Comparison of silvicultural and natural disturbance effects on terrestrial salamanders in northern hardwood forests

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ARTICLE INFO

ABSTRACT

In forested ecosystems timber harvesting has the potential to emulate natural disturbances, thereby maintaining the natural communities adapted to particular disturbances. We compared the effects of even-aged (clearcut and patch cut) and uneven-aged (group cut, single-tree selection) timber management techniques with natural ice-storm damage and unmanipulated reference forest sites on red-backed salamanders. We used cover boards and litter searches to survey for salamanders in northern hardwood forests in New Hampshire, USA. We estimated abundance while accounting for detection probability using the Dail–Madsen open population model. We found significant reduction in salamander abundance in recent group cuts, patch cuts, and clearcuts compared to reference forest sites, and significant but less effect of single-tree selection and ice-storm damage. Our results contribute to the evidence of detrimental effects of even-aged harvests on salamander abundance, but in contrast to most previous research, we also found lower abundance in sites following uneven-aged harvest practices when we accounted for detection probability. To more accurately reflect the total effect of harvests on salamanders, we also employed a parametric, nonlinear hierarchical model to estimate edge effects while accounting for imperfect detection. We found that group cut, patch cut, and clearcut logging reduced salamander abundance 34 m into the surrounding forest. These edge effects can greatly expand the total area affected by logging, especially in the northeastern US where cuts tend to be relatively small. This novel method for estimating edge effects will allow managers to directly calculate the total effects on populations for various size and shape harvesting plans.

1. Introduction

Disturbance is one of the primary factors that regulate natural populations, structure communities, and maintain biodiversity. Because local communities are thought to be adapted to natural disturbance regimes, a common goal of ecosystem management is to replicate natural disturbances (e.g. Buddle et al., 2006; Perry, 1998). Nevertheless, emulating natural disturbances with management practices can be difficult because effects on populations and communities can vary by habitat or the type, frequency, and severity of the disturbance (Runkle, 1985). Therefore, to properly inform forest management it is important to quantify the effects of various disturbances, such as from severe winds, insect outbreaks, wildfire, landslides, and ice-storms and compare them to silvicultural practices.

Much of the research directly comparing natural and anthropogenic disturbances has focused on wildfire (e.g. Buddle et al., 2006; Simon et al., 2002) and wind (e.g. Greenberg, 2001; Lain et al., 2008) in relation to prescribed burns and timber harvests. However, wind and ice storms are the major causes of natural disturbance in northern hardwood forests (Lorimer and White, 2003). Ice storms, which generally result in small canopy gaps, are a frequent disturbance agent occurring every 1–25 years in northern hardwood forests (Irland, 2000). The frequency of severe storms including snow and ice storms in New England are expected to increase given climate change predictions (Frumhoff et al., 2007). In contrast to ice storms, stand-replacing natural disturbances, such as major fires and hurricanes, which create large gaps, occur relatively infrequently (return times of 100–1000 years) in the temperate forests of northeastern North America (Runkle, 1985). Correspondingly, clearcutting is an intensive silvicultural practice which involves the removal of the entire canopy at longer harvest rotations, whereas single-tree selection and group selection cuts result in small gaps in the canopy, more similar to most natural disturbance in the region, and require logging a greater area of forested land, and shorter time between re-entry to stands (Walker, 1999).

Disturbance that opens gaps in the canopy increases light penetration (Minckler et al., 1973) and rain throughfall (Heatwole, 1962), and can have direct consequences on other abiotic factors

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such as soil moisture, leaf litter depth, and soil temperature (Johnson et al., 1985; Minckler et al., 1973). Relative changes in abiotic factors are likely dependent on gap size with larger gaps having greater reductions in soil moisture (Troendle, 1970) and leaf litter depth (Johnson et al., 1985), and increases in soil temperature (Marquis, 1967) compared to smaller gaps (Phillips and Shure, 1990). Additionally, the resulting amount of course-woody debris is a function of natural disturbance type and silviculture practices. The differential impacts on microhabitat characteristics due to differences in forest disturbance area and intensity may result in varying effects on wildlife populations.

Plethodontid salamanders are particularly sensitive to changes in forest conditions (Peterman et al., 2013; Welsh and Droege, 2001) and may be differentially affected by various forest disturbances. Salamanders are influenced by several habitat characteristics that can be altered immediately following a forest disturbance (Ash, 1997; Crawford and Semlitsch, 2008a; Tilghman et al., 2012), including temperature (Feder and Pough, 1975), soil moisture (Heatwole and Lim, 1961), density of understory vegetation (Brooks, 1999), the number, area, or volume of coarse woody debris (CWD; Brooks, 1999; Mathis, 1990), and leaf-litter depth (Crawford and Semlitsch, 2008a; Pough et al., 1987).

In addition to the general effects of large-scale disturbance such as clearcutting, these disturbances create an environmental gradient from the interior of the disturbed area extending out into the surround undisturbed forest. This edge gradient varies in light, temperature, moisture, vapor pressure deficit, humidity, and shrub cover (Matlack, 1993) and can extend 50 m or farther from the edge (Chen et al., 1999; Matlack, 1993; Murcia, 1995). The width of these edge effects has important conservation implications because the effects of disturbance can extend beyond the area directly disturbed. Among wildlife, amphibians are especially sensitive to increased light, temperature, and reduced moisture associated with forest edges around recent timber harvests (Crawford and Semlitsch, 2008a; deMaynadier and Hunter, 1998). The effect of forest edges on amphibian abundance varies by location and season (Baker and Lauck, 2006; deMaynadier and Hunter, 1998; Schlaepfer and Gavin, 2001) and by species (deMaynadier and Hunter, 1998; Urbina-Cardona et al., 2006). In the northeastern United States, amphibian abundance, especially of forest dependent species, is reduced 20 – 35 m into the forest surround timber harvests (DeGraaf and Yamasaki, 2002; deMaynadier and Hunter, 1998). Amphibians are also known to change their movement patterns in response to forest-open-canopy edges (Graeter et al., 2008; Popescu and Hunter, 2011; Rothermel and Semlitsch, 2002), potentially contributing to observed abundance distributions along edge gradients.

