



Research Article

Short-Term Response of *Dicamptodon tenebrosus* Larvae to Timber Management in Southwestern Oregon

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ABSTRACT In the Pacific Northwest, previous studies have found a negative effect of timber management on the abundance of stream amphibians, but results have been variable and region specific. These studies have generally used survey methods that did not account for differences in capture probability and focused on stands that were harvested under older management practices. We examined the influences of contemporary forest practices on larval *Dicamptodon tenebrosus* as part of the Hinkle Creek paired watershed study. We used a mark–recapture analysis to estimate *D. tenebrosus* density at 100 1-m sites spread throughout the basin and used extended linear models that accounted for correlation resulting from the repeated surveys at sites across years. Density was associated with substrate, but we found no evidence of an effect of harvest. While holding other factors constant, the model-averaged estimates indicated; 1) each 10% increase in small cobble or larger substrate increased median density of *D. tenebrosus* 1.05 times, 2) each 100-ha increase in the upstream area drained decreased median density of *D. tenebrosus* 0.96 times, and 3) increasing the fish density in the 40 m around a site by 0.01 increased median salamander density 1.01 times. Although this study took place in a single basin, it suggests that timber management in similar third-order basins of the southwestern Oregon Cascade foothills is unlikely to have short-term effects of *D. tenebrosus* larvae. © 2011 The Wildlife Society.

KEY WORDS *Dicamptodon tenebrosus*, forest management, mark–recapture, Oregon, Pacific giant salamander, stream amphibians.

Previous studies have identified stream amphibians as potentially sensitive bioindicators of forest condition (Welsh and Ollivier 1998) and may compose greater than 90% of the predatory biomass (Murphy and Hall 1981). Multiple studies have examined the effects of timber harvest on stream amphibians in the United States (see DeMaynadier and Hunter 1995 and Kroll 2009 for reviews) and many but not all have focused on clear-cut harvests. In the Pacific Northwest, most of the studies have been observational and correlative in nature, and the effects of forestry on stream amphibians vary between studies and regions (Murphy and Hall 1981, Corn and Bury 1989, Diller and Wallace 1996, Welsh and Lind 2002, Stoddard and Hayes 2005). For example, several studies occurring in coastal streams traversing harvested forests have found a negative relationship between stream amphibians and unconsolidated geologies (Diller and Wallace 1996, Wilkins and Peterson 2000), but a study in an unharvested preserve found stream amphibians to be relatively abundant in coastal streams on unconsolidated

geologies (Adams and Bury 2002). Several studies have found a negative relationship between presence or abundance of stream amphibians and previous timber harvest in the Pacific Northwest (Corn and Bury 1989, Stoddard and Hayes 2005), but stream amphibians are sometimes abundant in second-growth stands (Diller and Wallace 1996, 1999; Wilkins and Peterson 2000) and site level factors may mediate the effects of timber harvest (Bull and Carter 1996, Raphael et al. 2002, Welsh and Lind 2002).

Timber harvest is thought to affect stream amphibians through multiple routes that can generally be characterized as short- or long-term effects (Bury and Corn 1988). Many of the short-term effects of clear-cut timber harvest are thought to result from changes in energy input into the stream (Bury and Corn 1988). When the canopy is removed from a stream, there is a decrease in allochthonous inputs, but increased solar radiation commonly results in increased primary production and insect biomass (Kiffney et al. 2003, Vannote et al. 1980). These effects should decrease as the canopy reestablishes (Bury and Corn 1988). Forest management practices that reduce the size of clear-cut units, require rapid replanting, retain buffers along streams, and restrict the proximity of recent harvests to one another may help limit or localize the potential impacts of changes in energy input; though the effects of changes in management practices

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remain largely untested (Olson et al. 2007). The long-term effects of timber harvest are thought to be caused by habitat alteration, such as altered stream sedimentation, large wood input, allochthonous inputs, and microclimate and may take a relatively long time to return to preharvest conditions (Bury and Corn 1988).

