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STAGE-SPECIFIC AND INTERACTIVE EFFECTS OF SEDIMENTATION AND TROUT ON A HEADWATER STREAM SALAMANDER

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Abstract. In species with complex life cycles, stage-specific effects of environmental conditions combine with factors regulating stage-specific recruitment to determine population-level response to habitat disturbance. The abundance of the stream salamander *Gyrinophilus porphyriticus* (Plethodontidae) is negatively related to both logging-associated sedimentation and brook trout (*Salvelinus fontinalis*) in headwater streams throughout New Hampshire, USA. To understand the mechanisms underlying these patterns, we investigated stage-specific and interactive effects of sedimentation and brook trout on *G. porphyriticus*. We conducted quantitative surveys of salamanders, brook trout, and substrate embeddedness in 15 first-order streams and used a controlled experiment to test the direct and interactive effects of these factors on larval growth and survival. *G. porphyriticus* larvae and adults had opposite patterns of response to sediment and brook trout. Multiple regression analysis of our survey data indicated that abundance of larvae was negatively related to brook trout abundance, but unrelated to substrate embeddedness. In contrast, abundance of adults was primarily related to substrate embeddedness. Consistent with the field pattern of larval abundance, brook trout had a negative effect on growth and survival of larvae in the experiment. However, there was no effect of sediment and no interaction between brook trout and sediment. Larval and adult abundances were not significantly correlated in the study streams, indicative of the independent effects of sedimentation and brook trout on *G. porphyriticus* populations. These results suggest that adult resistance to fish may facilitate *G. porphyriticus* coexistence with brook trout, and that larval resistance to sedimentation can buffer populations from extinction in fishless streams impacted by logging. In streams with brook trout, where larval abundances are low, reductions in adult abundance caused by logging impacts may pose a risk to species persistence. Our findings underscore the value of information on species life history, demography, and community ecology in assessing sensitivity to anthropogenic perturbation.

Key words: *amphibian; brook trout; demography; forestry;* Gyrinophilus porphyriticus; *life history; logging; salamander;* Salvelinus fontinalis; *sedimentation; stream; timber harvest.*

INTRODUCTION

Many river- and stream-dwelling organisms have complex life cycles involving discrete transitions in morphological, physiological, and behavioral traits, including individual size, diet, microhabitat use, and vagility (Wilbur 1980, Resh and Rosenberg 1984, Duellman and Trueb 1986, Moyle and Cech 1988, March et al. 1998). As a result, stage-specific sensitivities to habitat alteration may interact with species demography to determine population-level response (Jager 2001, Jonsson and Ebenman 2001, Marsh 2001). Depending on the rate of habitat recovery and regulation of stage-specific recruitment rates (Wilbur 1980, 1996, Caswell 2001), resistance to perturbation of one stage may be sufficient to buffer populations from local extinction (Heppell et al. 2000, Biek et al. 2002, Lytle 2002). Likewise, high sensitivity to perturbation of multiple stages is likely to greatly increase population-scale extinction risk (Jonsson and Ebenman 2001, Marsh 2001). Despite these implications, stage-specific responses to disturbance of stream habitat have not been addressed in past studies, which have either focused on a single life-history stage (e.g., Morse et al. 1993, Reeves et al. 1993, Baxter et al. 1999, Gillespie 2002), or lumped stages into species-level indices of response (e.g., Diller and Wallace 1996, Lowe and Bolger 2002, Williams et al. 2002).

