (W.H. Lowe, unpublished data). Consistent with undisturbed headwater streams throughout New Hampshire (Lowe and Bolger, 2002), Merrill Brook displayed low conductivity (12.0–15.0  $\mu\text{S}$ ), slight acidity (pH of 5.0–6.0), high dissolved oxygen content (80–90% saturation), and moderate mid-day temperatures (13.0–17.0 °C) in the summer. Other salamanders, including *Eurycea bislineata* and *Desmognathus fuscus* (both Plethodontidae), were rarely encountered in Merrill Brook. The experiment examining interactions between *G. porphyriticus* larvae and adults was conducted along Alder Brook, a first-order stream located 3 km from Merrill Brook.

#### *Physical Habitat Assessment*

To quantify mesohabitat availability in Merrill Brook, I characterized the mesohabitat type of each 10-m reach of the 1000-m study section based on visual estimates of predominant flow, gradient and substrate conditions (modified from Montgomery and Buffington, 1997). Pools were defined by evidence of scour caused by obstruction, blockage, merging of flows, or constriction, and were dominated by cobble substrate (64–256 mm in diameter). Runs were defined by low gradient and laminar flow, and were dominated by gravel-pebble substrate (2–64 mm). Riffles were defined by moderate gradient and turbulent flow, and were dominated by cobble substrate (64–256 mm). Cascades were defined by high gradient and highly turbulent flow, and were dominated by boulder-bedrock substrate (>256 mm).

#### *Salamander Surveys*

Six salamander surveys of the study section of Merrill Brook were conducted during three-day periods in mid-June, mid-July and mid-August of 2000 and 2001. A cover-controlled active search sampling method was used (Heyer et al., 1994). Moving upstream, I turned rocks between 64 and 256 mm in diameter (cobble: Platts et al., 1983) within the channel and along the edge. Surveys continued until 1200 rocks had been turned. The presence of cobble in all mesohabitat types allowed me to maintain a constant effort of just over one rock per meter of stream length.

I used an aquarium dip-net to capture salamanders, including those flushed by the current. All larvae and adults of *G. porphyriticus* were measured (SVL, to the nearest 1 mm), weighed (to the nearest 10 mg), and unmarked animals were individually marked by subcutaneous injection of a fluorescent elastomer (Northwest Marine Technologies, Shaw Island, Washington, USA).

I also recorded the length-by-longest-dimension (mm, equivalent to maximum diameter) of each cobble particle under which I found an individual of *G. porphyriticus*. To test for bias against one of the two life history stages caused by turning only cobble-sized rocks, I used a Kolmogorov-Smirnov test to assess whether or not there was a difference between the size distributions of rocks under which larvae were found and under which adults were found. A significant difference between these two distributions would suggest that larvae and adults of *G. porphyriticus* have different cover-size preferences, and indicate that my survey approach may have been biased.

Mesohabitat use by larvae and adults of *G. porphyriticus* was quantified as the number of previously unmarked individuals found in each of the four mesohabitat types, combining individuals across survey dates. The mesohabitat of each individual was described according to predominant flow, gradient and substrate conditions within 5 m downstream and 5 m upstream of the point of capture. To assess mesohabitat association, I tested the prediction that mesohabitat use by larvae and adults differed from mesohabitat availability in Merrill Brook using likelihood ratio G-tests (Sokal and Rohlf, 1995). If larvae and adults were to have random distributions with respect to mesohabitat types, then the number of observations in each mesohabitat type would be proportional to the relative availability of each mesohabitat type in the stream (i.e., the ratio of the number of 10-m intervals of the study section exhibiting a particular mesohabitat type to the total number of 10-m intervals in the study section).

Log-transformed SVL and mass measurements from previously unmarked individuals were used to calculate size-corrected mass (log mg), an index of body condition (Green, 2001; Jakob et al., 1996). Analysis of covariance

(ANCOVA) was used to assess variation among mesohabitat types in size-corrected mass of larvae and adults. The mesohabitat type where an animal was found and survey year were entered as sources of variability in the ANCOVA model. Prior analyses indicated that survey year was a significant source of variability in the condition of *G. porphyriticus* individuals in Merrill Brook (Lowe, 2003). SVL was entered as a continuous covariate. In *a posteriori* comparisons, Tukey honestly significant difference (HSD) tests were used to identify mesohabitat pairs that differed in mean larval or adult condition (Sokal and Rohlf, 1995). By restricting analyses of mesohabitat association and body condition to unmarked animals, I controlled for the lack of independence among observations of the same individual over time. Overall patterns of salamander movement in Merrill Brook (Lowe, 2003) indicated that the probability of an individual moving to a different mesohabitat unit during the 2-year sampling period was low.