Short-term impacts should be apparent soon after timber harvest, and could be sensitive to differences in management practices. For example, practices that retain a buffer along a stream may cause different short-term effects on stream temperature and riparian microclimate than those that allow harvest to the stream bank (reviewed in Olson et al. 2007). In Oregon, best management practices are least restrictive on private forest lands (Olson et al. 2007), maximizing the possibility of detecting impacts, if present. We examined the short-term effects of timber harvest on *Dicamptodon tenebrosus* in a second-growth, private forest, managed for industrial timber production as part of the Hinkle Creek paired watershed study. Our objectives were to 1) determine short-term influences of forest management on the density of *D. tenebrosus* larvae by comparing sites pre- and post-harvest; 2) determine if local habitat factors such as substrate composition, fish density, or overhead stream cover are correlated with the density of larval *D. tenebrosus*; and 3) determine how location within the basin, as determined by the amount of upstream area drained, affects *D. tenebrosus* larval densities and interacts with other covariates.

STUDY AREA

Hinkle Creek is a third order basin located on the western slope of the Cascade Mountains in Douglas County, Oregon, approximately 40 km northeast of the city of Roseburg (Fig. 1). The drainage is split between the North (873 ha) and South (1,060 ha) forks of Hinkle Creek. Elevations in the basin ranged from approximately 400 m to 1,250 m above sea level.

The Hinkle Creek basin is located in a transitional snow zone, with most precipitation occurring between fall and spring. Precipitation at 839 m elevation was 1,242 mm in water year (1 Oct through 30 Sep) 2004, 1,300 mm in water year 2005, 1,908 mm in water year 2006, and 1,470 mm in water year 2007. The Hinkle Creek basin is privately owned, almost entirely by Roseburg Forest Products, and is managed primarily for timber production. Vegetation in the Hinkle Creek basin was dominated by 60-year old, harvest-regenerated Douglas-fir (*Pseudotsuga menziesii*). Riparian vegetation was comprised mainly of red alder (*Alnus rubra*) with an understory of sword fern (*Polystichum munitum*) and huckleberry (*Vaccinium parvifolium*) along the larger streams, and mainly of Douglas-fir along headwater streams. In 2001, 5 years prior to study initialization, 119 ha of forest were clear-cut harvested in 3 units located in the south fork basin (approx. 11% of basin area; Fig. 1). Outside of these harvested units stand age was uniform across the basin at the start of the study.

In the fall 2005 through spring 2006, 161 ha (approx. 15% of basin area) were clear-cut harvested in 5 units in the South Fork catchment of Hinkle Creek; the North Fork was left