A stage-specific approach may be crucial to understanding the effects of timber harvest, a major source of disturbance to upland stream ecosystems. A general conceptual model of the impacts of timber harvesting on the physical habitat of small streams (e.g., fine sediment dynamics, channel unit structure, discharge regime, riparian canopy cover) has been described (Garman and Moring 1991, Waters 1995, Hartman et al. 1996, Williams et al. 2002), and there is a growing body of research documenting correlations between

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these habitat alterations and species abundance (Anderson 1992, Harding et al. 1998, Welsh and Ollivier 1998, Lowe and Bolger 2002). However, the responses of stream species to the physical impacts of logging have varied substantially among studies and regions (Murphy et al. 1981, Bisson and Sedell 1984, Wilzbach 1985, Bury and Corn 1988, Hicks et al. 1991, Reeves et al. 1993), and models designed to predict species abundance based on physical habitat have performed poorly in streams other than those for which they were developed (Fausch et al. 1988, Hawkins et al. 2000, Holm et al. 2001). These shortcomings suggest that we need a more mechanistic understanding of the relationship between logging and stream organisms, both to accurately assess the threat to species persistence in diverse systems and to accurately interpret information provided by biotic indicators of stream habitat perturbation (Karr and Chu 1999, Hilty and Merenlender 2000). We investigated two potentially important aspects of species response to logging-induced stream habitat perturbation: direct effects that are life-history stage-specific and community-mediated indirect effects.

The stream salamander *Gyrinophilus porphyriticus* (Plethodontidae) is particularly well suited for a stage-specific and community-dependent approach to the study of species response to stream habitat disturbance. *G. porphyriticus* has strictly aquatic larvae and highly aquatic adults that use spaces among rocks in the streambed as refuges and foraging locations (Bishop 1941, Resetarits 1991, 1995, Petranka 1998). Total *G. porphyriticus* abundance in New Hampshire headwater streams was shown to be negatively related to substrate embeddedness (a measure of fine sediment accumulation among the larger substrate particles of the streambed) associated with timber harvest activities, and to the presence of brook trout (*Salvelinus fontinalis*) (Lowe and Bolger 2002). However, aspects of *G. porphyriticus* natural history indicate that these impacts may be stage specific. Adult *G. porphyriticus* are large (60–120 mm snout–vent length [SVL]), and therefore require large interstitial spaces that become rare as sediment accumulates in streams (Waters 1995, Montgomery and Buffington 1998, Shannon 2000). Smaller interstitial spaces usable by larvae (25–60 mm SVL) are likely to remain available across a wider range of substrate embeddedness conditions. Therefore, we expected adult abundance to respond more strongly than larval abundance to direct effects of sedimentation. While sediment may not have a strong direct effect on larvae, we predicted it to have a community-mediated negative indirect effect by reducing the overall availability of refuges in the stream and thereby increasing the exposure of larvae to brook trout predation (Jeffries and Lawton 1984, Kerfoot and Sih 1987). As a consequence of adult size, and resulting low susceptibility to predation by gape-limited brook trout (Power 1990, 1992), we did not expect adult abundance to be related to brook trout abundance.

In the current study, we used data from intensive sampling of 15 *G. porphyriticus* populations and a controlled experiment to assess the contributions of life-history stage-specific and interactive effects of sedimentation and brook trout to patterns of total *G. porphyriticus* abundance. We also hoped to provide general insight into the demographic structure of *G. porphyriticus* populations by investigating the correlation between larval and adult abundances in the study streams.

Methods

Study organism and study sites

G. porphyriticus belongs to the family Plethodontidae, the lungless salamanders. This species is found in cool, well-oxygenated, low-order streams along the Appalachian uplift, from central Alabama to southern Quebec (Bishop 1941, Petranka 1998). The larval period is ~3–4 years and sexual maturation occurs within one year of metamorphosis (Bishop 1941, Bruce 1980). Mark–recapture data indicate that the yearly survival probability of both larvae and adults is ~0.70 (Lowe, 2003).

