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# Local and Landscape-Scale Predictors of Salamander Abundance in New Hampshire Headwater Streams

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**Abstract:** We investigated the response of *Gyrinophilus porphyriticus* (Plethodontidae), the spring salamander, to timber harvest in headwater streams in New Hampshire (U.S.A.). We conducted cover-controlled, whole-stream surveys for *G. porphyriticus* in 25 first-order streams in drainages encompassing a range of timber-harvest histories. Streams in two different landscape configurations were chosen, isolated, or paired, based on the presence or absence of a confluent first-order stream—a potential source of immigrants. We analyzed salamander abundance with respect to logging history, presence of the brook trout (*Salvelinus fontinalis*), salamander population connectivity, and other measures of physical habitat and aquatic conditions. In stepwise multiple-regression analysis, the best multivariate model of *G. porphyriticus* abundance included fish presence/absence; effect category, a combined function of years since harvest and substrate embeddedness by fine sediment; and landscape configuration. These three factors explained 74% of the variation in *G. porphyriticus* abundance. *G. porphyriticus* was less abundant in streams where fish were present, likely because of predation by *S. fontinalis* or asymmetric competition between these species. Abundance also declined with increasing substrate embeddedness and/or decreasing years since harvest, indicating an effect of fine sediment inputs and harvest history on this species. Finally, *G. porphyriticus* was less abundant in isolated streams than in paired streams. This result suggests that landscape-scale population connectivity may buffer this species from the negative effects of local (i.e., stream-scale) habitat perturbation. We hope this work will encourage others to develop multiscale models of land-use effects on stream biota and thereby ultimately increase the range and effectiveness of conservation strategies for these species.

Predictores Locales y a Escala de Paisaje de la Abundancia de Salamandras en Arroyos de New Hampshire

**Resumen:** Investigamos la respuesta de *Gyrinophilus porphyriticus* (Plethodontidae), la salamandra de arroyo, a la cosecha de madera en arroyos de New Hampshire (E.U.A.). Realizamos muestreos de *G. porphyriticus* en 25 arroyos primarios que drenan sitios con distintas historias de cosecha de madera. Se seleccionaron arroyos en dos distintas configuraciones de paisaje, aislados o apareados, con base en la presencia o ausencia de arroyos primarios confluentes: una potencial fuente de inmigrantes. Analizamos la abundancia de salamandras en relación con la historia de explotación, la conectividad de la población de salamandras, presencia de la trucha (*Salvelinus fontinalis*) y otras medidas del hábitat físico y de las condiciones del agua. En los análisis de regresión múltiple por pasos, el mejor modelo multivariado de la abundancia de *G. porphyriticus* incluyó la presencia/ausencia de peces, la categoría de efecto (una función combinada de años desde la cosecha y la incrustación de sedimento fino en el sustrato) y la configuración del paisaje. Estos tres factores explicaron el 74% de la variación en la abundancia de *G. porphyriticus*. *G. porphyriticus* fue menos abundante en arroyos con presencia de peces, probablemente debido a la depredación de *S. fontinalis* o la competencia asimétrica de estas dos especies. La abundancia también declinó con el incremento de incrustación de sedimentos finos en el sustrato y/o un menor tiempo desde la cosecha, lo que indica un efecto de los aportes de sedimento fino y la historia de explotación sobre esta especie. Finalmente, *G. porphyriticus* fue menos abundante en arroyos aislados que en los apareados. Este resultado sugiere que la conectividad de la población a nivel de paisaje puede proteger a la especie de los efectos negativos de perturbaciones locales del

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*hábitat (i.e. a nivel de arroyo). Deseamos que este trabajo motive a otros a desarrollar modelos multiescales de los efectos del uso de suelo sobre la biota de arroyos y por lo tanto incrementar el rango la efectividad de las estrategias de conservación para estas especies.*

## Introduction

The response of a population to anthropogenic disturbance is in part a function of the local physical and biotic changes created by the disturbance event. It is often difficult to isolate anthropogenic effects on populations without knowledge of the nonanthropogenic factors that cause variation in the distribution and abundance of the focal species (Wiens 1996). One problem that arises is that research on these nonanthropogenic population and community-level controls often occurs at relatively small spatial scales in the laboratory or field, usually under relatively homogeneous conditions. The scale of disturbance or management activities is often much larger, however, and encompasses a greater range of system variation (O'Neill et al. 1997; Kunin 1998). This mismatch in scale creates uncertainty over whether local-scale results provide a reliable evaluation of the effect of larger-scale disturbances and management activities (Wennergren et al. 1995; Folt et al. 1999).