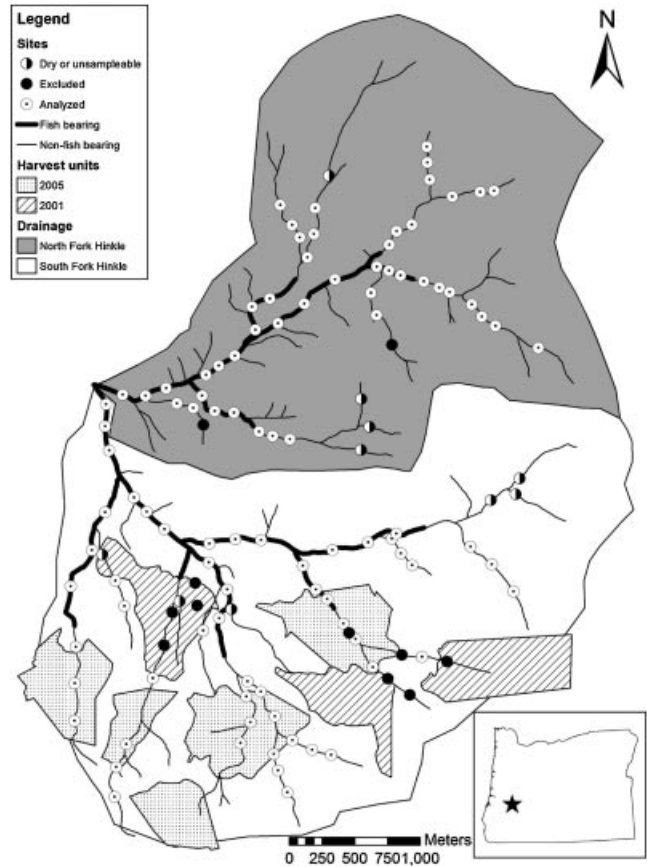


Figure 1. Map of sites surveyed for *Dicamptodon tenebrosus* in the Hinkle Creek Basin, Oregon in 2004–2007. White dots with dark centers represent sites that were able to sample in all 4 years and that were used in the analysis. Half black dots represent sites that were excluded from sampling because they were dry or unsamplable in the first year, and black dots represent sites that were excluded from the analysis because they were either in harvest units that occurred prior to study initiation or were unsamplable in all 4 years.

unharvested (Fig. 1). Harvests occurred along fishless, head-water streams that did not require buffer strips containing merchantable overstory conifers under Oregon Forest Practice Rules (Oregon Administrative Rules 2006). Site preparation, including the use of a broad spectrum herbicide, occurred in the fall of 2006, with harvested units being replanted with Douglas-fir in the winter of 2007. Contemporary forest management practices for clear-cuts on private forests limit harvest unit size to <48.6 ha, require rapid forest replanting after harvest, restrict the proximity of harvests to one another until site is successfully reforested (a maximum of 6 years), limit heavy machine usage and herbicide application in or near streams, and regulate road placement and construction (Oregon Administrative Rules 2006).

METHODS

Study Design

We sampled streams from late June through mid-September of 2004–2007. We defined segments as the reach of stream between 2 major tributaries and used a Geographic

Information System (GIS) and stream layers obtained from Roseburg Forest Products to determine segment length. We were interested in effects of cutthroat trout (*Oncorhynchus clarki*) presence on the density of *D. tenebrosus*, so we added a segment break at the upstream end of fish distributions. The fish were mostly cutthroat trout but also included a small number of steelhead trout (*Oncorhynchus mykiss*). We compiled fish data from single pass electroshocker sampling of streams carried out in late summer for a parallel study (late Aug–Sep; Bateman et al. 2005; Berger and Gresswell 2009; R. Gresswell and D. Bateman, U.S. Geological Survey, unpublished data). At 2 sites, crews were unable to sample for fish in 2006 and 2007 because these areas fell in or near harvest units and slash prevented access to the streams. Fish crews sampled these sites in 2008 and 2009, so we averaged these densities from these 2 years and used the average as the densities in 2006 and 2007.

Starting at the downstream end of a segment, we placed 3 sites at 0.25, 0.5, and 0.75 of the mapped length of the segment; this ensured a relatively even distribution of sites throughout the stream network. We did not visit first order segments that were <500 m in mapped length, because many of the mapped headwater segments were dry. If a site occurred in an area that was too steep to sample safely or too deep to sample effectively (>60 cm deep), we sampled the nearest position suitable for sampling.

We sampled 37 stream segments in the basin. Mean segment length was 811 m (range = 352–1,342 m). To limit potential confounding effects, we excluded data from sites within segments that were harvested prior to study initiation. We were interested in comparing pre- and post-harvest data, so we also excluded sites that we were unable to sample all 4 years. These sites were located in low-order streams that were dry in some sample years. With these exclusions, we used 100 sites in our analysis; 47 sites in the North Fork and 53 sites in the South Fork. There was no timber harvest in the North Fork basin, so all sites there were outside of harvest units and were considered reference sites. Because the basins were even-aged stands spread over a small area the vegetation and geologies of the control and treatment forks are similar. In the South Fork of Hinkle Creek, 11 sites were in units harvested between fall 2005 and spring 2006, and 8 were 500 m or less downstream of the harvested units.