Although declines of amphibian abundance following timber harvest are documented throughout the United States (e.g. deMaynadier and Hunter, 1995; Petranka et al., 1993; Tilghman et al., 2012), few studies have directly compared the effects of natural forest disturbances with different forest management practices on amphibians (but see Greenberg, 2001; Strojny and Hunter, 2010). Our objectives were to (1) compare the short-term impacts of various forest harvesting practices and natural ice-storm damage on the red-backed salamander (*Plethodon cinereus*) in northern hardwood forests, and (2) examine how salamander abundance varies along the edge gradient from cut interior to surrounding forest, while accounting for imperfect detection.

2. Methods

2.1. Study design

We established study sites in northern hardwood forest within the White Mountain National Forest (WMNF), New Hampshire. The forest canopy was dominated by American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), and sugar maple (*Acer saccharum*). These mature hardwood forests developed from woods selectively harvested between 1887 and 1916 (Belcher, 1980). Our sites were located in undisturbed forest, recently harvested forest, and mature forest recently damaged from ice storms and ranged in elevation from 226 to 573 m and varied in slope and aspect. All harvests were conducted in the winter of 1998–1999. Undisturbed forest sites ($n = 8$) consisted of stands not harvested in the past 60 years and without recent ice damage. Previous research has demonstrated no difference in salamander populations between old growth forests and 60 year-old secondary forests (Petranka et al., 1993; Pough et al., 1987). Harvested sites consisted of clearcuts ($n = 2$), patch cuts ($n = 5$), group selection ($n = 2$), and single-tree selection harvests ($n = 4$). Harvests were located low to moderately steep slopes to minimize runoff. Primary orientation of harvests varied within treatments. Most treatments had replicate sites with aspects that ranged in all cardinal directions, with the exception that group selection cuts and clearcuts were predominately in south- and east-facing orientations because there were only 2 replicated of each.

Silvicultural treatments were classified according to White Mountain National Forest management definitions (USDA Forest Service, 1986). Clearcuts and patch cuts (even-aged management practices) resulted in the removal of all merchantable trees down to 5 cm, with clearcuts ranging in size from 4 to 12 ha and patch cuts ranging from 1 to 4 ha. Uneven-aged management includes single-tree selection and group selection. Single-tree selection involves removal of individual trees based on characteristics such as quality and size, whereas group selection removes trees in small groups resulting in gaps 0.1–0.8 ha in size. Specifically at our study locations, the reference stands and pre-harvest areas had a mean basal area of 30.3 m² ha⁻¹, which was reduced by approximately 25% to a mean of 22.8 m² ha⁻¹ in the single-tree selection harvested stands.

In January 1998, a 100-year ice-storm hit the northeast United States and parts of eastern Canada, affecting principally mature northern hardwood forests at elevations between 300 and 800 m. More than 6.9 million ha of northern hardwood and spruce-hardwood forest were affected in New England and New York (Lorimer and White, 2003). Of the 430,000 ha of forest in New Hampshire, approximately 27% of the trees received light or moderate damage and 23% were seriously damaged. In New Hampshire, the average crown loss within damaged areas was 64% per individual tree (Miller-Weeks and Eagar, 1999). Ice-storm damage maps obtained from the USFS were used to identify areas of severe storm damage. Ice-storm damaged sites ($n = 9$) were chosen based on both proximity to harvest sites and accessibility (total $N = 30$ sites) and occurred on sites with aspects in all cardinal directions except west.

In each clearcut, patch cut, and group cut, we centered a transect at the harvest edge , which extended 80 m into harvest and 80 m into surrounding forest perpendicular to the harvest edge. We established sampling plots at the harvest-forest edge (0 m) and at 20 m intervals in both directions. An additional plot was located 10 m into the forest to help estimate a more precise edge effect. Group cuts and one patch cut were too small for plots to be located 80 m from a forest edge; therefore, these transects were truncated 40 or 60 m into the cut. At undisturbed, ice-storm damage, and single-tree selection sites, we randomly located the first plot and established three additional plots 20 m apart in random directions.

2.2. Salamander sampling

At each plot, we sampled red-backed salamander abundance using artificial cover objects (ACOs) and 1 m² area constrained

searches. ACOs consisted of five rough-cut pine boards (2–1 m × 20 cm × 2.5 cm and 3–1 m × 30 cm × 2.5 cm) placed at each sampling plot within each site. Meter square sampling quadrats were located adjacent to the ACOs on a randomly selected side. All cover objects and leaf-litter within sampling quadrats were turned over and searched down to the humus layer (Oa layer). We conducted diurnal searches at each plot in all 30 sites 3–4 times during each of 4 primary sampling periods (10 June – 23 July 1999; 03 September – 19 October 1999; 05 June – 21 July 2000; 28 August – 11 October 2000). Because heavy rainfall increases salamander activity, we did not sample within 24 h of a rain event in order to maintain consistency (Hyde and Simons, 2001). Captured salamanders were weighed to the nearest 0.01 g using a Pesola® spring scale and snout-vent length and total length were measured to the nearest 0.01 mm using calipers.