In addition to local physical and biotic factors, the response of a population to disturbance can also be influenced by larger-scale phenomena, particularly landscape-scale population dynamics (Hanski & Gilpin 1991; Hanski 1998). Population connectivity may increase both local resilience to habitat degradation and regional resistance to species extinction (Tilman et al. 1994; Kareiva & Wennergren 1995; Mills & Allendorf 1996; Wiens 1997; Hanski 1998). If dispersal is high, disturbance may not be reflected in local abundances (Robinson et al. 1995). If dispersal is low, population recovery may be dispersal-limited and lag behind the physical recovery of the habitat (Amarasekare 1998). Dispersal frequency is determined by the intrinsic vagility of the focal species and the landscape-scale distribution of subpopulations (Gadgil 1971; Horn 1983).

The effects of forestry activities on ecosystems is one area in which conservation biologists are interested in evaluating effects on populations (Hagan et al. 1997; Maschinski et al. 1997; Steventon et al. 1998; Taulman et al. 1998; Hayward et al. 1999). Stream organisms in particular are often the target of study (Murphy et al. 1981; Hicks et al. 1991; Anderson 1992; Bisson et al. 1992; Reeves et al. 1993); stream amphibians are one group of organisms that have received little attention in these efforts, yet may well be a sensitive indicator of logging impacts (Corn & Bury 1989; Welsh & Ollivier 1998). The only published studies linking specific logging effects on stream habitat to a response in stream amphibians have been conducted in the Pacific Northwest. These studies

have shown that some stream amphibians occur at lower abundance in streams where recent timber harvest or road-building activities have resulted in the accumulation of fine sediments (Corn & Bury 1989). To our knowledge, only one published study has focused on the response of stream amphibians in the eastern United States to logging (Stiven & Bruce 1988), and none has examined the response of these species to specific logging-associated changes in the stream habitat. This is in contrast to the considerable attention given to the response of salamanders to logging-associated changes in terrestrial habitat in the eastern United States (Petranka et al. 1993, 1994; Ash & Bruce 1994; Petranka 1994; deMaynadier & Hunter 1995, 1998; Ash 1997).

The need to address this geographic gap in our knowledge of the conservation biology of stream amphibians is underscored by recent evidence of the long-term effects of land-use history on the invertebrate community of eastern streams (Harding et al. 1998), by the failure of generalizations from stream studies in the Pacific Northwest to hold in other regions (e.g., Berg et al. 1998), and by evidence that the effect of specific disturbances on streams varies across regions (Hicks et al. 1991). There is also a lack of ecological research on stream amphibians in the northeastern United States. Although natural-history information is available (Bishop 1941; Hunter et al. 1992; Taylor 1993; Andrews 1995), managers, scientists, and naturalists in this region currently have little foundation on which to develop management approaches and build public awareness and appreciation of these species.

In addition to this geographic limitation, understanding the response of stream amphibian populations to disturbance has been limited by a historical focus on the local-scale ecological interactions and effects of disturbance. Although prior studies have shown landscape-scale population dynamics to be important among amphibians, these studies have been almost exclusively restricted to pond-breeding species (Gill 1978; Berven & Grudzien 1990; Sjogren-Gulve 1994; Hecnar & MCluskey 1996, 1997; Dodd & Cade 1998; Skelly et al. 1999). Studies of stream amphibians have usually selected the stream reach as the unit of observation, a relatively small longitudinal segment of the larger stream, generally defined by homogeneous physical features. This scale of observation has been extremely important in identifying mechanisms of species interaction, both among salamander species (Hairston 1987) and between salamanders and fishes (Resetarits 1991; Kats & Sih 1992; Storfer & Sih 1998), and in documenting the local effects

of habitat perturbation (Hawkins et al. 1983; Corn & Bury 1989; Welsh & Ollivier 1998). But by not considering the role of landscape-scale population dynamics, this approach may have failed to provide a complete picture of the controls on salamander distribution and abundance in streams.

The headwater stream drainages of the northeastern United States provide an ideal system for exploring the link between local and landscape-scale controls of the distribution, abundance, and response to disturbance of stream amphibians. In this region, stream-amphibian diversity is concentrated in headwater drainages (Hunter et al. 1992; Taylor 1993; Andrews 1995). The primary disturbance in these areas, both currently and historically, is timber-harvesting activities (Miller et al. 1998). Harvest practices have been linked to a wide array of habitat effects in lotic systems, both within the riparian zone and the stream channel itself (Hawkins et al. 1983; Reid & Dunne 1984; Garman & Moring 1991; Meehan 1991; Reid 1993; Hartman et al. 1996). These effects include the accumulation of fine sediments, reduction in the input of coarse woody debris, alteration of the water-temperature regime, and desiccation of riparian groundcover.