#### *Experimental Analysis of Adult-Larval Interactions*

In July and August of 2001, I conducted a three-week experiment to assess the effects of adult *G. porphyriticus* on the survival, growth, and activity of larval conspecifics. Experimental units were 250-l, flow-through artificial stream pools set on the bank of Alder Brook. I used garden pools constructed of black, high-density polyethylene. Pools were 3-m long by 1-m wide with a central section 0.5 m deep surrounded by a peripheral ring 0.25-m deep. Pools were gravity fed from the main stream channel and flow was 6 l per minute. Substrate composition was standardized by first adding a base mixture of equal volumes of untreated playground sand and gravel (modified from Resetarits, 1991). I then randomly assigned 12 rocks of between 64 and 256 mm in diameter (cobble) to each pool. Enclosures were open to colonization by stream invertebrates and input of falling terrestrial litter and invertebrates. They were left to reach equilibrium physical conditions for one week prior to the beginning of each experiment and this was confirmed by repeated sampling of temperature, dissolved oxygen, pH, and conductivity. I never detected a dif-

ference between physical conditions in the pools and conditions in the stream.

Two conspecific adult densities were applied to pools containing three *G. porphyriticus* larvae (25–45 mm SVL), with six replicates per treatment level. Adult densities were zero and two individuals (80–100 mm SVL). Densities of larvae and adults were selected based on mark-recapture estimates of local densities in the field (Lowe, 2003; Lowe et al., 2004). Larvae were within the size-range of salamanders found in the guts of adult *G. porphyriticus* (16–52 mm SVL, Bishop, 1941; Wright and Haber, 1922). Both larvae and adults were assigned to pools randomly with respect to size.

I assessed larval activity based on four observations of each pool during the experiment. Observations were made at night between 2200 and 2400 h and were randomized so that all pools were visited in a night, but in a random order (modified from Resetarits, 1991). Observation-nights occurred at five-day intervals over the course of the experiment. Observations consisted of five-minute visual searches using a headlamp. The frequency that at least one larva was observed in a visit was the measure of activity level in a pool (e.g., if one or more larvae were observed on two of the four visits, then activity level was 0.50). At the conclusion of each experiment, mean proportional growth (change in mass [mg] =  $[\text{mass}_{\text{final}} - \text{mass}_{\text{initial}} / \text{mass}_{\text{initial}}]$ ) and proportional survival were calculated for *G. porphyriticus* larvae in each pool. To maximize the accuracy of growth estimates, mass measurements were taken using an electronic balance after each larva was lightly swabbed to remove external moisture. The effect of conspecific adults on larval survival was analyzed using contingency table analysis with Fisher's exact test (Sokal and Rohlf, 1995). Larval growth and activity were analyzed using analysis of variance (ANOVA). In the analysis of activity, I corrected for the number of surviving larvae in each pool by including survival as a factor in the ANOVA model.

## RESULTS

### *Mesohabitat Association*

Larvae and adults of *G. porphyriticus* showed evidence of mesohabitat association (larvae,  $G = 52.39$ ,  $df = 3$ ,  $P < 0.0001$ ; adults,

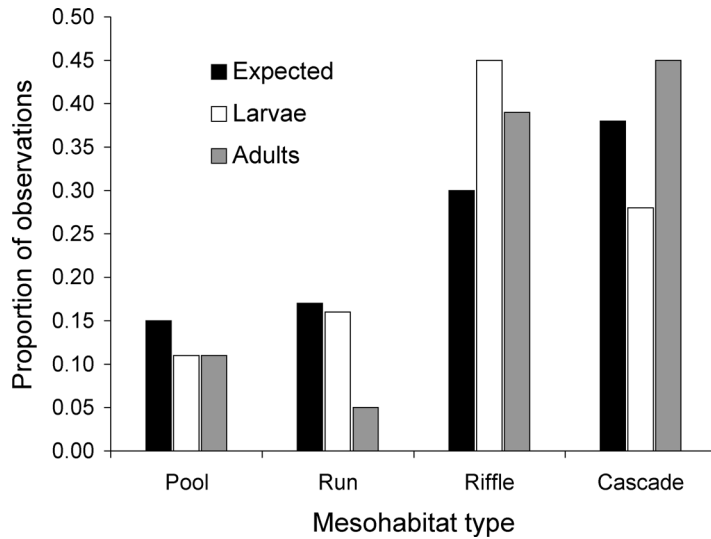


FIG. 1.—Proportions of expected and actual observations of *Gyrinophilus porphyriticus* larvae and adults in four mesohabitat types within a 1000-m section of Merrill Brook. Proportions were derived from total sample sizes of 116 larvae and 231 adults.