2.3. Habitat characteristics

We measured habitat variables concurrently with salamander sampling. Within the 1-m^2 quadrats, we sampled habitat characteristics likely to influence salamander distribution including percent canopy cover, leaf-litter depth, soil moisture, soil temperature, and soil pH (e.g. Crawford and Semlitsch, 2008a; Heatwole, 1962; Wyman, 1988). Leaf-litter depth (Oi layer) was determined by pressing a ruler through the litter layer to the Oe layer and recording the height of uncompressed leaf-litter. Because humus layer depths were highly variable, soil temperature was taken at a constant depth of 3.5 cm below the soil surface. We measured percent canopy cover at each plot using a spherical densiometer.

We collected soil samples from the humus layer in plastic bags and analyzed them in the lab for soil moisture and pH. Gravimetric moisture content was determined by oven drying 20 g of wet soil at 29 °C for 48 h and reweighing the sample to determine the amount of moisture per dry soil weight (g water/g dry soil; Jarrell et al., 1999). For soil pH, we air-dried, sifted (2-mm sieve), and suspended soil samples in a 1:10 solution of distilled water (2 g of soil in 20 ml of water) by shaking samples for one minute. The soil samples rested for 30 min prior to measurement with a calibrated Orion 240A pH meter and triode probe (adapted from Davey and Conyers, 1988). Because soil moisture varies temporally more than soil pH, we measured soil moisture during every sampling occasion but measured soil pH every other sampling occasion.

2.4. Statistical analysis

For all statistical analyses, we used the combined count of ACOs and litter searches within a plot on a given day. Previous experience suggested that immediately after rain salamanders may move out from cover objects and into the leaf litter but as the leaf litter dries animals move back under cover objects and if the soil continues to dry, salamanders may move belowground, reducing

detection probability. Therefore, by combining litter and ACO searches and not sampling within 24 h of rain, we maximize our capture consistency (less variable detection). When comparing the effects of natural disturbance and various forest harvest techniques we limited the data in the group cut, patch cut, and clearcut sites to plots 20–80 m into the cuts. Data from plots at the edge and into the surrounding forest were only used for testing edge effects (see below). To account for varying detection probability across time and space, we used the Dail–Madsen hierarchical model for open populations when comparing treatment effects (Dail and Madsen, 2011). Using this model, we assumed population closure during the 4 primary periods, but allowed the populations to vary between primary periods. Four latent parameters were estimated: Abundance (N_i), Recruitment (γ), Survival (ω), and Probability of Detection (p). We constructed 6 a priori models with different combinations of covariates describing the latent parameters, assuming a Poisson distribution (Table 1). We fit these models using a maximum likelihood approach implemented in the R package unmarked (Fiske and Chandler, 2011). We assumed an autoregressive function for abundance where recruitment is modeled as $\gamma * N_{i,t-1}$, where t is the primary period. We selected the best model based on the lowest AIC value and considered a model well supported if the ΔAIC values were >2 for all the other models (Burnham and Anderson, 2002).

Group cuts, patch cuts, and clearcuts are useful, traditional categories for silviculture, but these categories represent breaks in a continuum of harvest sizes. We were also interested the effect of harvest size as a continuous measure of timber harvest on salamander abundance. Therefore, we conducted a post hoc linear mixed model regression of abundance derived from the best Dail–Madsen model as a function of cut size using plot as a random effect. We conducted this analysis using the nlme package in R (Pinheiro and Bates, 2000; Pinheiro et al., 2013).

To examine how salamanders were distributed from within recently logged habitat into the surrounding forest (edge-effects), we employed an N-mixture model (Royle, 2004), using data from the group cuts, patch cuts, and clearcuts. We only used data from fall 2000 for this analysis because a nonlinear N-mixture model would be too complicated to fit using an open-population model, which necessitates estimating more latent parameters. The fall 2000 sample period had four repeated observations of all plots, whereas the other closed periods often had only three observations per plot; therefore, the fall 2000 period had more data to estimate the nonlinear parameters.

Salamander captures followed a logistic pattern with respect to distance from the forest-cut edge; with few captures 80 m into the harvest area and increasing captures around the harvest edge and finally plateauing farther into the forest. To model this pattern, we used a four point logistic function,

$$N_i = C + \frac{A - b_{site_i}}{1 + e^{-(x_i - D)/B}} \tag{1}$$

Table 1
Hierarchical models of abundance, recruitment, survival, and detection as a function of forest disturbance treatment (Trt), soil pH, leaf litter depth (Litter), soil moisture (Moist), canopy cover (Canopy), day of the year (DOY), soil temperature (Temp) and number of natural cover objects searched (NCO).

	Abundance	Recruit	Surviv	Detection
Treatment models				
Global	Trt + pH + Litter + Moist	Canopy	Canopy	Canopy + DOY + DOY^2 + Temp + Temp^2 + Moist + NCO
Simple abundance	Trt	Canopy	Canopy	Canopy + DOY + DOY^2 + Temp + Temp^2 + Moist + NCO
Simple abundance and detection	Trt	Canopy	Canopy	Canopy + Temp + Temp^2 + Moist
Simple survival and recruitment	Trt + pH + Litter + Moist	1	1	Canopy + DOY + DOY^2 + Temp + Temp^2 + Moist + NCO
Simple	Trt	1	1	Canopy + Temp + Temp^2 + Moist
Null	1	1	1	1
Edge effect model				
Logistic Edge Effects	C + (A − b)/(1 + exp(−(Dist−D)/B))	–	–	Canopy + Temp + Temp^2 + Moist + NCO