The objective of our study was to identify the predictors of abundance of the spring salamander, *Gyrinophilus porphyriticus* (Plethodontidae), in first-order streams throughout New Hampshire. Streams were located in drainages encompassing a chronosequence of harvest histories. Because first-order headwater streams are manageable, hydrologically independent sampling units, we could examine the response of stream-amphibian populations to timber-harvest activities at the scale of the whole stream. Because headwater streams occur in spatially nested sets, forming a "streamscape" of potential habitat patches, we were able to assess the role of spatial controls on the response of stream amphibians to these harvest activities. This was accomplished by choosing streams in two different landscape configurations, isolated and paired, based on the presence of a confluent first-order stream, a potential immigrant source. The limited dispersal potential of the focal species and the uncoupled habitat conditions in the individual streams of a pair could generate a differential response to disturbance in isolated and paired streams.

Existing research and theory provided us with an initial set of factors likely to affect salamander abundance in streams in New Hampshire: logging history and the quantity of fine sediments in the stream channel, the presence of fish predators, and the degree of population connectivity. To investigate the roles of these factors, we conducted salamander surveys in headwater streams throughout New Hampshire. Streams varied in logging history, presence or absence of brook trout (*Salvelinus fontinalis*), and presence or absence of a direct connection to another first-order stream. We used these survey

data to test the following predictions. The abundance of the stream salamander *G. porphyriticus* is lower in (1) streams in drainages that have been logged more recently or have experienced more sedimentation, (2) streams with brook trout than in streams without trout, and (3) isolated streams than in paired streams.

Moreover, we sought insight into whether the findings from local-scale studies (Resetarits 1991; Welsh & Ollivier 1998) provide useful predictors of salamander abundance at local and regional scales. Specifically, we asked whether or not local variables are sufficient predictors of abundance or whether landscape-scale variables that capture population connectivity provide additional predictive power.

## Methods

### Study Organism

*Gyrinophilus porphyriticus* belongs to the family Plethodontidae, the lungless salamanders. It is a large salamander (11–21 cm total length [TL]) usually found in cool, well-oxygenated, low-order streams. This species has a relatively long larval period of approximately 3–4 years (Bishop 1941; Bruce 1980), and no published estimates of its lifespan are available. Although both larval and adult *G. porphyriticus* are highly aquatic, there are anecdotal reports of adults found on the forest floor outside riparian corridors (J. S. Andrews & H. M. Wilbur, personal communication). Gut content analysis shows that *G. porphyriticus* larvae in New Hampshire feed primarily on aquatic invertebrates, including beetles, caddisflies, and dipterans, and secondarily on larval two-lined salamanders (*Eurycea bislineata*) (Burton 1976; W.H.L. & D.T.B., unpublished data). Adults feed on a diverse assemblage of both terrestrial and aquatic invertebrates (Burton 1976; W.H.L. & D.T.B., unpublished data).

### Study Area

We selected study streams based on our initial predictions that *G. porphyriticus* abundance would be influenced by recent timber-harvest activities and associated sedimentation and by the landscape position of the focal stream. We were unable to select streams based on fish occurrence, which left this factor to chance. Initial assessment of harvest history was based on records provided by land managers. Landscape configuration was characterized as either isolated or paired, both delimited downstream by a confluence with a larger-order river (Fig. 1).

Streams were located on lands owned and managed by Dartmouth College, the U.S. Forest Service, and the Society for the Protection of New Hampshire Forests (SPNHF). We surveyed 37 first-order streams throughout New Hampshire. Twelve streams were subsequently