Based on results of a previous study (Lowe and Bolger 2002), we selected 15 first-order study streams throughout New Hampshire, USA, covering a gradient of logging-associated substrate embeddedness (the proportion of substrate with visible vertical surfaces buried in silt or sand; Welsh et al. 1997) and both with and without brook trout (trout occupancy estimated in visual surveys). These stream drainages were moderately sloped (2–4% slopes), and small (<1 km^2 drainage area), with mixed stands of ~50% hardwoods (*Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, *Betula papyrifera*) and 50% softwoods (*Picea rubens*, *Abies balsamea*, *Tsuga canadensis*). Experiments were conducted along Alder Brook, a first-order stream in northern New Hampshire.

Field surveys

We established a 100 m long survey section in each study stream, starting 25 m upstream of the confluence of the first-order study stream with a larger stream. We conducted 4 salamander surveys of these 15 sections at 3-wk intervals beginning in mid-June and ending in late August of 2000 using a cover-controlled active-search sampling method (Heyer et al. 1994). Moving upstream, one rock between 64 and 256 mm in diameter (cobble; Platts et al. 1983) was turned per meter of stream length. Rocks were selected across all lateral microhabitats (i.e., bank, edge, channel) and were not embedded in fine sediments. An aquarium dip net was used to capture salamanders, including those flushed by the current.

These data were used to estimate total, larval, and adult abundance values (mean number of individuals/

survey section from four sampling dates) for each stream. All *G. porphyriticus* were also individually marked by subcutaneous injection of a fluorescent elastomer (Northwest Marine Technologies, Shaw Island, Washington, USA). To assess the influence of catchability on variation in indices of *G. porphyriticus* abundance, we tested for a correlation between mean abundance values and the number of individually marked animals in the response groups (i.e., total, larvae, adults) in each stream (Pledger and Efford 1998).

Substrate embeddedness was measured visually within 6 randomly placed 1 m wide transects extending between the bank-full channel edges of the stream (edges at high-flow conditions as indicated by evidence of scour; Welsh et al. 1997, Lowe and Bolger 2002). To estimate brook trout abundance, we conducted electrofishing censuses of the 100-m study sections during a 1-wk period in late August of 2000. These censuses involved multiple-pass removal using a BP-12 backpack electroshocker (Smith-Root, Incorporated, Vancouver, Washington, USA) set to 500V DC. Fish captured in each pass were anesthetized using MS-222 (Argent Chemical Laboratories, Incorporated, Redmond, Washington, USA). They were then counted, weighed, measured, and returned to the stream. A modified Zippin maximum likelihood method was used to estimate brook trout abundance (number of individuals/survey section) and the standard error of abundance (Carle and Strub 1978).

Stage-specific effects of sedimentation and brook trout

Pearson product-moment correlations were calculated between mean larval and adult *G. porphyriticus* abundance estimates and between mean substrate embeddedness and brook trout abundance. Stepwise multiple regression analysis with backward elimination (P to remove variables = 0.05; Kleinbaum et al. 1998) was then used to identify the primary predictors of total, larval, and adult *G. porphyriticus* abundance from the set of independent variables including mean substrate embeddedness, brook trout abundance, and the interaction of these two factors. To achieve normality, mean substrate embeddedness was arcsine square-root transformed and brook trout abundance was square-root transformed. The stepwise multiple regression analysis was performed with PROC REG of SAS (SAS Institute 1990). We analyzed the residuals of all regression models to confirm normality and constant variance (Kleinbaum et al. 1998). The relationships between larval and adult *G. porphyriticus* abundance and significant predictors from the final models were examined directly using univariate regression methods.

Experimental test of sedimentation and brook trout effects

We conducted controlled experiments to examine direct and interactive effects of sedimentation and brook trout on larval *G. porphyriticus* growth and survival. Experimental units were 250-L flow-through artificial stream pools set on the bank of Alder Brook. Prior observations indicated that *G. porphyriticus* larvae did not avoid pool mesohabitat (W. H. Lowe, *unpublished manuscript*). We 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/min. Substrate composition was standardized by first adding a base mixture of equal volumes of untreated playground sand and gravel (modified from Resetarits 1991). We 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 for 1 wk to reach equilibrium physical conditions prior to the beginning of each experiment, and this was confirmed by repeated sampling of temperature, dissolved oxygen, pH, and conductivity. We never detected a difference between physical conditions in the pools and in the stream.