where N_i is the predicted abundance for plot i at distance x, A is a y-scale parameter (upper asymptote control), B is the rate parameter, C is the asymptote in the harvests (lower asymptote control; carrying capacity in the even-aged harvests), D is x-shift parameter (inflection point), x_i is the distance from the forest-cut edge at plot i (negative into the harvest, positive into the forest), and b_{site_i} is the random effect of site. We assumed that error was distributed following a Poisson distribution. We defined the detection level of the model as:

$$logit(p_{ij}) = \alpha + \beta_1 SoilT_{ij} + \beta_2 SoilT_{ij}^2 + \beta_3 Moist_{ij} + \beta_4 NCO_{ij} \qquad (2)$$

where α is the overall mean detection probability on the logit scale, β_1 is the regression coefficient for the effect of soil temperature at plot i during observation j, and β_2, β_3, and β_4 are the regression coefficients for soil temperature squared, soil moisture, and the number of cover objects searched, respectively. We did not include day of the year as a detection covariate in this model because data were only from fall 2000 and the effects of day would be difficult to distinguish from temperature over this short time period. We estimated parameters within a Bayesian framework using Gibbs sampling in program JAGS through the rjags package (Plummer, 2012) in program R (R Development Core Team, 2012). To improve model convergence we set the mean asymptote in the forest (carrying capacity [K]), equal to the mean of the reference sites in fall 2000 from the previous analysis ($K = 30$). We set $A = K - C$ and chose non-informative priors for C and all other parameters (Appendix A). We also standardized all covariates to have a mean of 0 and standard deviation of 1, except distance which was not necessary to standardize for convergence. We used uniform priors of 0–30, 0–10, and −20–20 for B, C, and D, respectively. For inference, we ran 100,000 iterations of 4 chains after discarding the first 100,000 iterations and saved every 100th iteration following the burn-in, resulting in a posterior distribution of 4000 values for each parameter. We determined that the Markov chain had converged based on visual inspection of the traceplots and testing that the Gelman–Rubin statistic, $\hat{R}$, was <1.1 for all parameters (Gelman and Hill, 2007).

3. Results

We captured a total of 1593 red-backed salamanders between 1999 and 2000 across all plots and seasons. The *simple abundance model* (Table 1) describing salamander abundance, survival, recruitment, and detection model had the best support (AIC weight = 0.760; Table 2). Based on the 95% confidence intervals, we found significant differences in abundance across the forest treatments (Fig. 1). Storm damage sites had fewer salamanders than reference sites (40% lower than reference) and single-tree selection sites had fewer salamanders than storm damage sites (60% lower than reference). The group cut, patch cut, and clearcut treatments supported fewer salamanders than the single-tree selection treatment, but did not differ significantly from each other (88% lower than reference; Fig. 1). Although percent canopy cover was included in the best model, it was not a significant predictor of survival, recruitment, or detection (Table 3). The effects of treatment on abundance were consistent over time, although the uncertainty increased over time except in the even-aged treatments (Fig. 1). Mean detection probability per individual per survey across years and seasons was 4.45%. Detection increased with soil moisture and number of cover objects searched (Fig. 2). Detection followed quadratic effects of day of the year (minimum on 01 August) and temperature (maximum at 14.3 °C). Additionally, using a mixed model approach, we found no significant effect of cut size on abundance of salamanders ($t_{df=24}$, $P = 0.5331$, random plot SD = 0.5675). No trend of cut size on abundance was visually apparent in any primary period (Fig. 3).

Table 2
Comparison of models estimating abundance, recruitment, survival, and detection of red-backed salamanders using AIC.

Model	nPars[a]	AIC	ΔAIC	AICwt	cumWt
Simple abundance	18	2496.45	0	7.60E−01	0.760
Global	21	2498.75	2.3	2.40E−01	1.000
Simple	13	2524.44	27.99	6.40E−07	1.000
Simple abundance and detection	14	2527.91	31.46	1.10E−07	1.000
Simple survival and recruitment	19	*Inestimable*			
Null	4	*Inestimable*			

[a] nPars = number of parameters in the model.
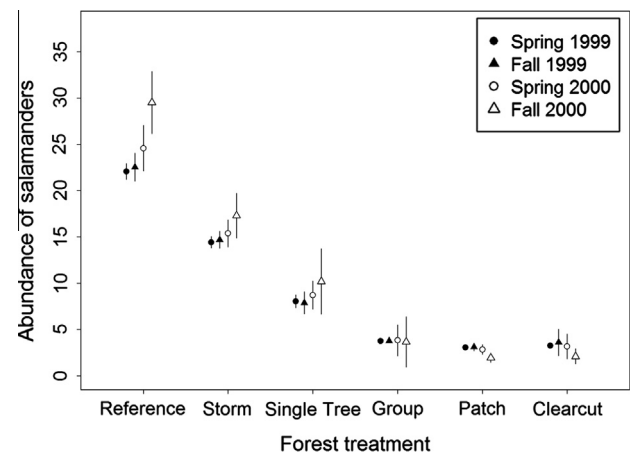
Fig. 1. Abundance of red-backed salamanders in each forest treatment in spring and fall of 1999 and 2000. Estimates and 95% confidence intervals were estimated using a Dail–Madsen Model (Dail and Madsen, 2011) to account for variable detection probability.

Table 3
Coefficient estimates from the best model (lowest AIC) and associated standard errors (SE), z-scores, and P-values (significant < 0.05).