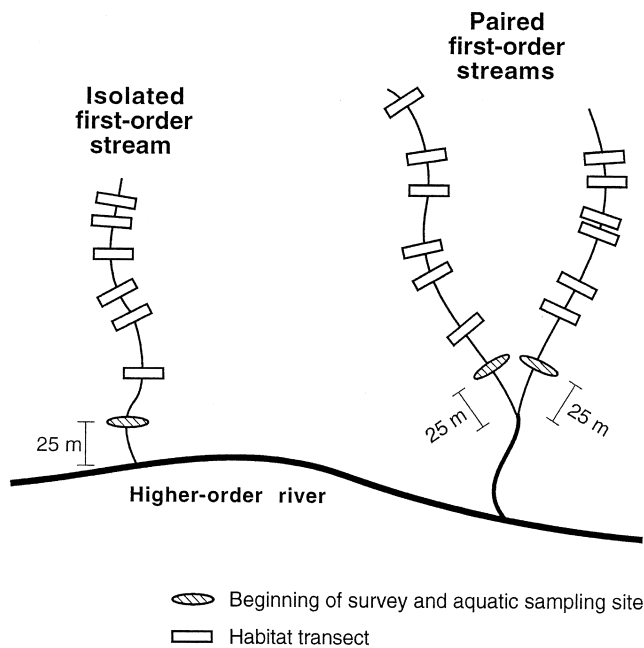


Figure 1. Schematic representation of sampling design used to determine the primary predictors of *G. porphyriticus* abundance in first-order streams throughout New Hampshire.

eliminated from analyses for one of the following two reasons: (1) stream drained a marsh or pond, thus greatly differentiating its structural and aquatic habitat conditions from those of streams arising directly from overland flow (Wotton 1988, 1995; Allan 1995) and (2) obvious signs of timber-harvest activity (e.g., patches of harvested trees, skidder trails, dirt roads) were observed within the drainage at the time of the survey, but no record of this activity was available. Eight of the remaining streams were located in the northern end of the state (on the Dartmouth Second College Grant) north of the town of Errol. Thirteen streams were located in the middle of the state on the White Mountain National Forest in the vicinity of the towns of Woodstock and Plymouth. Four streams were on SPNHF reserves in the southern end of the state east of the town of Keene. The general terrain of these drainages was moderately to steeply sloped. The temperate hardwood forest of these sites consisted of approximately 25% hardwood forest, 25% softwood forest, and 50% mixed forest. The primary hardwood species included *Acer saccharum*, *Betula alleghaniensis*, *Fagus grandifolia*, *Betula papyrifera*, and *Populus tremuloides*. The softwood component was composed primarily of *Picea rubens* and *Abies balsamea*.

### Amphibian Surveys

All amphibian surveys took place during July and August 1999. Amphibian surveys began 25 m upstream of the

confluence with either a higher-order river (isolated streams) or with another first-order stream (paired streams; Fig. 1). We used a cover-controlled active-search sampling method (Heyer et al. 1994). Moving upstream, we turned cover objects at a constant rate across all lateral microhabitats (i.e., bank, edge, channel). Cover objects were rocks between 64 and 256 mm in diameter not embedded in fine sediments. We used an aquarium dip net to capture salamanders, including those flushed by the current. Surveys continued until 100 cover objects had been turned. These surveys encompassed multiple mesohabitat units (i.e., pool, run, riffle, cascade; Welsh et al. 1997) and were therefore designed to characterize abundance at the scale of the whole stream. Surveys generally ended at or near the most upstream perennial reach of the stream. To eliminate variation from among-observer differences in the sampling of cover objects, W.H.L. conducted all amphibian surveys.

All salamander larvae and adults were identified to species, and these data were used to calculate an index of species abundance (individuals/survey). Species encountered included *G. porphyriticus*, *Desmognathus fuscus*, and *Eurycea bislineata* (all Plethodontidae). Here we analyzed only *G. porphyriticus* abundance. *D. fuscus* was found extremely infrequently in our surveys. *E. bislineata* was present in all surveyed streams, and its abundance was negatively correlated with the abundance of *G. porphyriticus* (W.H.L. & D.T.B., unpublished data). Based on previous studies (Hairston 1987; Resetarits 1991) and the small size and relatively terrestrial nature of *E. bislineata*, we had no reason to expect that the abundance of this species would affect the abundance of *G. porphyriticus*. Therefore, abundance data for *E. bislineata* were not included in the analysis of *G. porphyriticus* abundance.

To evaluate the repeatability of survey results and among-stream differences in the relationship between number of *G. porphyriticus* captured in surveys and actual abundance, we surveyed a subset of seven representative streams three times during July and August 2000, uniquely marking all individuals (W.H.L. & D.T.B., unpublished data). The mean coefficient of variation ( $\pm 1$  SE) for *G. porphyriticus* abundance from these repeated surveys was 16.39% ( $\pm 2.03$ ). Mean number of *G. porphyriticus* captured per survey was significantly correlated with the total number of uniquely marked individuals in these streams ( $n = 7$ ,  $r = 0.95$ ,  $p = 0.001$ ). These data suggest that the number of *G. porphyriticus* individuals captured per survey is a reliable index of the relative abundance of that species in the stream

### Habitat Assessment

We characterized the harvest history within each drainage or subdrainage (i.e., the drainage of an individual stream in our paired configuration) by the number of

years since the last harvest activity. Drainages that had never been harvested were assigned a value of 34 years since last harvest, the value of the drainage with the earliest recorded harvest date. Harvest activities included clearcutting, removal cuts, salvage cuts, commercial thinning, individual tree selection, and group selection.