We marked sites and recorded their positions with a Global Positioning System (GPS) unit. In the summer following timber harvest (2006), we visited sites in harvest units 1 week prior to sampling and moved or cut slash when necessary to allow net placement for sampling. Sampled sites spanned the wetted width of the stream and were 1-m long. We initially used a site length of 1 m to optimize site occupancy for an occupancy analysis (MacKenzie et al. 2003, 2006), but after exploratory analysis we elected to use density and recorded the length and width, at both ends of the site, to calculate the site area. We placed block nets (4-mm mesh) at each end of each site, and sampled stream amphibians within the area between the nets. When obstacles, such as boulders or downed wood, precluded sampling reaches 1 m in length, we sampled the smallest possible area >1 m in length that

allowed us to place nets. We used a light touch method (adapted from Bury and Corn 1991 and Adams and Bury 2002) to minimize habitat disturbance among sampling events. After visually inspecting the site and capturing any amphibians that were visible, we systematically surveyed the site starting at the downstream net and moving upstream. The surveyor overturned easily movable surface items so that any amphibians present would be washed into 4-mm mesh handheld nets or captured by hand. We left large or heavily embedded objects in place, but thoroughly searched their peripheries. We only searched the surface layer and returned all objects to where we found them. At the completion of a pass, we checked the downstream net for stream amphibians that were washed undetected past the surveyor.

We marked individuals with a unique toe clip that allowed us to identify individuals if they were recaptured that year. After sampling and data collection, we released animals back into the site. Ten minutes after we released captures, or 10 minutes after we completed the previous pass if there were no captures, a different member of the crew sampled the site. We repeated this process until 3 passes were completed. Due to the temporary nature of the toe clips, we did not mark animals captured on the third pass. Our use of block nets combined with the short time intervals ensured closure within a year. In streams >2 m in width, 2 surveyors sampled the site, splitting the width equally. We conducted work under a Oregon State University Institutional Animal Care and Use Committee permit (3047).

Prior to net placement and surveying we collected site habitat data. At each site, we recorded site length (m), site width (m), and visual estimates of the stream area composed of large wood (%), stream area composed of organic debris (%), and cover >1 m above stream (%). For stream area compositions and overhead cover we estimated the percentages as <5%, 5–10%, and subsequent 10% intervals; we used the mid-point of each category during analysis. At each site, we split the area along the downstream boundary into 0.3 m by 0.3 m squares. We categorized the 2 most prevalent substrates classes (dominant and subdominant) into 12 categories based on Cummins (1962). We calculated the average substrate size (henceforth average size dominant, average size subdominant) using the mid-point of the size range of each category or the following assigned sizes: bedrock = 0 mm, silt-clay = 0.1 mm, fine sand = 0.5 mm, mm, and boulder = 350 mm. We also calculated the proportion of squares where the dominant and subdominant particles were classified as small cobble or larger (henceforth proportion cobble or boulder). We did not include bedrock in the proportion of small cobble or larger, because it generally does not provide cover a stream amphibian can use. Using a GIS with data layers obtained from Roseburg Timber Products we determined the amount of upstream area drained at each site.

Analysis

Mark-recapture analysis.—We estimated abundance of *D. tenebrosus* for each site each year using a Huggins (1989) closed, single season mark-recapture model with

covariates in Program MARK (White and Burnham 1999). In each year, we captured 5 or fewer *D. tenebrosus* either undergoing metamorphosis or in the adult stage and these were included in the analysis. We used a single season approach because the marks we used were temporary and unlikely to be visible in subsequent years. Due to the low number of captures at each site, we grouped sites to estimate capture probabilities, but allowed capture probability to vary among sites by including covariates in the models.