	Estimate	SE	z	P(>|z|)
Abundance:				
(Intercept)	3.088	0.362	8.53	1.42E−17
Storm damage	−0.418	0.118	−3.54	4.04E−04
Single-tree selection	−0.969	0.2	−4.85	1.25E−06
Group cut	−1.763	0.518	−3.4	6.69E−04
Patch cut	−1.921	0.382	−5.03	4.97E−07
Clearcut	−1.809	0.442	−4.09	4.27E−05
Recruitment:				
(Intercept)	−6.028	0.734	−8.208	2.24E−16
Canopy cover	0.368	0.398	0.926	3.54E−01
Apparent survival:				
(Intercept)	6.00386	0.734	8.1767	2.92E−16
Canopy cover	−0.00821	0.42	−0.0196	9.84E−01
Detection:				
(Intercept)	−3.06728	0.3677	−8.3422	7.29E−17
Canopy	−0.00198	0.0827	−0.0239	9.81E−01
DOY	−2.85861	0.7038	−4.0617	4.87E−05
DOY^2	2.917	0.7156	4.0766	4.57E−05
Temperature	1.65217	0.3361	4.9153	8.87E−07
Temperature^2	−1.81178	0.3633	−4.9873	6.12E−07
Moisture	0.11507	0.0486	2.3663	1.80E−02
NCO	0.14179	0.0448	3.1666	1.54E−03

Modeling a logistic curve to the edge data, we found the interior of the harvest (lower asymptote) supported approximately 2 salamanders per 1.3 m^2 of cover boards and 1 m^2 of natural habitat, whereas the forest supported a mean of 30 salamanders (Fig. 4).

Salamanders reached 95% of forest carrying capacity 34 m (95% CI; 33.5 – 36.5) into the forest (Fig. 1). During this sampling period (fall 2000), we found that soil temperature significantly affected detection probability as indicated by the 95% credibility intervals not overlapping zero (Table 4). The effect of temperature on detection followed a quadratic function with peak detection at 13.1 °C, which is similar to but slightly lower than the predicted peak temperature of 14.3 °C across all years and seasons. During fall 2000, soil moisture and number of natural cover objects searched did not significantly affect detection probability (Table 4).

4. Discussion

We found that red-backed salamander abundance decreased as intensity of the forest disturbance increased. Natural ice-storm damage reduced salamander abundance by approximately 35% and single-tree selection harvesting reduced salamander abundance by 62%, whereas group cuts, patch cuts, and clearcuts reduced abundance by approximately 85% compared with reference forests. Interestingly, the effects of silviculture treatments on salamanders did not fall out along traditional even- and uneven-aged management practices. Group cuts had similar effects to even-aged practices of patch cuts and clearcuts, whereas single-tree selection harvests had significantly less effect on red-backed salamander abundance and their effects were between those of the even-aged practices and natural storm damage. Our estimates of declines in abundance are slightly greater than typically observed for salamanders following logging. Estimates from a meta-analysis suggest short term effects of partial cuts generally reduce salamander abundance by 51% and clearcuts initially (<5 years) reduce abundance by 62% (95% CI = 29–80%; Tilghman et al., 2012). Additionally, timber harvests in cool climates, like the northern hardwood forests of this study, tend to have less effect on abundance of salamanders than harvest in warmer areas. Red-backed salamanders have only had moderate declines following logging compared with other salamanders in other studies, despite their small body size (Tilghman et al., 2012). Sampling methods can affect the perceived declines, suggesting that variable detection probability could contribute to differences in the
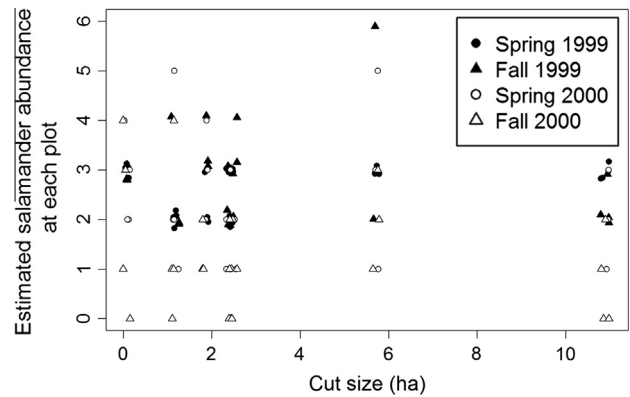

Fig. 3. Estimated abundance of red-backed salamanders at each plot in group cut, patch cut, and clearcut treatments as a function of cut size. Estimates at each plot are presented for each primary period (spring and fall in 1999 and 2000) derived from the Dail–Madsio model.

observed magnitude of population declines in previous studies (Royle and Dorazio, 2008; Tilghman et al., 2012). We used two sampling methods (ACOs and litter searches) and accounted for imperfect detection, whereas other studies may have underestimated declines in abundance due to lumping detection and population processes, which may explain why we found greater initial declines than previous studies.