All fish observations were recorded during the amphibian surveys. We incorporated fish presence in our analysis as a categorical variable (fish, fishless). An average ( $\pm 1$  SE) of 3.53 ( $\pm 0.64$ ) individuals was observed in streams where fish were present. Streams where no fish were sighted during the survey were classified as fishless. Sporadic fish captures during the surveys and quantitative electrofishing in several streams (Hogan 2000) suggest that the brook trout was the only fish species present in these streams. Hogan's (2000) electrofishing data also confirmed our fish/fishless designations for three streams. Although our surveys are insufficient to prove that fishless streams are absolutely fishless in all cases, they are sufficient to demonstrate a substantial difference in potential fish pressure between fish and fishless streams.

To guard against the possibility of missing important variables other than those we hypothesized were important, we also collected data on a set of variables related to the substrate composition, structural habitat, and aquatic conditions of the focal streams (Table 1). Cover and structural habitat variables were measured in six randomly placed habitat transects in each stream (Fig. 1). Transects were 1 m wide and extended between bank-full channel edges (edges at high-flow conditions as indicated by evidence of scour). The proportion of cover in four categories (Table 1; from Platts et al. 1983) and the proportion of embedded cover within each transect were estimated visually. Embedded cover objects were those whose visible vertical surfaces were buried in either silt or sand (modified from Welsh et al. 1997). Reach-scale mesohabitat, defined as the channel area 5 m upstream and downstream of the transect, was categorized as pool, run, riffle, or cascade, based on predominant flow and gradient conditions (modified from Montgomery & Buffington 1998). Pool-dominant reaches were defined by evidence of scour caused by obstruction, blockage, merging of flows, or constriction. Runs were defined by low-gradient and laminar flow, riffles by moderate-gradient and turbulent flow, and cascades by high-gradient and highly turbulent flow. Stream width (m) was measured between bank-full edges. Habitat conditions recorded at these transects were pooled within streams to get mean stream-scale estimates.

Aquatic conditions, including dissolved oxygen (% saturation), conductivity ( $\mu\text{S}$ ), acidity (pH), and water temperature ( $^{\circ}\text{C}$ ), were collected at a single position at the beginning of the survey (Fig. 1). Dissolved oxygen, conductivity, and water temperature were measured with a YSI multimeter (YSI, Inc., Yellow Springs, Ohio). Acidity

**Table 1.** Habitat variables measured in first-order streams throughout New Hampshire.

Habitat variables	Units
Cover*	
gravel-pebble (2.0–64.0 mm)	proportion
cobble (64.0–256.0 mm)	proportion
boulder-bedrock (>256.0 mm)	proportion
coarse woody debris	proportion
embeddedness	proportion
Structural characteristics	
predominant mesohabitat	pool, run, riffle, cascade
width	meters
Aquatic conditions	
dissolved oxygen	percent saturation
conductivity	$\mu\text{S}$
acidity	pH
water temperature	$^{\circ}\text{C}$
Other measurements	
brook trout	fish/fishless
landscape configuration	isolated/paired
elevation	meters
harvest history	years since harvest

\*Values in parentheses refer to diameters of mineral-cover size categories.

was also determined in the field with a portable pH meter (Oakton, Inc., Vernon Hills, Illinois). The elevation (m) of the starting point of each survey was determined with an altimeter (Thommen, Inc., Waldenburg, Switzerland).

### Statistical Analysis

We conducted pairwise correlation analyses of all continuous habitat variables (Table 1) to evaluate multicollinearity. We then used principal component analysis to reduce multicollinearity among variables (Gunst & Mason 1980; Kleinbaum et al. 1998). Groups of autocorrelated variables were replaced by the fewest uncorrelated, continuous components needed to encompass more than 75% of the variability of the original set of predictors or by categorical variables. We used the average-linkage hierarchical clustering method (Sokal & Michener 1958; Milligan 1980; SAS Institute 1995) to dichotomize principal component scores into categorical variables when scores appeared to be aggregated and categorization improved the interpretability of the resulting variable. In this clustering method the distance between two clusters is the average distance between pairs of observations, one in each cluster.

