

Efficacy of riparian buffers in mitigating local population declines and the effects of even-aged timber harvest on larval salamanders

William E. Peterman^{*}, Raymond D. Semlitsch

University of Missouri-Columbia, 105 Tucker Hall, Division of Biological Sciences, United States

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ABSTRACT

Headwater streams are an important and prevalent feature of the eastern North American landscape. These streams provide a wealth of ecosystem services and support tremendous biological diversity, which is predominated by salamanders in the Appalachian region. Salamanders are ubiquitous throughout the region, contributing a significant biomass that supports ecological and ecosystem processes. One of the greatest threats to salamanders is loss of headwater-riparian habitat through timber harvest. In this study, we measured larval salamander abundance at five headwater streams with different riparian buffer widths retained following logging. By sampling larval salamanders using leaf litter bags, we assessed the impacts of even-aged timber harvest on aquatic larval salamander abundances, where it was found that larvae are negatively impacted by increased stream sedimentation and a decrease in riparian buffer width. We found that retention of a 9-m buffer was effectively no different than complete removal of all riparian forest, and as such, current regulations to protect headwater streams are ineffectual. Furthermore, no significant differences were observed between the 30 m buffer treatment and uncut control treatments suggesting that a 30 m or larger riparian buffer may assuage the in-stream effects of riparian timber harvest. Management guidelines for Appalachian forests should be revised to accommodate the biology of plethodontid salamanders.

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1. Introduction

One of the most prominent land uses affecting wildlife is timber harvest (e.g., Gram et al., 2003; Goldstein et al., 2005; Gitzen et al., 2007; Olson and Weaver, 2007), which results in temporary loss of forests and can negatively impact aquatic habitats (e.g., Swank et al., 2001; Wilkerson et al., 2006; Jackson et al., 2007). Headwater streams are a prevalent aquatic habitat on the landscape in the eastern United States and are estimated to account for at least three-quarters of overall stream and river channel length within the region (Meyer and Wallace, 2001; Peterman, 2008). Headwaters provide important ecosystem services including flood control, sediment retention, water purification, cycling of nutrients and transfer of energy to downstream ecosystems, and support of biological diversity (Vannote et al., 1980; Ward, 1989; Meyer and Wallace, 2001; Gomi et al., 2002). Many of these processes are

facilitated by, or dependent on intact riparian zones, which are also important for moderation of air and water temperatures, maintenance of soil moisture, and retention of sediments and nutrients from runoff (Brosnoff et al., 1997; Swank et al., 2001; Stoddard and Hayes, 2005; Wilkerson et al., 2006).

Numerous taxa including fish, birds, small mammals, reptiles, and amphibians have an intimate association with headwater streams, riparian forests, and the processes therein (Hairston, 1987; Burbrink et al., 1998; Jones et al., 1999; Maisonneuve and Rioux, 2001; Iwata et al., 2003; Shirley and Smith, 2005). Salamanders are the most abundant vertebrate organisms in eastern North American headwater-riparian habitats (Burton and Likens, 1975), where they contribute a significant biomass and are integral to ecosystem processes (Hairston, 1987; Wyman, 1998; Davic and Welsh, 2004; Peterman et al., 2008). In the Appalachian region, stream salamanders form assemblages that are comprised of five to nine species from the genera *Desmognathus*, *Eurycea*, *Gyrinophilus*, and *Pseudotriton*. All of these genera are stream dependent salamanders of the family Plethodontidae and most of the species (except *D. aeneus* and *D. wrighti*) have biphasic life cycles consisting of an aquatic larval stage and a terrestrial adult stage (Petranka, 1998). As such, salamanders have been recommended as viable indicators of

^{*} Corresponding author. Current Address: Indiana State University, Indiana School of Medicine-Terre Haute, 135 Holmstedt Hall, Terre Haute, IN 47809, United States. Tel.: +1 812 237 8301; fax: +1 812 237 7646.

E-mail address: bill.peterman@gmail.com (W.E. Peterman).

stream quality and ecosystem integrity (Welsh and Droege, 2001; Southerland et al., 2004).