In July and August 2000, we conducted two 14-d experiments applying sediment and brook trout treatments to larval *G. porphyriticus*. A randomized complete block design was employed with time as the blocking factor. Within each block, two substrate embeddedness levels and two brook trout densities were applied to pools containing three *G. porphyriticus* larvae (25–45 mm SVL and 590–4800 mg $\text{mass}_{\text{initial}}$), with three replicates per treatment level per block. The number of larvae added per pool was based on mark–recapture estimates of local larval densities (Lowe, 2003). Sediment treatments replicated mean proportions of embedded substrate in streams impacted and unimpacted by timber harvest activities: 0.30 in unimpacted streams and 0.60 in impacted streams (Lowe and Bolger 2002). These treatments were applied by burying the vertical surfaces of 4 of 12 cobble particles in low embeddedness treatments and 8 of 12 particles in high embeddedness treatments in 2 and 4 L of high quality, untreated playground sand, respectively. Fish densities were zero or one adult brook trout (90–120 mm fork length). The experimental trout density (0.33 individuals/m^2) was comparable to mean trout density ($\pm$1 SE) in trout-occupied study streams (0.29 $\pm$ 0.06 individuals/m^2, reach length = 100 m, mean width = 1.61 $\pm$ 0.08 m; see Fig. 1 for trout abundances). Salamanders and fish were randomly assigned to pools.

At the conclusion of each experiment, mean proportional growth ($\text{mass}_{\text{final}} - \text{mass}_{\text{intitial}}/\text{mass}_{\text{intitial}}$, averaged across surviving individuals) and proportional survival of larvae were calculated for each pool. For growth calculations, individual larvae were identified using pre-existing epidermal discolorations recorded at the beginning of the experiment. The effects of embeddedness and brook trout on larval growth and sur-

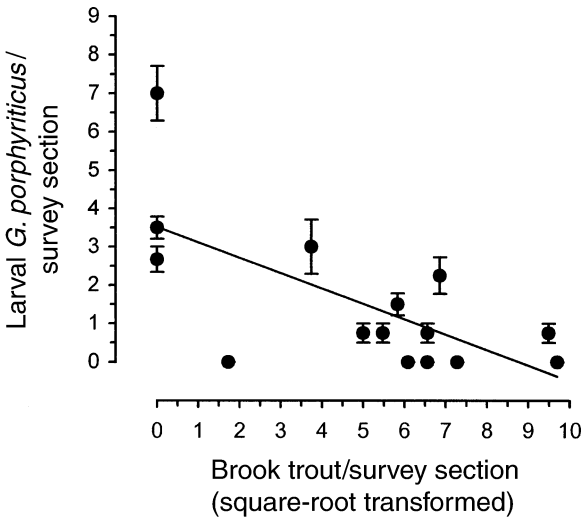

FIG. 1. Relationship between brook trout abundance (no. individuals/survey section, square root-transformed) and larval *Gyrinophilus porphyriticus* abundance (number of individuals/survey section from four sampling dates [mean ± 1 SE]) in 15 study streams located throughout New Hampshire, USA. The line resulting from the best-fitting regression model (Table 1) is plotted.

vival were analyzed using two-way analyses of variance (ANOVA) of the full factorial model. Because block effects were not close to significant in analyses of larval growth and survival ($P > 0.1$), block was not included as a factor in the final statistical models. Logistic regression was used to test for an effect of larval size (log SVL, mm) on survival in pools with trout, controlling for the lack of independence within pools by including pool as a source of variability in this model.