We used stepwise multiple-regression analysis, with  $p$  to enter and remove variables of 0.10 (Kleinbaum et al. 1998), to identify the most predictive multivariate model of *G. porphyriticus* abundance from the resulting set of independent variables; it was performed with PROC REG of SAS (SAS Institute 1985). We incorporated cate-

gorical variables, such as predominant mesohabitat, brook trout, and landscape configuration, into this analysis by assigning binary, linearly independent dummy variable sets (Draper & Smith 1981; Neter et al. 1985). To test for significant interactive effects among key predictors identified in the initial stepwise regression procedure, we ran a second stepwise analysis on a model including the key predictors and all two-way interactions among these predictors. We analyzed the residuals of all regression models to confirm normality and constant variance (Kleinbaum et al. 1998). We examined partial  $p$  values and least-squares means of *G. porphyriticus* abundance from the best multivariate-regression model to determine the relationship between *G. porphyriticus* abundance and individual variables.

## Results

### Autocorrelation among Variables

Two sets of predictors were highly autocorrelated. One set included years since harvest and substrate embeddedness ( $n = 25$ ,  $r = -0.55$ ,  $p < 0.01$ ). The second set included the proportional coverage of the three mineral-substrate size categories we sampled (Table 1). Specifically, the proportional coverage of the gravel-pebble size class was significantly autocorrelated with both the proportion of cobble ( $n = 25$ ,  $r = -0.57$ ,  $p < 0.01$ ) and the proportion of boulder-bedrock coverage ( $n = 25$ ,  $r = -0.47$ ,  $p < 0.05$ ).

### Principal Components and Cluster Analysis

In a principal component analysis of the harvest history and substrate embeddedness variables, the first principal component encompassed 77% of the variability in these conditions (eigenvalue = 1.55). Cluster analysis separated surveyed streams into two groups with regard to the harvest history-embeddedness principal component. These groups, which we refer to as effect categories (less affected vs. more affected), were included in the stepwise regression analysis as a categorical variable. Average years since harvest ( $\pm 1$  SE) in less-affected streams was 29.54 ( $\pm 2.36$ ) and 11.25 ( $\pm 2.14$ ) in more-affected streams. Average substrate embeddedness values ( $\pm 1$  SE) in less-affected and more-affected streams were 0.27 ( $\pm 0.04$ ) and 0.62 ( $\pm 0.04$ ), respectively. All streams in drainages that had never been harvested were in the less-affected category.

In a principal component analysis of the three mineral-substrate coverage variables, the first and second principal components encompassed 95% of the variability in these conditions (eigenvalues = 1.64 and 1.21, respectively). Both were included in the stepwise multiple-regression procedure as continuous variables.

### Predictors of *G. porphyriticus* Abundance

Stepwise multiple regression analysis resulted in a multivariate model of *G. porphyriticus* abundance that confirmed our hypotheses about the key predictors of the abundance of this species in New Hampshire streams. This model included fish presence, effect category, and landscape category as key predictors (Table 2). Partial  $p$  values from this multivariate model indicated significant independent relationships between *G. porphyriticus* abundance and each of these three variables (Table 2). Partial-regression correlations and least-square means of *G. porphyriticus* abundance indicated that this species was less abundant in streams where fish were present, less abundant in more-affected than in less-affected streams, and less abundant in isolated than in paired streams (Table 2; Fig. 2). The subsequent stepwise regression analysis including fish, landscape category, effect category, and all two-way interactions between these predictors in the set of potential predictors resulted in the same multivariate model as described above and no significant interactions.

## Discussion

Our results suggest that the presence of brook trout, harvest-history, and/or related fine-sediment inputs are important local controls on the abundance of the spring salamander *G. porphyriticus* in New Hampshire headwater streams. The presence of a confluent first-order stream was associated with higher salamander abundance, suggesting that population connectivity may buffer salamander populations from logging-induced effects or other stream-scale disturbances.

Prior research has documented negative effects of *S. fontinalis* fingerlings and adults on the survival, growth, and behavior of *G. porphyriticus* larvae (Resetarits 1991; Gustafson 1994; Resetarits 1995), and these interactions may underlie the observed association between the species in New Hampshire streams. But our own observation of predation by adult *G. porphyriticus* on fingerling *S. fontinalis* (W.H.L. & D.T.B., unpublished data) and the general lack of information on the role of adult *G. porphyriticus* in interactions with *S. fontinalis* leave the details of this association open to question. Specifically, we still do not know the potential for coexistence of *G. porphyriticus* and *S. fontinalis* under "balanced" size structures—in the presence of both large and small size classes of both species—or for negative effects of *G. porphyriticus* adults on *S. fontinalis* survival and growth.