Despite the acknowledged importance of salamanders, little attention has been given to stream breeding salamanders with regards to anthropogenic land uses. Numerous studies have shown that fully terrestrial salamanders (*Plethodon*) are sensitive to upland forest alterations (e.g., Petranka et al., 1993; Ash and Bruce, 1994; Herbeck and Larsen, 1998; Reichenbach and Sattler, 2007) and that salamanders requiring streams for aquatic larvae are particularly susceptible to human development and impervious surfaces (Willson and Dorcas, 2002; Price et al., 2006; Miller et al., 2007). However, the impacts of managed timber harvest on stream salamanders within riparian zones has largely been ignored, receiving some consideration on the west coast (e.g., Vesely and McComb, 2002; Stoddard and Hayes, 2005; Olson and Weaver, 2007) while populations in eastern forests have been largely unstudied (but see Crawford, 2007). This is of particular concern in the Appalachian region where logging at various intensities has occurred for decades (Brown, 2000).

When affected by riparian zone modification, salamander populations may exhibit one or more of several possible responses, including local population declines (Petranka et al., 1993; Ash, 1997; Herbeck and Larsen, 1998; Perkins and Hunter, 2006), modified movement patterns (Johnston and Frid, 2002), increased competition (Hairston, 1980), evacuation of altered habitat (Peterman, 2008), changes in growth and fitness (Beachy, 1997; Lowe et al., 2004; Peterman, 2008), or changes in genetic diversity (Stiven and Bruce, 1988; Curtis and Taylor, 2004). Rapid land development and natural resource utilization trends are unlikely to change, highlighting the need to find a balance that allows for continued land use while preserving the integrity and function of ecosystems.

The purpose of our research was to evaluate the effectiveness of forested riparian buffers in preserving stream salamander populations following recent even-aged timber harvest events. Specifically, the relative abundance of larval salamanders and environmental variables were measured at headwater streams with riparian forest buffers of varying widths. We used regression analyses with an information-theoretic approach to determine the environmental and habitat variables that most affected salamander populations and to determine the efficacy of riparian buffers in mitigating the impacts of even-aged timber harvest along headwater streams.

2. Methods

2.1. Study area

In order to determine the effects that riparian buffer width has on stream salamander populations, we monitored five southern Appalachian headwater streams. These streams drained small watersheds (<10 ha) within the Wayah Ranger District, Nantahala National Forest, Macon County, North Carolina, U.S.A., all of which had previously been harvested 70–80 years prior to this study. These sites were harvested using a 2-age shelterwood harvest (even-aged timber harvest), where a few mature trees were left for regeneration purposes. Timber harvest resulted in one of four riparian zone alterations: 0 m forest retained (complete upland forest harvest), 9 m forest retained, 30 m forest retained, and control (no upland forest removal). These logging treatments were completed on both sides of the stream within the stream watershed and extended for 200 m parallel to the stream and 200 m perpendicular to the stream. Harvest of the 0 m and 9 m sites occurred between October 2005 and May 2006 and harvest of the 30 m site occurred between June and September 2006.

2.2. Sampling protocol

We sampled larval salamander populations by dividing each stream into three 40 m sampling blocks that consisted of four 10 m subsections; each block was separated by 40 m. We monitored two control streams (controls 1 and 2), one 0 m buffer, one 9 m buffer, and one 30 m buffer stream from May to August 2007, but only the 0 m, 9 m, and Control 1 streams were monitored in 2006. Salamanders were captured using leaf litter bags (Pauley and Little, 1998; Waldron et al., 2003) made from 1.9 cm² polypropylene mesh. To make a leaf litter bag, mesh was cut to 75 cm × 75 cm squares and packed with dry leaf litter. The corners of the mesh were then pulled together and secured with plastic cable ties (Waldron et al., 2003). Sixteen bags were systematically distributed throughout each sampling block (4 per 10-m subsection) and a total of 48 leaf litter bags were deployed at each study site. Litter bags were set 10–14 days prior to initial sampling and were sampled weekly in 2006 and bi-weekly in 2007 by shaking them over a white tray (eight and five sample periods, respectively). Water and sediments collected in the trays were then poured through a 15 cm × 20 cm baitnet. All captured salamanders were identified to species, measured for total length (TL), snout-vent length (SVL), weighed, marked, and released at the point of capture. Salamanders were weighed using a digital balance with 0.001 g resolution (My Weigh, model GemPro 250), measured to the nearest 0.01 mm using digital calipers (Storm, model STO3C301) and then marked by clipping the tip of the tail fin of larval Blue Ridge two-lined salamanders (*Eurycea wilderae*) or clipping a toe on black-bellied salamanders (*Desmognathus quadramaculatus*).