RESULTS

Field surveys

Mean estimates of total, larval, and adult *G. porphyriticus* abundance were significantly correlated with the number of uniquely marked individuals in these groups in each stream (Pearson product-moment correlations: total, $r = 0.98$, $N = 15$, $P < 0.001$; larvae, $r = 0.97$, $N = 15$, $P < 0.001$; adults, $r = 0.98$, $N = 15$, $P < 0.001$), indicating that our measures of relative abundance were accurate and not strongly influenced by variation in animal catchability. Other salamanders encountered in surveys included *Desmognathus fuscus* and *Eurycea bislineata* (both Plethodontidae). *D. fuscus* was rare. *E. bislineata* was present in all surveyed streams.

Mean substrate embeddedness of streams ranged from 0.08 to 0.77 (Fig. 2). Brook trout were found in 12 of the 15 streams, with a total of 498 individuals captured. Electrofishing mortality was low (3 fish). Estimated trout abundances in the 100-m survey sections ranged from 0 to 94 individuals (Fig. 1), with fish size ranging from 31 to 180 mm fork length and 0.51–63.6 g. A second round of electrofishing in August 2002 obtained similar results (K. H. Nislow and W. H. Lowe, *unpublished data*), indicating that differences among sites are consistent across years. Given the size ranges observed both across and within sites, we assume that multiple age classes were present in all of the streams where fish were found. Brook trout was the only fish species found in these surveys.

Stage-specific effects of sedimentation and brook trout

Consistent with our predictions, *G. porphyriticus* larvae and adults had opposite patterns of response to sediment and brook trout abundance (Table 1). Larval abundance was negatively related to brook trout abundance (Fig. 1), and unrelated to embeddedness. In contrast, adult *G. porphyriticus* abundance was primarily related to substrate embeddedness (Fig. 2). However, contrary to our prediction, there was no interactive effect of substrate embeddedness and brook trout abundance on larval *G. porphyriticus* abundance (full-model multiple regression: substrate embeddedness × brook trout abundance, $F = 0.61$, df = 1, 11, $P = 0.45$). Total *G. porphyriticus* abundance (i.e., larvae and adults combined) was negatively related to both substrate embeddedness and brook trout abundance (Table 1). We observed no significant correlation between brook trout abundance and embeddedness (Pearson product-moment correlation: $r = 0.33$, $N = 15$, $P = 0.23$), justifying our use of these variables as independent predictors in the regression models. In accord with the differential responses of the two stages, mean larval

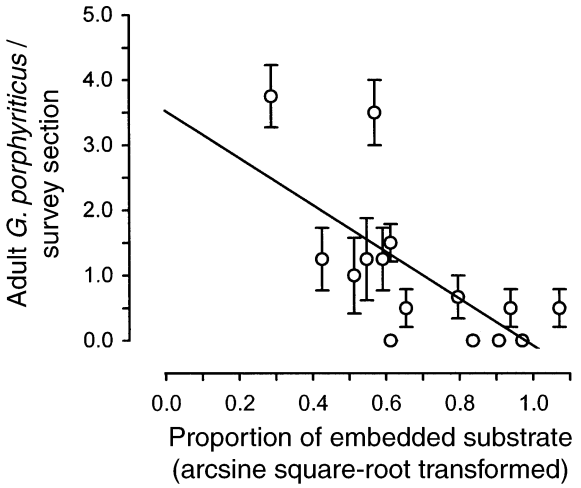

FIG. 2. Relationship between substrate embeddedness (mean proportion of embedded substrate particles from six stream transects, arcsine square root-transformed) and adult *Gyrinophilus porphyriticus* abundance (number of individuals/survey section from four sampling dates [mean ± 1 SE]) in 15 study streams located throughout New Hampshire, USA. The line resulting from the best-fitting regression model (Table 1) is plotted.

TABLE 1. Results of multiple regression analyses of the relationships between substrate embeddedness (mean proportion of embedded substrate particles from six stream transects, arcsine square-root transformed) and brook trout abundance (no. individuals/survey section, square-root transformed) and total, larval, and adult *Gyrinophilus porphyriticus* abundance (mean no. individuals/survey section from four sampling dates) in 15 study streams.