Our estimates of abundance in the different treatments are robust to variation in detection probability. As expected, salamander detection increased with soil moisture and number of cover objects searched. Detection was also highest in the spring and fall, but decreased in the summer (end of spring sampling and beginning of autumn sampling), and peaked at intermediate temperatures with an optimum at 14.3.0 °C. Canopy cover varied within and across treatments and also across seasons, but did not significantly affect the probability of detection. It is possible that reduced activity associated with higher temperatures in the group cuts, patch cuts, and clearcuts is one of the mechanisms causing initial post-harvest declines. The mean (16.9 °C) and maximum (32.1 °C) temperatures
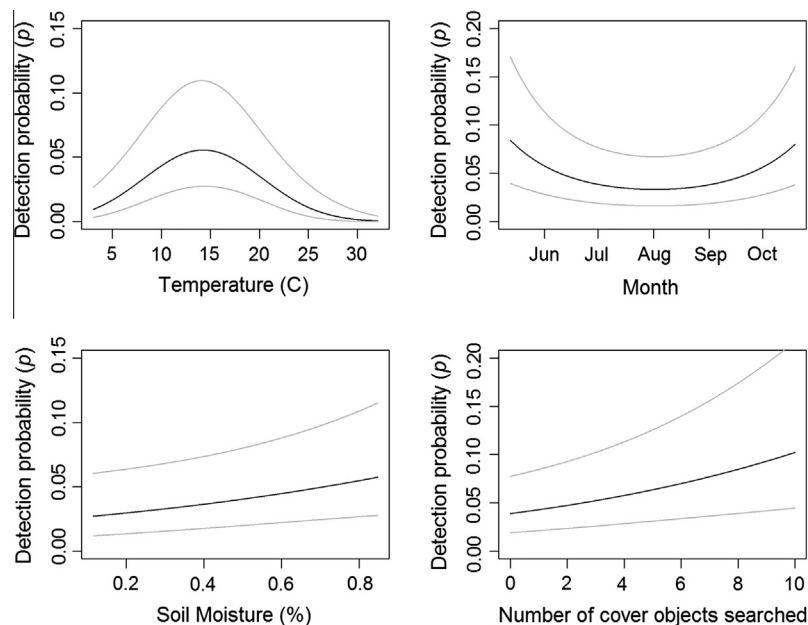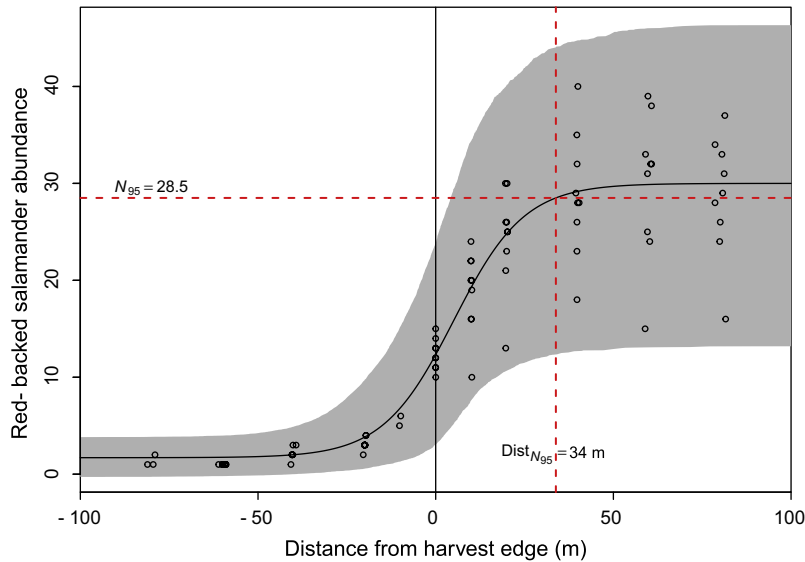

Fig. 2. Effects of soil temperature, day of the year (plot by month), soil moisture, and number of cover objects searched on red-backed salamander detection probability per individual per search. Black line = mean estimate, gray lines = 95% confidence bands.

Fig. 4. Predicted red-backed salamander abundance over a timber harvest-forest edge using a Bayesian analysis of a hierarchical N-mixture model with a logistic function of distance. The harvest-forest edge is centered at zero with negative distances into the cuts and positive distance into the forest. The solid black line is the mean prediction with the 95% credibility region shaded in grey. Open circles represent the mean estimates of abundance at each plot. The vertical, red dashed line is the mean distance where the population reaches 95% of forest carrying capacity, corresponding to horizontal dashed line. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 4
Bayesian parameter estimates and 95% credibility intervals for logistic N-mixture model of salamander abundance in detection during fall 2000 across a harvest-forest edge.

Parameter	Mean	SD	2.5%	97.5%
Abundance:				
A	28.300	1.060	25.688	29.767
B	9.974	3.620	4.153	18.132
C	1.700	1.060	0.233	4.312
D	5.064	5.101	−4.869	15.644
Random site SD	8.257	3.629	3.080	16.861
Detection:				
Intercept	−3.291	0.167	−3.608	−2.966
Temp	−0.146	0.125	−0.402	0.089
Temp2	−0.184	0.095	−0.377	−0.004
Moist	0.078	0.093	−0.099	0.264
NCO	0.141	0.090	−0.034	0.320

we observed in these cuts were below the critical thermal maximum for red-backed salamanders, but the thermal maximum is also a function of moisture and acclimation (Spotila, 1972). High temperature fluctuations in clearcuts and patch cuts may prevent metabolic acclimation to higher maximum temperatures (Bobka et al., 1981; Brown and Fitzpatrick, 1981; Homyack et al., 2010). Additionally, reduced activity in hotter sites following timber harvest may limit foraging time and contribute to population declines following timber harvest (Leclair et al., 2008; Taub, 1961). Overall, red-backed salamanders are expected to have approximately 33% higher metabolic rates in recent clearcut habitats (Homyack et al., 2011). Future research would benefit from recording more detailed soil temperature data in conjunction with salamander activity, metabolic rates, foraging success, and dietary assimilation in response to forest disturbance. This would help elucidate the mechanisms underlying forestry effects on amphibian population declines (Semlitsch et al., 2008, 2009).