$G = 129.82$ ,  $df = 3$ ,  $P < 0.0001$ ; Fig. 1). Both stages were found more frequently in riffles than expected based on availability. Both stages used pools at a frequency slightly lower than availability. Larvae were found less frequently in cascades than expected and adults were found less frequently in runs than expected. Totals of 116 previously unmarked larvae and 231 previously unmarked adults were encountered in surveys of the 1000-m study section of Merrill Brook. The size range of larvae captured in these surveys was 28–80 mm SVL. The size range of adults was 60–112 mm SVL. Mesohabitat use by larvae and adults of *G. porphyriticus* did not differ by year or month ( $\chi^2$  tests:  $P > 0.05$ ). There was no difference between the size distributions of rocks under which larvae and adults were found (Kolmogorov-Smirnov test:  $P > 0.05$ ). The size range of rocks under which both larvae and adults were found was 70–250 mm.

There was no significant variation among mesohabitat types in the condition of larvae of *G. porphyriticus* ( $F_{3,111} = 1.0$ ,  $P = 0.40$ ). Variation in adult condition among mesohabitat types was marginally significant ( $F_{3,226} = 2.62$ ,  $P = 0.05$ ). Adult condition was higher in riffles than in cascades (Tukey HSD:  $P < 0.05$ ). No other mesohabitat pairs differed in adult

condition. The functional relationships between log SVL and log mass of *G. porphyriticus* larvae and adults were linear (W.H. Lowe, unpublished data) and correlations between log SVL and the residuals of these regressions were not significant (Pearson product-moment correlations: larvae,  $r < 0.0001$ ,  $P = 1.0$ ,  $n = 116$ ; adults,  $r < 0.0001$ ,  $P = 1.0$ ,  $n = 231$ ) (Green, 2001).

#### Adult-Larvae Interactions

Adult *G. porphyriticus* had no effect on the survival (Fisher's exact test:  $P = 0.23$ , one-tailed test) or mean proportional growth ( $F_{1,10} = 0.63$ ,  $P = 0.45$ ) of conspecific larvae in the controlled experiment (Fig. 2). The presence of adults tended to increase the activity of larvae, but this effect was only marginally significant ( $F_{1,9} = 5.29$ ,  $P = 0.05$ ). A single larva was depredated in two pools with adults. This was confirmed by identifying larval remains in the gut contents of adults at the conclusion of the experiment. Gut contents were sampled using a nonlethal method of stomach flushing. There was no significant interactive effect of treatment and initial size (SVL, mm) on larval growth (ANCOVA:  $F_{1,30} < 0.001$ ,  $P = 0.98$ ),

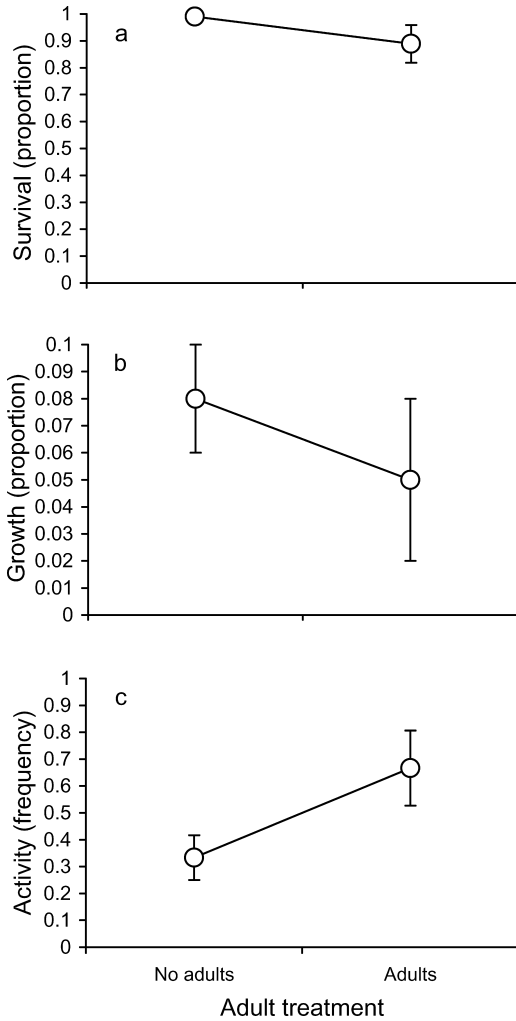


FIG. 2.—Effects of adult *Gyrinophilus porphyriticus* on the (a) mean survival ( $\pm 1$  SE), (b) mean proportional growth ( $[\text{mass}_{\text{final}} - \text{mass}_{\text{initial}}]/\text{mass}_{\text{initial}}$ ) and (c) activity of conspecific larvae.

indicating that larval growth response to conspecific adults did not depend on larval size.