Model variables	*b*†	R^2	*P*
Total *G. porphyriticus* abundance			
Mean substrate embeddedness, brook trout abundance	−, −	0.71	<0.01
Larval *G. porphyriticus* abundance			
Brook trout abundance	−	0.45	<0.01
Adult *G. porphyriticus* abundance			
Mean substrate embeddedness	−	0.47	<0.01

† Indicates whether regression coefficient was positive or negative.

and adult abundances were not significantly correlated in the study streams ($r = 0.49$, $N = 15$, $P = 0.06$).

Experimental test of sedimentation and brook trout effects

Experimental results were consistent with results of field surveys. There was a significant negative effect of brook trout on growth and survival of *G. porphyriticus* larvae in the experimental mesocosms (Fig. 3, Table 2). Proportional growth (mean ± 1 SE) was −0.002 ± 0.02 mg in the absence of trout and −0.07 ± 0.01 mg in the presence of trout. Proportional survival was 1.0 ± 0.0 in the absence of trout and 0.53 ± 0.09 in the presence of trout. In contrast, sediment had no direct effect on larval growth or survival. Contrary to our predictions, but consistent with field survey results, there was also no interactive effect of substrate embeddedness and brook trout on larval growth or survival. Results did not differ when larval survival was analyzed as a categorical response variable using multiple logistic regression (SAS Institute 1990). Survival was unrelated to larval size in pools with fish (logistic regression: $\chi^2 = 0.19$, $N = 36$, $P = 0.66$).

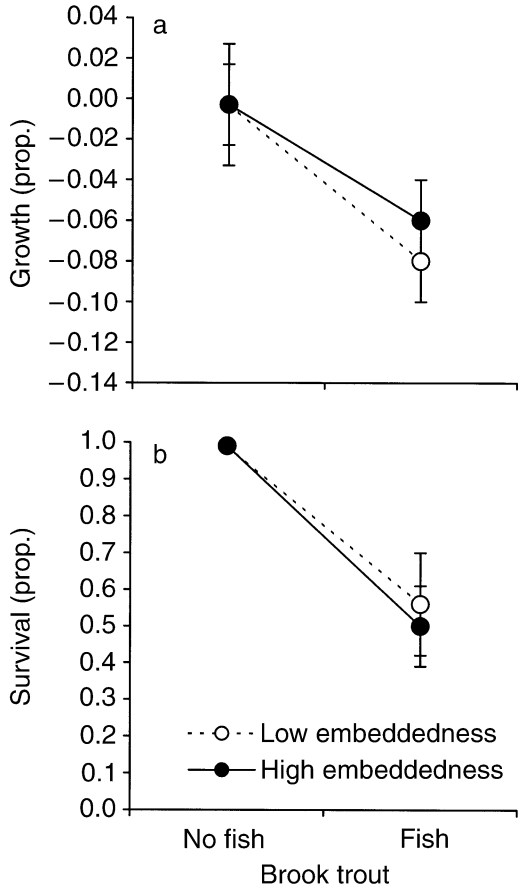

FIG. 3. Effects of substrate embeddedness, a measure of fine sediment accumulation in the stream bed, and brook trout abundance on (a) mean proportional growth ($[\text{mass}_{\text{final}} - \text{mass}_{\text{initial}}]/\text{mass}_{\text{initial}}$; ±1 SE) and (b) proportional survival (±1 SE) of *Gyrinophilus porphyriticus* larvae.

DISCUSSION

Results of this study support the hypothesis that larval and adult *G. porphyriticus* respond differently to sedimentation and brook trout in headwater streams of the northeastern USA. Both field and experimental data indicated that *G. porphyriticus* larvae are neither directly nor indirectly affected by substrate embeddedness, but are negatively affected by brook trout. In contrast, adult *G. porphyriticus* are primarily affected by substrate embeddedness. Combined with the lack of a significant correlation between larval and adult abundance in the 15 study streams, this difference in stage-specific response to sedimentation and brook trout also indicates a surprisingly high level of independence in the status of these two life-history stages.