The negative relationship we observed between time since harvest and substrate embeddedness is supported by studies of the accumulation of fine sediments in streams following timber harvest and associated road-building activities (Reid & Dunne 1984; Garman & Moring 1991;

**Table 2.** Summary step history from the stepwise multiple-regression analysis of *G. porphyriticus* abundance in first-order streams throughout New Hampshire.

Step	Model variables	b <sup>a</sup>	partial p	r <sup>2</sup> (adjusted)	p
1	Brook trout <sup>b</sup>	+	—	0.5	<0.0001
2	Brook trout, effect category <sup>c</sup>	+, +	0.0001, 0.003	0.65	<0.0001
3	Brook trout, effect category, landscape configuration <sup>d</sup>	+, +, +	<0.0001, 0.005, 0.009	0.74	<0.0001

<sup>a</sup>Indicates whether regression correlation was positive or negative.

<sup>b</sup>Fish vs. fishless.

<sup>c</sup>More affected vs. less affected.

<sup>d</sup>Isolated vs. paired.

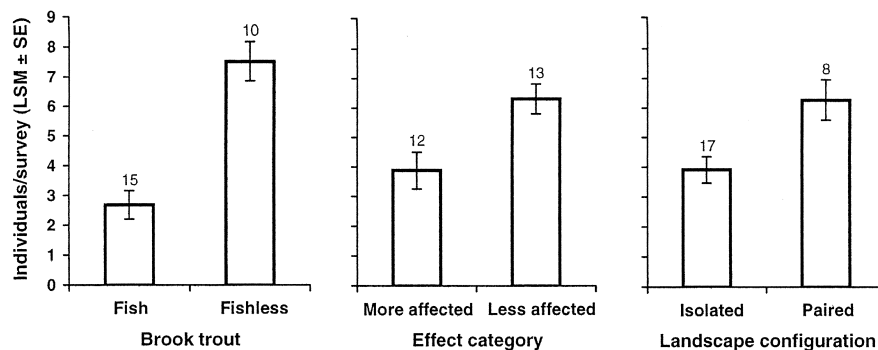
Meehan 1991; Reid 1993; Waters 1995; Hartman et al. 1996). After the initial input, sediments are resuspended and flushed downstream over time, a process mediated by the regional discharge regime and the morphology of the drainage (Waters 1995; Montgomery & Buffington 1998). Consequently, fine sediment in the stream declines with time elapsed since the last disturbance.

A negative relationship between substrate embeddedness and *G. porphyriticus* abundance is consistent with studies of the effects of fine-sediment inputs on stream amphibian species in the Pacific Northwest (Hawkins et al. 1983; Bury & Corn 1988; Corn & Bury 1989; Welsh & Ollivier 1998). Reduction in habitat availability resulting from the filling of interstitial spaces used by *G. porphyriticus* is a likely mechanism underlying this relationship. Experimental analysis of interstitial refuge selection in this species confirms a preference for spaces  $\geq 1$  cm in depth (Shannon 2000), which are likely to become rare as fine sediments accumulate in streams.

A reduction in interstitial refuge availability could increase adult and larval mortality from natural disturbances (e.g., high-flow events; Hart & Finelli 1999) or from increased predation rates in streams where *S. fontinalis* is present (Sih et al. 1988; Sih & Kats 1991). *G. porphyriticus* is known to feed heavily on aquatic invertebrates in New Hampshire streams (Burton 1976), so a bottom-up mechanism of effect, whereby fine sediments limit food resources, is also possible. Fine sediment in streams is known to impair photosynthesis by periphyton (Ryan 1991). Reduced periphyton productivity may lead to reduced densities of grazing insects (Anderson 1992; Rosenberg & Resh 1993). When resuspended in the flowing water, fine sediments may also increase the

downstream drift rate of aquatic invertebrates (Ryan 1991), thereby potentially reducing both grazer and nongrazer densities. Reproduction could also be impaired if sediments are deposited on salamander eggs or restrict access to egg-laying sites on the undersides of stream rocks (Bishop 1924; Bruce 1978). Further research is needed to identify the ecological mechanisms and the demographic changes that lead to lower *G. porphyriticus* abundances in recently harvested drainages.