#### DISCUSSION

Larvae and adults of *G. porphyriticus* exhibited different patterns of mesohabitat association. In addition to a strong positive association with riffles shared by both stages, larvae were negatively associated with cascade mesohabitat (high gradient, turbulent flow, large substrate), while adults were negatively

associated with run mesohabitat (low gradient, laminar flow, small substrate) (Fig. 1). My experimental results suggest that the negative association of larvae with cascade mesohabitat was not caused by negative effects of adults on the survival, growth, or activity of larvae. However, this negative association may result from other consequences of interactions between the two stages that were not examined in this experiment (e.g., effects of adults on the foraging success, dispersal, or microhabitat requirements of larvae). The negative mesohabitat associations of both larvae and adults also may be related to a difference between runs and cascades in the size structure of interstitial habitat, resulting in different interstitial habitat availabilities for the two life history stages.

For *G. porphyriticus*, the availability of interstitial habitat in a reach is a function of two factors: the size distribution of the substrate (Gordon et al., 1992; Vogel, 1994) and the size of the individual. Salamanders cannot use interstitial spaces that are smaller than they are, and they avoid spaces that are much larger than they are (C.B. Shannon, unpublished data), which may not provide the tactile cues that a fossorial species like *G. porphyriticus* uses to identify suitable interstitial habitat. Consequently, the availability of interstitial habitat for larvae and for adults is probably very different in cascade and run mesohabitat. The size distribution of interstitial spaces in cascades, dominated by boulder/bedrock substrate, is likely skewed toward large spaces that are not usable by larvae. Likewise, the size distribution of interstitial spaces in runs, dominated by pebble/gravel substrate, is likely skewed toward small spaces that are not usable by adults. Although use of pool and riffle mesohabitat by larvae and adults differed from availability, the stages showed similar associations with these two mesohabitat types (i.e., negative association with pools and positive association with riffles; Fig. 1). These results may be related to the intermediate-sized cobble substrates that predominate in pools and riffles, creating interstitial habitat of similar suitability for both larvae and adults.

Body condition of larval *G. porphyriticus* did not differ among mesohabitat types and the difference in adult condition (riffle > cascade) was not strongly supported and was inconsis-

tent with the mesohabitat associations exhibited by this stage (i.e., adults did not avoid cascades more strongly than they avoided pools or runs). In addition to the experimental results, these data further elucidate the mechanism underlying the mesohabitat associations of the two *G. porphyriticus* life history stages. These results suggest that observed mesohabitat associations may be the result of passive dispersal or settlement processes in the stream, and unrelated to individual performance in the different mesohabitat types (Fonseca and Hart, 2001; Lewin, 1986). Alternatively, individual performance may be so closely linked to mesohabitat that animals distribute themselves within the stream such that body condition is equalized among mesohabitat types (Fretwell and Lucas, 1970; Palmqvist et al., 2000; Tyler and Gilliam, 1995). Further research is required to assess the relative importance of passive sorting processes and active habitat selection in structuring the within-stream distribution of larvae and adults of *G. porphyriticus*.

Given that *G. porphyriticus* is notorious for its habit of eating other salamanders in southern Appalachian systems (Bruce, 1972, 1979; Petranka, 1998), the lack of an effect of adults on the survival, growth, and activity of conspecific larvae is surprising. These results are consistent with research documenting dominance of invertebrate prey in northern populations of *G. porphyriticus* (Burton, 1976), but whether this dominance is the cause or consequence of a lack of adult predation on conspecific larvae remains in question. It is possible that adults in northern populations of *G. porphyriticus* preferentially select invertebrate prey over conspecific larvae. However, adults in New Hampshire do prey on other salamander species (Burton, 1976), suggesting that a mechanism limiting negative interactions between the stages may exist. Behavioral differences (Elliott et al., 1993; Hileman and Brodie, 1994), size-mediated microhabitat segregation (i.e., occurring within all mesohabitat types, Sih et al., 1988; Wissinger, 1992), or species-specific chemical cues (Elliott et al., 1993; Kats et al., 1994) may act to reduce negative intraspecific interactions.