Responses exhibited by larval and adult *G. porphyriticus* were consistent with our hypothesis that the differing interstitial habitat requirements of these two stages mediate the effects of sedimentation. The lack of relationship between substrate embeddedness and larval abundance supports our prediction that reduction in interstitial habitat caused by sediment accumulation does not directly limit larval abundance. In contrast, a reduction in large interstitial spaces as fine sediments accumulate in the stream may increase adult mortality during high-flow events (Harr 1986, Chapman and Kra-

TABLE 2. Results of ANOVAs of the effects of substrate embeddedness and brook trout abundance on larval *Gyrinophilus porphyriticus* mean proportional growth ($[mass_{final} - mass_{initial}]/mass_{initial}$) and proportional survival in experimental stream pools.

Source	df	MS	*F*	*P*
Growth				
Substrate embeddedness	1	0.0002	0.06	0.81
Brook trout	1	0.02	9.32	<0.01
Substrate embeddedness × brook trout	1	0.0002	0.08	0.79
Error	18	0.003		
Survival				
Substrate embeddedness	1	0.01	0.09	0.76
Brook trout	1	1.34	27.26	<0.0001
Substrate embeddedness × brook trout	1	0.01	0.09	0.76
Error	20	0.05		

mer 1991, Matthaei and Townsend 2000), or increase exposure of adults to non-fish predators (Uhler et al. 1939, Brodie et al. 1979). Bishop (1941) observed aggressive interactions among *G. porphyriticus* adults indicative of territoriality, a characteristic likely to reinforce the negative effects of sedimentation by preventing multiple adults from using the same refuge. Alternatively, sediment may change the availabilities of adult prey resources through effects on the invertebrate community (Burton 1976, Ryan 1991, Waters 1995, Kerby and Kats 1998). Further investigation is required to test these alternative hypotheses and to directly assess changes in the size structure and availability of interstitial habitat accompanying sediment accumulation.

Sediment and brook trout did not have a significant interactive effect on larval *G. porphyriticus* abundance in the field or on larval growth and survival in experimental enclosures, refuting the prediction that reduced availability of refuges increases the negative effects of brook trout on larvae. These results suggest that refuges are not sufficiently reduced in streams impacted by sedimentation to exacerbate the already strong effects that brook trout have on larval *G. porphyriticus*, or that refuges are not involved in the relationship between trout and *G. porphyriticus* larvae. Resistance of larvae to reduced availability of refuges may be a consequence of larval predator-avoidance behavior (Sih et al. 1988, Brodie et al. 1991, Sih and Wooster 1994). If larvae limit foraging to the area surrounding a known refuge, thus maintaining access to that refuge, then the negative effects of brook trout would only increase when the number of larvae exceeds the number of available refuges. Behavioral interactions among larvae may further regulate response to reduced refuge availability (Camp and Lee 1996, Wiltenmuth 1997). Larval tolerance of the proximity of conspecifics would increase the proportion of embedded substrate particles required to produce a significant sediment × brook trout interaction. Multiple larvae were frequently found under the same rock during stream surveys (W. H. Lowe, *personal observation*), suggesting that this stage may be tolerant of conspecific proximity.