2.3. Environmental data

We measured environmental variables at 15 sample points, each spaced 10 m apart within sampling blocks three times during the study. Environmental measures were collected from each site within 24 h of each other to limit temporal variation. Percent canopy coverage was estimated from the center of the stream using a spherical crown densiometer. Sedimentation was quantified as the percentage of surface sediment covering the streambed, and was measured using a 50 cm × 50 cm quadrat that was divided into 25 equal-sized square sections. Leaf litter mass was estimated by measuring the wet-weight of drained leaf litter and other organic debris collected from within a 0.25 m² area at the aquatic-terrestrial interface using a 2-kg Pesola® spring scale. Coarse woody debris was visually estimated on a five-point scale with 0 defined as no coarse woody debris and 4 defined as extensive woody debris spanning the width of the stream. Water temperatures were collected hourly from one location in the middle of the 200 m study stream using HOBO® data loggers (Onset, model UA-002-64).

2.4. Data analysis

To assess salamander abundance in relation to riparian forest modification and environmental variables, we used an information-theoretic approach to model selection (Burnham and Anderson, 2002). The information-theoretic approach allows one to select a “best” model and to rank the remaining models and its use is suggested for observational studies where other hypothesis testing methods may lead to data dredging and over-fitted models (Burnham and Anderson, 2002). Fourteen *a priori* models incorporating uncorrelated habitat variables were developed to test hypotheses predicting stream salamander abundance from 2007 data (Table 1). These *a priori* models were developed based on

Table 1
A priori regression models and justification of their use

| Model name | Model terms ^a | Justification |
|-----------------|--|---|
| Width | Width | May affect leaf litter deposition and stream substrate characteristics |
| Depth | Depth | May affect water flow rate and microhabitat characteristics |
| Leaf Litter | Leaf litter | Primary nutrient source in allochthonous-based headwater streams and important for salamander refugia (Petranka, 1998; Wallace et al., 1999) |
| Sediment | Sediment | Fills interstitial spaces utilized as refugia by larval salamanders (Smith and Grossman, 2003) |
| CWD | Coarse woody debris | May provide refugia as well as nutrient source for salamander prey |
| Buffer width | Buffer width | Affects sediment influxes into streams, water temperatures, allochthonous inputs, and riparian microclimate (Swank et al., 2001; Gomi et al., 2006) |
| Sample period | Date | Salamanders may show seasonal shifts in activity pattern (Petranka, 1998) |
| Sample location | Block | Salamanders may differentially utilize upstream and downstream reaches (Bruce, 1986; Bruce, 1988) |
| Site | Buffer width + block | Salamanders inhabiting different stream reaches may be differentially affected by loss of riparian habitat |
| Site effect | Buffer width + sediment | Salamanders may be impacted by sediment influxes that are known to increase following loss of riparian habitat (Welsh and Ollivier, 1998; Smith and Grossman, 2003) |
| Microhabitat | Leaf litter + CWD + sediment | Characteristics that may influence larval salamander habitat use and foraging |
| Stream profile | Leaf litter + CWD + sediment + width + Depth | An assessment of the measured stream characteristics on larval salamanders |
| Global model | All single parameters | A full assessment of salamander abundance with regard to all biotic and abiotic site characteristics |
| Null model | N/A | Salamander abundance may be random with regard to measured variables |

^a The number of parameters estimated (K) for each model is equal to the sum number of terms listed for each model plus one.

published literature on the effects of riparian forest modification as well as pilot data collected in 2006.