Improved estimates of abundance by accounting for detection allowed us to identify reduced abundance following disturbances of natural and human origin. This is in contrast to previous studies, which were unable to detect differences between natural

disturbance and reference sites. Greenberg (2001) found no significant difference in amphibian abundance and species richness among canopy gaps created by wind, salvage logged gaps, and undisturbed forests. Strojny and Hunter (2010) also found no difference in adult red-backed salamander captures under canopy gaps of natural or timber harvest origin in a Maine, USA mixed coniferous-deciduous forest. Nevertheless, there were marginally-significant reductions in captures of immature red-backed salamanders in large gap harvests and natural gaps compared with reference forests and between large and small harvest gaps (Strojny and Hunter, 2010). Furthermore, they caught fewer metamorph frogs of three species (genus: *Lithobates*) and fewer spotted salamanders (*Ambystoma maculatum*) in large timber harvest gaps compared with small timber and natural gaps (Strojny and Hunter, 2010). Similarly, we found far fewer captures in the group cuts, patch cuts and clearcuts, compared to the reference sites. Interestingly, the harvest gaps in Maine (~500–2000 m²; Strojny and Hunter, 2010) were similar in size to the group cuts in our study (611 m² and 778 m²), and they did not detect declines in red-backed salamander abundance whereas we did. The reason for these differences is unclear but may be due to habitat or climate differences or because detection probability was not accounted for in the Maine study.

The reduction in salamanders in even-aged management stands is not surprising as our results contribute to a growing number of studies that show declines in salamander activity, abundance, and species diversity in response to even-aged forest harvests (e.g. deMaynadier and Hunter, 1995; Semlitsch et al., 2009; Tilghman et al., 2012). The effects of even-aged harvest on amphibians can persist for decades, particularly for terrestrial, woodland salamanders (e.g. Connette and Semlitsch, ; Crawford and Semlitsch, 2008b; Petranka, 1994). In general, partial canopy harvest, thinning, and understory removal have less effect on amphibians in the terrestrial habitat than even-aged harvests (e.g. Messere and Ducey, 1998; Pough et al., 1987; Semlitsch et al., 2009). Harpole and Haas (1999) and Knapp et al. (2003) found significant declines in salamander abundance after canopy removal. In contrast, a multi-region comparison of clearcutting, partial canopy thinning, and uncut reference forest treatments found universally negative

effects of clearcutting on terrestrial amphibian abundance, movement, and vital rates (Semlitsch et al., 2009). Less consistent are the effects of partial cutting, which can have negative, positive, or no effect depending on the species and response metric (Semlitsch et al., 2009). For example, previous studies found no effect of partial timber harvest on red-backed salamanders (Patrick et al., 2006) or western slimy salamanders (*P. albagula*) (Hocking et al., 2013). However, in a follow-up study to Patrick et al. (2006), there was a slight decrease in abundance of amphibians, including red-backed salamanders, over a six year period in the partial harvest sites (Popescu et al., 2012). Additionally, captures of the closely related western red-backed salamander (*P. vehiculum*) decreased following a thinning timber harvest, but no decrease was observed for other amphibian species (Grialou et al., 2000). In summary, stand thinning and single-tree selection harvests likely lead to moderate declines in woodland salamander (*Plethodon spp.*) abundance in the first few years after harvesting, but these effects are less severe than with larger timber harvests and may not be fully identified without accounting for variable detection probability. Some species may continue to decline in abundance beyond the first few years, before beginning to recover as the forest regenerates (Popescu et al., 2012) and the effect size may be dependent on summer temperatures (Tilghman et al., 2012).

Long-term effects of ice-storm damage and uneven-aged timber management on red-backed salamanders and other amphibian species remain to be tested. Additionally, we did not evaluate soil compaction or the effects of physical timber removal on salamanders or their habitat. Logging roads can have lasting detrimental effects on Plethodontid salamander populations (Semlitsch et al., 2007). Therefore, construction of logging roads necessary to remove timber from a large area under single-tree selection management could reduce salamander abundance over an extended timeframe. The effect of compaction associated with logging roads may have different effects depending on landscape physiognomy and soil type. In addition to compaction, repeated entry of areas for single-tree selection and group timber harvests is predicted to cause significantly greater soil loss than other harvesting practices (approximately 12,100 kg/ha more loss than clearcut over 100 yr rotation; Hood et al., 2002). Woodland salamanders are sensitive to leaf litter cover and soil moisture associated with organic soil horizons. Increased erosion over time may increase the long-term severity of single-tree selection harvests on red-backed and other woodland salamanders. While single-tree selection harvests may mimic the initial effects of ice-storm damage on canopy openings and salamander abundance, the increased soil compaction and erosion differentiate the long-term effects of single-tree selection and natural disturbance. In contrast, the effects of storm damage and single-tree selection may be shorter than in the other cuts because the canopy can rapidly grow to fill in the gaps. This will reduce solar radiation reaching the forest floor and thereby reduce the risk of desiccation for salamanders. There is some evidence that woodland salamanders, including red-backed salamanders, recover at similar, or slightly faster, rates following group harvesting than following clearcutting (Homyack and Haas, 2009). Further research is warranted in this area to understand how recovery times depend on harvest technique in combination with rotation times, climatic conditions, landscape physiognomy.

To determine the full extent of timber harvest impacts, it is important to consider the effects extending beyond the boundary of the harvest. We found that the detrimental effects of even-aged timber harvest on red-backed salamander abundance extends 34 m (33.5–36.5 m) into the surrounding forest. This estimate is similar to, but more precise and objective than, other studies of edge effects on red-backed salamanders which estimated edge effects of approximately 20–25 m (DeGraaf and Yamasaki, 2002;

deMaynadier and Hunter, 1998) and our results are the first to account for imperfect detection. These estimates represent the edge effects during the first two years after timber harvest. It is likely that the severity of the edge effect decreases more quickly over time than the other harvest effects as trees and shrubs at the edge of the forest grow rapidly to fill in gaps. As the forest edge becomes thicker, the solar radiation and wind penetrating the forest is reduced, thereby reducing the risk of desiccation and heat stress on salamanders in the forest edge. However, the time to recovery may depend on the quality and configuration of habitat in the landscape.