Higher abundance of *G. porphyriticus* in nonisolated, first-order streams suggests that between-stream dispersal dynamics may influence the response of this species to habitat degradation associated with harvest activities. Specifically, our data suggest that the presence of a confluent first-order stream buffers *G. porphyriticus* populations against the negative effects of habitat disturbance, such as fine-sediment inputs. This pattern could be produced by transient source-sink dynamics (Pulliam 1988; Holt 1997), with dispersal from adjacent unlogged streams augmenting abundance in recovering streams until the physical recovery of the stream returns it to source status. In a related mechanism, dispersal might help prevent local population extinction in the disturbed streams via the rescue effect (Brown & Kodric-Brown 1977; Gotelli 1991; Amarasekare 1998). These mechanisms remain speculative, however, because we do not know the extent or the pathway of interstream dispersal. If interstream dispersal does occur, we expect this population buffering to occur as long as effects on habitat are not highly spatially and temporally autocorrelated between the subdrainages of stream pairs (Pulliam 1988; McPeck & Holt 1992; Palmqvist & Lundberg 1998; Koenig 1999).



**Figure 2.** Relationships between *G. porphyriticus* abundance (individuals/survey [least-squares mean  $\pm$  SE]) and brook trout, effect category, and landscape configuration of first-order streams in New Hampshire. Least-squares means (LSM) are from the multivariate regression model including all three predictors. Numbers above bars indicate the number of streams in each category.

It may be possible to differentiate between these different scenarios of landscape-scale population dynamics by quantifying landscape-scale genetic population structure. Although there is evidence that stream-salamander populations from the same watershed are more closely related than populations from adjacent watersheds over large distances (i.e., >5 km between populations; Voss et al. 1995), molecular data have not yet been used to assess genetic structure among stream-salamander populations in adjacent, hydrologically independent streams at a smaller scale (i.e., <1 km among populations; Stiven & Bruce 1988; Routman et al. 1994; Storfer 1999; White et al. 2000). This level of spatial resolution will be required because any demographically significant dispersal by *G. porphyriticus* or other stream amphibians is almost certainly restricted to this scale (Barbour et al. 1969; Barthalamus & Bellis 1972; Dougherty & Sheldon 1982; Bruce 1986).

## Conclusion

Our results suggest that reach-scale studies can provide useful predictors of salamander abundance at whole-stream and regional scales. Specifically, our data suggest that the negative effects of *S. fontinalis* on *G. porphyriticus* are not limited to experimental mesocosms or individual reaches within the stream, but can be observed over extensive sections of first-order streams. Likewise, the effects of logging and sedimentation on *G. porphyriticus* are in evidence at both whole-stream and regional scales.

In addition to confirming the regional applicability of findings from previous reach-scale studies, our results provide a more complete perspective on the ecology and conservation biology of stream amphibians than has previously been available. Specifically, our results suggest that the effects of logging activities on stream salamanders need to be interpreted in light of both community factors (fish/fishless) and landscape connectivity. Without consideration of this full suite of controls, Type I or Type II errors could easily result. Our results also point to potentially important relationships among these controls. For example, if between-stream movement in *G. porphyriticus* is primarily overland, the location of harvest blocks, harvest treatment, and timing of application may affect ground-cover moisture dynamics and, ultimately, dispersal success in this species. Likewise, the outcome of interactions between *S. fontinalis* and *G. porphyriticus* may vary over time as fine sediments move through the stream and the availability of interstitial refugia changes, thereby tightly linking population viability and community dynamics with land-use history. We hope our findings will encourage investigation of these hypotheses.

Our study provides support for the utility of stream amphibians as indicators of land-use effects on stream

ecosystems (Corn & Bury 1989; Welsh & Ollivier 1998). We believe that it also provides a model for multiscale approaches to understanding the response of stream biota to anthropogenic disturbance. Although in recent years the effects of land use on stream organisms have been increasingly realized (Zwick 1992; Allan & Flecker 1993; Harding et al. 1998), the development of general predictive models of these effects has been slow. This lag can be attributed largely to the overwhelming physical and biological heterogeneity found in streams (Pringle et al. 1988; Palmer & Poff 1997; Ward 1998). Due to this heterogeneity, localized investigations are required for any mechanistic understanding of the effects of land use on stream organisms. Our results demonstrate, however, that an evaluation of these effects at the landscape scale, both in sampling design and integration of spatial population dynamics, also provides a valuable perspective. We hope this "streamscape" perspective will contribute to the development of multiscale conceptual models of land-use effects on stream biota that are generalizable across regions.

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