In order to select the model that best described salamander abundance, we used Akaike's information criterion (AIC). For each model, we calculated the corrected AIC (AIC_c) value, which measures model fit while correcting for small sample sizes (Burnham and Anderson, 2002). AIC_c values were calculated from log-linear regressions with a negative binomial distribution (two-lined salamanders) or Poisson distribution (black-bellied salamanders) using the generalized linear model in SPSS (v. 15.0). These distributions best fit the data for each species, respectively, resulting in significant model fitting when compared to an intercept only model. All candidate models were ranked according to their AIC_c value, with the best model having the smallest AIC_c value (Burnham and Anderson, 2002). We then calculated ΔAIC_c , which is the difference of each model from the best-fit model within the model set. To determine the weight of evidence for each model, Akaike weights (ω_i) were calculated (Burnham and Anderson, 2002). Lastly, we calculated odds ratios and 95% confidence intervals for model parameters from the best-supported models. Odds ratios allow for biological interpretation of β parameter estimates; for every unit change in a parameter's odds ratio, there is a one-unit change in the odds of the response variable (Keating and Cherry, 2004). An odds ratio of 1.0 indicates no difference between the proportion of sample points with or without salamanders, while odds ratios close to zero or substantially >1.0 indicates a large difference. Odds ratios less than 1.0 indicate a negative effect while ratios greater than 1.0 indicate a positive effect.

3. Results

In 2007, a total of 1402 larval salamanders (1262 two-lined salamanders and 140 black-bellied salamanders) were captured at five study streams (Fig. 1). Spring salamanders (*Cyprinophilus porphyriticus*) were also captured, but in numbers too small for data analysis. Larval two-lined salamanders were most abundant at the 30 m (413 larvae) and the control 1 and 2 streams (171 and 533 larvae, respectively), with very few captures occurring in the highly disturbed 0 m and 9 m sites (72 and 73 larvae, respectively). This trend was not seen in black-bellied salamanders as they were equally abundant at all sites (25–34 larvae per site). Similar post-treatment capture proportions among sites were observed in both

2006 and 2007 (Table 2), and capture proportions did not differ among years at sites that were monitored in both 2006 and 2007 (Table 2). In both years the control 1 site had a greater proportion of the two-lined salamander captures, while black-bellied salamander captures were relatively constant. Though the frequency of sampling differed between years, the relative proportion of two-lined salamander and black-bellied salamander

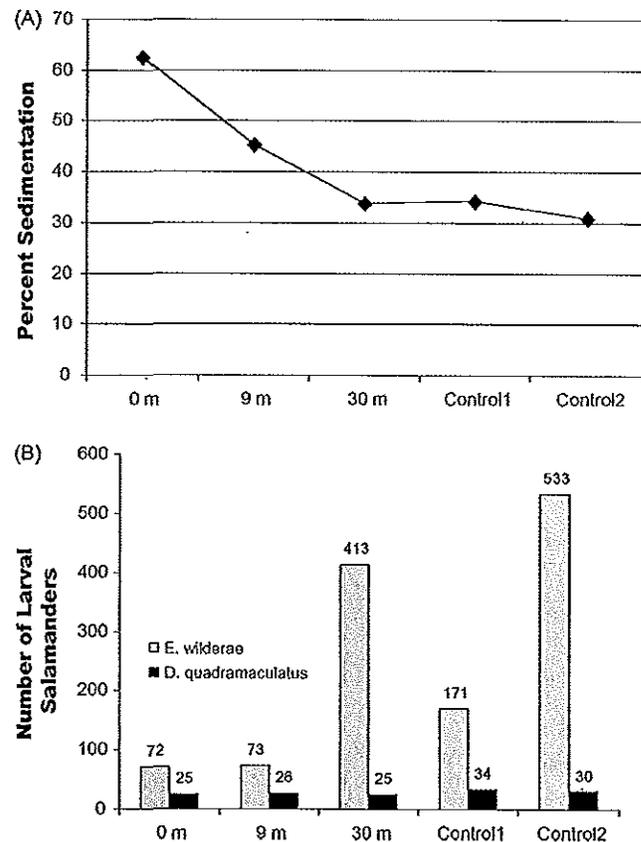


Fig. 1. Relationship between the (A) mean percent surface sedimentation and (B) the number of larval *Eurycea wilderae* and *Desmognathus quadramaculatus* captured in 2007 at each of five sites.