The potential for biased count data due to differences in detection associated with microhabitat alteration following logging has long been a point of contention (Ash, 1997; Petranka, 1994; Semlitsch et al., 2008). Our hierarchal parametric approach to estimating the edge effect has advantages over previously used nonparametric smoothing estimates such as Loess regression, smooth splines, or even generalized additive models (deMaynadier and Hunter, 1998; Schlaepfer and Gavin, 2001). We were able to account for variable detection probability, making our estimates robust to changes in behavior and detection associated with the environmental gradient. This parametric approach also allows us to explicitly calculate an edge effect. We defined the edge effect as the distance from the cut into the forest where the population reaches 95% of the carrying capacity, K (edge effect = 34 m). We could also easily calculate the distance when the population reaches 90% (26 m), 99% (50 m), or any other percent of carrying capacity. Additionally, using a parametric approach allows practitioners to calculate the area under the curve to determine the total effect of harvest on populations given the harvest size and shape (amount of edge and interior area). Managers can use this information to plan the spatial patterns for timber harvests. As with previous studies (Tilghman et al., 2012), we did not find an initial effect of harvest size on local salamander abundance; however, the logistic abundance distribution associated with cut-forest edge suggests that the combination of harvest size and shape should influence salamander abundance. Based on the logistic pattern of abundance across the edge gradient, cuts with high edge:interior ratios will have less detrimental effects within the harvested area but a larger area with reduced salamander abundance outside the harvested area than cuts with low edge:interior ratios. The balance of these contrasting effects depending on patch shape remain to be tested. Future studies on edge effects with other taxa would benefit from accounting for imperfect detection and using parametric models to explicitly define total harvest effects depending on the size and shape of harvested areas.

Reduced salamander abundance in the forest adjacent to the harvested area may be caused by reduced survival and vital rates due to abiotic habitat changes (Rittenhouse et al., 2009; Todd and Rothermel, 2006), but it may also be due to movement away from this edge habitat (Graeter et al., 2008; Semlitsch et al., 2008). In addition to avoid open habitat and edges, recent forest harvests and other open habitat can limit amphibian movement (Popescu and Hunter, 2011; Rothermel, 2004; Rothermel and Semlitsch, 2002), but this may depend on species, size-class, habitat, climate, and environmental conditions (Rittenhouse and Semlitsch, 2009; Rothermel and Semlitsch, 2002; Veysey et al., 2009). Limits and costs of movement, especially among small-bodied species and juveniles can lead to reduced connectivity of habitats (Popescu and Hunter, 2011; Rothermel, 2004). This may be of less importance for woodland salamanders with direct development, which do not make regular migrations from upland to aquatic breeding habitat, but it is important to consider the needs of multiple species when planning forest management. Even woodland salamanders without large migratory patterns need sufficiently connected habitat for dispersal to maintain genetic diversity and

supplement sink populations. Maintaining connectivity within harvested landscapes, as is done with smaller harvests, may allow for greater gene flow and genetic similarity among subpopulations (Gibbs, 1998). Although many forest-dependent amphibians avoid edge and open habitat, other species may be attracted to edges or have complex habitat requirements (Gascon, 1993; Hocking and Semlitsch, 2007; Urbina-Cardona et al., 2006). The needs of these species must be balanced with those of more strongly forest-dependent species, such as woodland salamanders for which timber harvest appears universally detrimental to varying degrees in the first post-disturbance decades.

5. Conclusions

Understanding the impacts of forest disturbance on red-backed salamanders is important if the guiding principal within a forest management plan is to maintain forest ecosystem integrity or minimize biological impacts. Current forest management plans usually consider biodiversity, the ecological function and integrity of the system, and the economic and social value of forest stands (Kessler et al., 1992). There is an increasing interest in replicating the impacts of natural disturbance regimes within forest management (Greenberg, 2001; Saunders and Arseneault, 2013; Simon et al., 2002). In our study, single-tree-selection harvests were most similar in salamander abundance to storm damage sites. This suggests that single-tree selection harvesting may reasonably mimic natural ice-storm disturbance for red-backed salamanders. Land managers wishing to replicate this type of natural disturbances may be able to use single-tree selection techniques, while not significantly reducing red-backed salamander populations in the short-term. Longer term effects may be of concern because of compaction and soil loss that can occur to a greater extent over time in uneven-aged management stands compared with natural disturbance or other forest management practices. Even-aged harvests may be used to create other wildlife habitat and to emulate stand-replacing natural disturbances (e.g. hurricanes, tornados, fire, etc.), but these practices will significantly reduce salamander abundance. Since ice-storms and individual tree deaths occur more frequently in northern hardwood forests than more severe, stand-replacing natural disturbances such as fire and intense wind storms (Lorimer, 1989), the impacts of single-tree selection may also more closely resemble the natural disturbance regime in the northeast (Lorimer, 1989). While more total area is affected by single-tree selection to obtain the same amount of timber, the initial ecological impacts of uneven-aged management on red-backed salamanders appear less severe in the northeast than even-aged management (Tilghman et al., 2012). Further research is needed to understand how the variety of forestry techniques used across the landscape, with standard rotation periods, effects amphibian populations over multidecadal time periods. Additionally, single-tree selection may result in higher proportions of less marketable tree species (e.g. Eastern Hemlock, American Beech) than larger harvest areas. Out study contributes to the understanding of short-term effects of ice-storm damage and various timber harvest practices on red-backed salamanders. Managers can use this information to balance other priorities including natural disturbance emulation, multi-species management, long-term effects on wildlife, erosion control, and the economics of various silvicultural practices.

Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2013.08.006.

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