As with any mesocosm study, it is important to consider how experimental conditions may have influenced the results (Skelly, 2002). It is

not possible to replicate the full complexity of the stream environment in artificial pools, and the duration of the experiment was limited to three weeks by the onset of flooding in September 2001. While these conditions may have contributed to the experimental results, I think it is unlikely that they alone accounted for the lack of negative effects of adult *G. porphyriticus* on the survival and growth of conspecific larvae. I selected the size of substrate used in the artificial pools to match the size of substrate in actual stream pools (i.e., cobble). As illustrated by the survey data, this substrate size may be equally suitable for *G. porphyriticus* larvae and adults, and therefore a good choice for examining interactions between the stages while controlling for the effects of physical habitat on the outcome of these interactions. If these interactions are sensitive to substrate conditions (e.g., if adults reduce larval survival in reaches dominated by boulder substrate) or to other reach-scale habitat conditions (e.g., water velocity, stream gradient), then it is possible that observed mesohabitat associations were related to variation among mesohabitat types in the outcome of interactions between the two stages.

An analysis of community  $\times$  habitat interactive effects was beyond the scope of this study, and in another study (Lowe et al., 2004) interstitial habitat availability did not influence interactions between brook trout and larvae of *G. porphyriticus*. However, the possibility of such interactive effects highlights an opportunity for future research. As stated in the introduction, there is a rich history of research in southern Appalachian systems examining how interspecific interactions structure species distribution in communities of stream salamanders (e.g., Hairston, 1987; Petranka, 1983). Individual size is often identified as an important predictor of the outcome of these interactions and, therefore, of the distribution of focal species and size classes (e.g., Beachy, 1991; Gustafson, 1994). More recently, studies have expanded our understanding of how physical conditions affect the distribution and abundance of stream salamanders (Barr and Babbitt, 2002; Bruce, 2003), particularly those physical conditions that are sensitive to anthropogenic impacts (Lowe and Bolger, 2002; Welsh and Ollivier, 1998). In spite of numerous threats to the physical habitat of southeastern

headwater streams (Meyer and Wallace, 2002; Morse et al., 1993), much of this recent work, including the research presented here, has taken place in systems lacking the diversity of stream salamanders found in the southern Appalachians. This has resulted in an opportunity to draw together these two lines of research by examining how physical conditions (e.g., stream pH, sedimentation, temperature) mediate outcomes of key interactions among stream salamander species in the diverse communities of the southern Appalachians.

There is growing evidence that stream amphibians are useful indicators of ecosystem stress (Corn and Bury, 1989; Lowe and Bolger, 2002; Stiven and Bruce, 1988; Welsh and Ollivier, 1998). To capitalize on this utility, it is necessary to design sampling protocols that accurately assess the status of stream amphibian populations (Heyer et al., 1994), a nontrivial requirement given the potential for life-history stage-specific responses to habitat perturbation in these species (Kerby and Kats, 1998; Lowe et al., 2004; Smith and Grossman, 2003) and the physical complexity of stream habitat (Frissell et al., 1986; Hawkins et al., 1993). My data indicate that incorporating reach-scale habitat structure into these sampling protocols is critical. Surveys of pools and riffles are likely to reflect the status of populations of *G. porphyriticus* accurately, but those conducted in runs and cascades will be biased against one of the two stages. Likewise, these results suggest that perturbations altering reach-scale habitat structure may differentially affect larvae and adults of *G. porphyriticus* (Gomi et al., 2002; Montgomery and Buffington, 1997).

By assessing competing hypotheses for determinants of within-stream distribution of salamander life-history stages, this study elucidates the relative importance of physical and biological conditions to one aspect of the ecology of these species. More generally, it illustrates the value of past work on both intra- and interspecific interactions among stream salamanders (e.g., Beachy, 1994; Hairston, 1987; Resetarits, 1991) as a source of community-based hypotheses against which alternatives can be tested (e.g., related to the physical habitat, water chemistry, or resource availability; Chamberlin, 1897). This study also offers a model for combining studies conducted at the

local scale (i.e., in experimental enclosures) and large scale (i.e., across an entire headwater stream) to elucidate general patterns of ecological organization in streams. I hope it will add to the growing body of multi-scale research needed to expand basic understanding of stream ecology and to manage stream systems exposed to spatially extensive disturbances (Fausch et al., 2002; Lowe, 2002; Power and Dietrich, 2002; Wiens, 2002).

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