Table 2
Comparison of larval salamander captures in 2006 and 2007

| Species | Site | 2006 | | 2007 | |
|---------------------------|-----------|-------|------------|-------|------------|
| | | Count | Proportion | Count | Proportion |
| <i>E. wilderae</i> | 0-m | 137 | 25.75 | 72 | 22.78 |
| | 9-m | 146 | 27.45 | 73 | 23.10 |
| | Control-1 | 249 | 46.80 | 171 | 54.12 |
| | Total | 532 | 100.00 | 316 | 100.00 |
| <i>D. quadramaculatus</i> | 0-m | 51 | 29.82 | 25 | 29.41 |
| | 9-m | 58 | 33.92 | 26 | 30.59 |
| | Control-1 | 62 | 36.26 | 34 | 40.00 |
| | Total | 171 | 100.00 | 85 | 100.00 |

Capture numbers cannot be directly compared between years due to differences in sampling frequency and methodology. The relative proportion (percent) of total larval captures for each species can be compared among sites and between years. The 30 m and control 2 sites were only sampled in 2007.

Table 3
Habitat variables measured at study streams

| Site | Habitat variable | N | Mean | Min | Max | S.E. |
|-----------|------------------|------|--------|--------|---------|--------|
| 0 m | Litter (g) | 45 | 12.60 | 0.00 | 220.00 | 5.205 |
| | CWD | 45 | 2.32 | 1.00 | 4.00 | 0.152 |
| | Canopy (%) | 45 | 79.11 | 49.04 | 93.76 | 1.492 |
| | Sediment (%) | 45 | 62.53 | 28.00 | 84.00 | 4.932 |
| | Temperature (°C) | 1000 | 16.84 | 14.33 | 19.76 | 0.037 |
| 9 m | Litter (g) | 45 | 43.11 | 0.00 | 330.00 | 7.855 |
| | CWD | 45 | 2.31 | 0.00 | 4.00 | 0.158 |
| | Canopy (%) | 45 | 85.90 | 68.80 | 97.92 | 1.193 |
| | Sediment (%) | 45 | 45.24 | 22.00 | 76.00 | 1.692 |
| | Temperature (°C) | 1000 | 16.59 | 14.52 | 18.62 | 0.027 |
| 30 m | Litter (g) | 45 | 378.00 | 120.00 | 780.00 | 21.338 |
| | CWD | 45 | 1.87 | 1.00 | 4.00 | 0.129 |
| | Canopy (%) | 45 | 92.70 | 83.36 | 97.92 | 0.525 |
| | Sediment (%) | 45 | 33.69 | 12.00 | 68.00 | 1.588 |
| | Temperature (°C) | 1000 | 15.68 | 13.37 | 18.37 | 0.032 |
| Control 1 | Litter (g) | 45 | 536.22 | 80.00 | 2500.00 | 57.031 |
| | CWD | 45 | 1.56 | 0.00 | 4.00 | 0.173 |
| | Canopy (%) | 45 | 94.92 | 84.40 | 98.96 | 0.442 |
| | Sediment (%) | 45 | 34.13 | 16.00 | 64.00 | 1.429 |
| | Temperature (°C) | 1000 | 15.13 | 12.21 | 17.09 | 0.029 |
| Control 2 | Litter (g) | 45 | 344.89 | 80.00 | 850.00 | 25.195 |
| | CWD | 45 | 1.64 | 0.00 | 4.00 | 0.153 |
| | Canopy (%) | 45 | 94.55 | 86.48 | 98.96 | 0.476 |
| | Sediment (%) | 45 | 30.84 | 10.00 | 56.00 | 1.616 |
| | Temperature (°C) | 1000 | 15.38 | 13.37 | 17.00 | 0.026 |

captures among sites and between years is consistent. As such, we feel confident that our methodology and results are expressive of the trends experienced by salamanders at each of these treatments.