The difference in predictors of larval and adult *G. porphyriticus* abundance and lack of a significant correlation between larval and adult abundances across study streams may be indicative of donor stage density-independent recruitment (McPeek and Peckarsky 1998, Caswell 2001). Although further research on the local demography of *G. porphyriticus* is needed, these data suggest that adult recruitment is partially independent of larval density and, likewise, that larval recruitment is partially independent of adult density. Factors that may exert donor-stage density-independent controls on larval and adult recruitment include availability of egg-laying sites (Holomuzki 1991), stream discharge (Kupferberg 1996), or availability of adult territories (Camp and Lee 1996, Wiltenmuth 1997). Variability in population size structure produced by factors other than sedimentation and brook trout abundance, such as population-level adaptation to the local hydrologic regime or climatic conditions (Bruce 1972), may have also contributed to the lack of correlation between larval and adult abundances. In another study, larval and adult *G. porphyriticus* were shown to exhibit similar patterns of movement along the stream corridor (Lowe 2003), suggesting that differences in population size structure were not a consequence of stage-specific dispersal behavior. Adult *G. porphyriticus* were also found to have no effect on larval growth or survival in experimental stream pools (W. H. Lowe, *unpublished manuscript*). Therefore, it is unlikely that the relationship between larval and adult abundances in the survey streams was a result of interactions between these two life-history stages.

These results help to answer the question of how *G. porphyriticus* is able to coexist with brook trout. Having shown strong negative effects of brook trout on *G. porphyriticus* larvae (Resetarits 1991, 1995), Resetarits (1995) concluded that the persistence of *G. porphyriticus* with brook trout is ''likely a complex function of the interactions between the life history and local demography of both [species].'' Our results provide empirical support for this hypothesis, suggesting that differential responses of *G. porphyriticus* life-history stages to brook trout are critical to the coexistence of

these two species. Preliminary evidence that recruitment of *G. porphyriticus* adults, the trout-resistant life-history stage, may be partially independent of larval density lends further support. These findings also corroborate the view that individual size and associated timing of metamorphosis are key structural variables in interspecific interactions involving stream amphibians (Wilbur and Collins 1973, Southerland 1986, Hairston 1987, Resetarits 1995) and are therefore fundamental determinants of the distribution and abundance of these species.

Implications

Increasingly, sedimentation is viewed as a pervasive threat to the ecological integrity of stream ecosystems (Waters 1995, Jones et al. 2000, USEPA 2000). There is growing evidence that stream amphibians are sensitive indicators of this form of stream habitat perturbation (Hawkins et al. 1983, Corn and Bury 1989, Welsh and Ollivier 1998, Lowe and Bolger 2002). The relatively narrow standard error intervals around mean *G. porphyriticus* abundance values (Figs. 1 and 2) are indicative of the repeatability of survey results, and thereby support the general utility of these species and our survey methods in stream monitoring programs. Our study also provides an empirical basis for improving these monitoring programs, indicating that stage-specific responses to sedimentation of focal species should be evaluated before large-scale sampling efforts are initiated. In addition to improving the accuracy of assessments of sedimentation intensity and extent, information on stage-specific response may enable researchers to increase the efficiency of sampling programs by focusing on an informative (i.e., sensitive) stage. For example, researchers can limit sampling to the subset of habitats within the stream used by that stage (e.g., edge, channel, pool, riffles; Platts et al. 1983, Frissell et al. 1986) and employ sampling techniques suited to that stage (Heyer et al. 1994, Hauer and Lamberti 1996).

The risk posed by logging activities to the persistence of *G. porphyriticus* populations is a function of both the sensitivities of individual life-history stages and the community composition of impacted streams. More specifically, larval resistance to the effects of sedimentation may buffer populations in fishless, logged drainages from local extinction. Likewise, reductions in adult abundance caused by logging impacts may pose an especially significant risk to *G. porphyriticus* persistence in streams with brook trout, where larval populations are already low. These results show that species life history, demography, and community ecology must be considered in assessing the threat to population persistence posed by habitat alteration in streams, as well as by other stressors in other systems. As a function of their complex life histories (Wilbur and Collins 1973) and community ecology (Hairston 1987, Wilbur 1997, Blaustein and Kiesecker 2002), amphibians are likely to be particularly susceptible to these mediators of population-level response to anthropogenic stressors.

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