Table 5
 β estimates and odds ratios for parameters in the most supported models predicting the presence of larval *Eurycea wilderae* and *Desmognathus quadramaculatus*

| Parameter | β | S.E. | Wald χ^2 | P-value | Odds ratio | 95% CI |
|--|----------------|-------|---------------|---------|------------|-------------|
| <i>E. wilderae</i> ^a | | | | | | |
| Sediment | -0.006 | 0.002 | 8.360 | 0.004 | 0.994 | 0.990–0.998 |
| Complete buffer | 0.179 | 0.085 | 4.430 | 0.035 | 1.196 | 1.012–1.412 |
| 30 m buffer | 0.272 | 0.072 | 14.399 | 0.000 | 1.313 | 1.141–1.511 |
| 9 m buffer | -0.133 | 0.101 | 1.739 | 0.187 | 0.876 | 0.719–1.067 |
| 0 m buffer | 0 ^c | - | - | - | - | - |
| <i>D. quadramaculatus</i> ^b | | | | | | |
| Date | 0.211 | 0.063 | 11.395 | 0.001 | 1.235 | 1.093–1.397 |
| Block | -0.083 | 0.026 | 9.940 | 0.002 | 0.921 | 0.875–0.969 |

Significant parameters are those whose 95% confidence intervals do not include 1.0.

^a The site effect model that included sediment and buffer width parameters was most supported.

^b Sample period and sample location were single parameter models including date and block, respectively, and were equally supported.

^c No parameter estimate because this was the reference value that the significance of the other buffer categories were based off of.

Table 4
Top four *A priori* regression models predicting abundance of larval *Eurycea wilderae* and *Desmognathus quadramaculatus* within five experimental streams in the Nantahala National Forest, North Carolina, USA

| Model | -2 log likelihood | K ^a | AIC _c ^b | Δ AIC _c ^c | ω_i ^d |
|---------------------------|-------------------|----------------|-------------------------------|--|-------------------------|
| <i>E. wilderae</i> | | | | | |
| Site effect | 692.09 | 5 | 1394.37 | 0 | 0.93 |
| Buffer | 696.16 | 4 | 1400.46 | 6.09 | 0.04 |
| Site | 695.85 | 3 | 1401.90 | 7.528 | 0.02 |
| Global | 690.46 | 11 | 1403.85 | 9.471 | 0.01 |
| <i>D. quadramaculatus</i> | | | | | |
| Date | 267.21 | 2 | 538.47 | 0 | 0.61 |
| Block | 267.90 | 2 | 539.85 | 1.381 | 0.31 |
| Global | 260.77 | 11 | 544.45 | 5.983 | 0.03 |
| Site | 267.14 | 3 | 544.49 | 6.024 | 0.03 |

The Global model fit the data for *E. wilderae* ($\chi^2 = 126.793$, d.f. = 9, $P < 0.001$, $n = 300$) and for *D. quadramaculatus* ($\chi^2 = 17.619$, d.f. = 9, $P = 0.040$, $n = 300$).

^a Number of parameters estimated in each model.

^b Akaike's Information criterion adjusted for small sample size.

^c The difference between the AIC value for a given model and the AIC value of the best approximating model for each data set.

^d Akaike weights. Probability that the current model (*i*) is the best-approximating model.

Habitat variables also differed among treatments. Average leaf litter and percent canopy cover were lower at the 0 m and 9 m treatment streams, while percent sedimentation and coarse woody debris (CWD) were greater at the 0 m and 9 m streams than at the 30 m or control streams (Table 3). Mean stream temperatures were substantially greater at the 0 m and 9 m streams.

Of the fourteen *a priori* models assessing the abundance of larval two-lined salamanders, the Site Effect model that incorporates buffer width and sediment parameters was the most supported ($\omega_i = 0.93$; Table 4). Sediment had a significant negative effect on larval presence, though the influence of sediment was minimal (odds ratio = 0.994; Table 5). Buffer width was also a significant variable in the model and buffer width greater than 9 m resulted in significantly more larval two-lined salamanders (Table 5). Buffer width was the most influential parameter in the model (odds ratio = 1.313 and 1.196 for 30 m and complete buffer, respectively; Table 5).

The presence of black-bellied salamanders at our study streams was best predicted by the Sample Period ($\omega_i = 0.61$) and Sample Location models ($\omega_i = 0.31$; Table 4), which were both single parameter models that had considerable support. The date of the sample period was positively associated with black-bellied salamander abundance, indicating that more larvae were captured later in the sampling season. In contrast, sampling block had a negative influence on black-bellied salamander abundance, indicating that more larvae were encountered in upstream reaches.

4. Discussion

Long-term studies in the Appalachian Mountains have documented the impacts of even-aged timber harvest on headwater streams and their invertebrate communities (Stone and Wallace, 1998; Swank et al., 2001), resulting in increased sedimentation, changes in nutrient cycling, and shifts in functional benthic feeding groups. Perhaps most significant of these findings is the long-term retention (up to 20 years) of sediments that were introduced to the stream following timber harvest (Swank et al., 2001). Of the parameters included in our regression analyses, sediment was the only significant habitat variable to predict a decrease in larval two-lined salamander abundance (Table 5). Increase in sedimentation was most evident at the 0 m and 9 m streams, while the 30 m and control streams showed relatively lower sediment levels (Fig. 1, Table 3). Two-lined salamander populations were also significantly greater at the 30 m and control streams that had wider riparian buffers, reduced sedimentation, lower water temperatures, and more allochthonous inputs (Table 3). Increased sedimentation is likely detrimental to larval two-lined salamanders because they are dependent on small interstitial spaces amongst the streambed cobble for refuge (Smith and Grossman, 2003). The loss of refugia could make two-lined salamanders more susceptible to predation from larger heterospecific salamander larvae such as spring salamanders and black-bellied salamanders (Beachy, 1994). If similar sedimentation dynamics measured by Swank et al. (2001) are realized at our experimental streams, depressed larval two-lined salamanders populations due to sedimentation may be expected for several years post-harvest, though it is important not to assess the long-term salamander population response to timber harvest strictly in terms of the larval life stage.

While sediment was a significant parameter in explaining two-lined salamander abundance in the Site Effect model, it had a relatively small influence (Table 5); buffer width had a much greater effect on salamander abundance. Odds ratios indicate that extending riparian buffers beyond 9 m resulted in a significant increase in the likelihood of high salamander abundance. These results suggest that there is an unmeasured aspect of riparian forest loss that is negatively affecting larval two-lined salamanders. As adults, two-lined salamanders are highly terrestrial, utilizing riparian habitat up to 100 m from the stream (Crawford and Semlitsch, 2007). As such, a significant reduction or complete loss of riparian habitat will likely affect two-lined salamander populations in the adult life stage more than the predominately aquatic black-bellied salamanders. Loss of adult age classes will further exacerbate local declines due to reduced reproductive output.

Larval black-bellied salamanders did not show the same responses to riparian timber harvest treatments as two-lined salamanders. Black-bellied salamanders appear to not be immediately affected by any of the measured habitat variables included in *a priori* habitat models, and abundance of black-bellied salamanders was relatively equal among the five study streams (Fig. 1). The significant parameters affecting black-bellied salamander populations were date and block (Table 5); more black-bellied salamanders were captured later in the collecting season and more were captured in upstream reaches than in downstream reaches. There is no obvious explanation for the date effect in black-bellied salamander abundance. It is possible that they exhibit a behavioral shift later in the active season whereby they change refugia and/or prey base. It cannot be excluded that black-bellied salamanders were artificially drawn to leaf litter traps due to the increased prey abundance that resulted from colonization by benthic invertebrates and larval two-lined salamanders. The observed greater abundance of black-bellied salamanders in

upstream reaches has been described by Bruce (1985), who noted that black-bellied salamanders tended to breed in the upper reaches of headwaters, resulting in more larvae in upstream reaches.

Since black-bellied salamanders are primarily found within 5 m of headwater streams (Crawford and Semlitsch, 2007; Peterman et al., 2008), they may be more resilient to immediate post-cut harvest effects. Though variation in abundance of black-bellied salamanders was not observed among buffer treatments as it was in two-lined salamanders, they are likely not immune to the long-term impacts of even-aged timber harvest. The long-term synergistic effects of both aquatic larval and terrestrial adult life stages being impacted by timber harvest are unknown for either species. Crawford (2007) showed that all stream salamanders, including two-lined salamanders, were significantly less abundant in even-aged forest stands less than 40 years in age as compared to stands that were more than 40 years old. Though black-bellied salamanders were not included in Crawford's (2007) study, Stiven and Bruce (1988) reported decreased abundances of black-bellied salamanders in recently cut plots, and they also showed losses of genetic diversity that correlated with historical land uses. Recovery of salamander populations to pre-harvest levels is likely dependent on multiple factors that include flushing of sediments from the stream bed and forest succession in the riparian habitat, which will provide increased canopy coverage, leading to increased leaf litter, soil moisture, and allochthonous inputs, as well as stabilization of both aquatic and riparian microclimates.

We recognize that our study lacks spatial replication, and as such, conclusions drawn from our data must be done so with caution. In an effort to alleviate this symptom and to fortify our results we added a second un-harvested control site to better encompass the natural variation of Southern Appalachian salamander populations. Given the constraints of our experimental design, we have done our best to accurately represent the trends and responses measured, but nonetheless know that a multi-year, replicated design would more strongly support our conclusions.

5. Conclusions and management implications

Current U.S. Forest Service regulations generally require a 30-ft (~9 m) buffer around low order headwater streams. If the purpose of these riparian buffers is to mitigate the impacts of land uses such as even-aged timber harvest and to preserve the health and function of headwater-riparian ecosystems, then it is clear that the current regulations requiring a 9-m buffer around low order headwater streams is insufficient. Our results showed no appreciable difference between the 0 m treatment with no riparian buffer and the 9-m buffer treatment with regards to two-lined salamander abundance (Fig. 1), which was significantly affected by an increase in sedimentation (Table 5). Though sedimentation was slightly reduced as a result of the 9 m buffer (Table 3), the reduction was insufficient to maintain larval two-lined salamander populations at a level equivalent to or greater than those measured at the 30 m or control treatments (Table 5).

More important than sedimentation was the significant effect of riparian buffer width on larval two-lined salamander abundance, suggesting that there were unmeasured effects of riparian habitat loss contributing to local population declines. We believe that the unmeasured effect of significance is the loss of breeding adult two-lined salamanders, which are highly dependent on riparian habitat (Crawford and Semlitsch, 2007). Unlike the 0 m and 9 m treatments, salamander abundance and habitat measures for the 30 m treatment did not significantly differ from the control treatments, but it must be reiterated that data presented here were collected following the first 2 years of timber harvest. Our research

and findings represent a brief snapshot of what will be an ongoing successional process. Since local population declines may not be realized immediately, it is critical to assess the impacts of timber harvest across all life stages so that the long-term demographic impacts of forestry are clearly understood.

Stream salamanders are highly dependent upon specific microclimates that are maintained by riparian forests (Crawford and Semlitsch, 2008). These microclimates can be significantly affected by edge effects, the extent and influences of which is an ever-present concern when dealing with the effectiveness of buffers. The distance that altered microclimate conditions can penetrate a forest vary (discussed in Olson et al., 2007). There is evidence that headwater streams themselves may help to buffer the effects of microclimate changes within 10 m of the stream (Anderson et al., 2007), but microclimates will vary beyond this. In their review of riparian forestry impacts on amphibian populations, Olson et al. (2007) suggest buffers of 40–100 m. These buffers are sufficient to preserve the majority of aquatic-riparian dependent species such as salamanders, but also allow timber harvest to occur in upland habitats. For the Appalachian region, Crawford and Semlitsch (2007) recommended preserving 42.6 m for core terrestrial salamander habitat with an additional 50 m buffer to ameliorate edge effects (92.6 m total).

Land use and natural resource extraction are unlikely to change in the near future. In order to progress and coexist with natural ecosystems that we are dependent upon, compromises must be made. Salamanders play an integral role in headwater stream ecology and it is important that we recognize that headwater streams provide ecosystem services that we depend upon (Meyer and Wallace, 2001; Davic and Welsh, 2004). We have shown that current regulations are insufficient to maintain headwater stream function and retain biodiversity. Though the 30-m riparian buffer assuaged the effects of even-aged timber harvest in the short-term, such a buffer is unlikely to maintain a salamander assemblage similar to one unaffected by timber harvest in the long-term (Crawford and Semlitsch, 2007, 2008). In order to find an adequate riparian buffer that balances ecosystem health and function with human utility, future research needs to assess the long-term impacts of even-aged timber harvest in relation to riparian buffers, monitoring both larval and adult life history stages through multiple generations.

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