We fit 11 a priori models in MARK hypothesized to explain capture and recapture probabilities. The terms included in these models were site area, mean dominant substrate size, mean subdominant substrate size, percentage large wood, percentage organic debris, and harvest status (Table 1A). We did not include a variable for fish, because our data represented the presence of fish around a site and not if fish were present at a site at the time of sampling. To test for effects of initial disturbance on capture probabilities, we fit the same set of models, but allowed the probabilities to vary over the 3 passes that occurred at each site. Due to the short time between passes, we did not expect the factors affecting the probability of initial capture to differ from those affecting the probability of recapture, so we used the same covariates, but allowed the probabilities to vary. Within each year, we ranked models with Akaike's Information Criterion for small sample sizes (AIC_c ; Burnham and Anderson 2002). Lower AIC_c values indicate a more parsimonious approximation of the data by a given model. We calculated the difference between a given model's AIC_c value and the model with the lowest AIC_c value in the set of models considered (ΔAIC_c ; Burnham and Anderson 2002). We evaluated the same set of models each year, and summed the ΔAIC_c value for each model across all 4 years. We used the model with the lowest summed ΔAIC_c to calculate the population estimates for each site across all years. Although the same model was used at all sites, the capture histories and covariates differed between sites and years resulting in unique population estimates.

In 2006, the mark–recapture models that allowed the initial capture and recapture probabilities to vary by pass failed to

converge so we only analyzed models where the probability of initial capture and recapture did not vary between passes. We did this to maintain consistency among the set of models considered between years and because there was not strong evidence that probability of capture and recapture varied by pass in other years. Given the short time between sampling occasions, it was highly unlikely that actual probabilities would vary greatly among passes. Also, in the years when models allowing the capture and recapture probabilities to vary by pass converged, these models always had higher AIC_c values than the same model where probabilities did not vary by pass.

Extended linear analysis.—We screened data for spatial autocorrelation using variograms created using methods developed by Ganio et al. (2005) to examine spatial patterns within a stream network. We used a GIS to calculate the distance between all sites following the stream network rather than using the Euclidian distances between sites. In 3 of the 4 years, there was no evidence of spatial autocorrelation between sites. In 2005, there was weak evidence of spatial autocorrelation. Based on these findings, we modeled for temporal, but not spatial, autocorrelation in further analyses. Modeling spatial autocorrelation in streams is complicated by potential differences in linkages in the upstream and downstream direction and the process is unclear for species where terrestrial migration is possible.

To assess variations in salamander densities, we fit extended linear models using restricted maximum likelihood via the *gls* function in S-Plus (TIBCO Software, Inc., Palo Alto, CA). The extended linear models we used are similar to mixed effects models in that they allow correlated and heteroscedastic errors, but they do not contain random effects like one would use for spatial autocorrelation (Pinheiro and Bates 2000). The response variable was the annual density estimates obtained from the mark–recapture analysis and was zero for sites where no captures occurred that year. We transformed population estimates into density estimates by dividing by the area of the site, and then natural log–transformed the data to stabilize the variance. We constructed the extended linear models to account for the

Table 1. Description and summary of variables used in A) mark–recapture analysis and B) extended linear analysis of *Dicamptodon tenebrosus* at Hinkle Creek, Oregon. We collected data from 2004 to 2007.

| Variable | Description | Mean | Range |
|----------------|---|-------|------------------------|
| A) | | | |
| Area | Area of site in m ² | 1.5 | 0.1–6.1 |
| InHU | Categorical variable describing if the site is in a harvest unit or not | | 0, 1 |
| Dom | Mean diameter of dominant substrate in cm | 1.3 | 0–3.5 |
| Subdom | Mean diameter of subdominant substrate in cm | 0.42 | 0–2.31 |
| LWD | % stream area composed of large wood | 0.061 | 0.025–0.65 |
| B) | | | |
| Upstr.area | Amount of upstream area drained by a site km ² | 2.02 | 0.084–10.8 |
| South | Categorical variable if site was located in the South fork basin | | 0, 1 |
| Year | Year data was collected | | 2004, 2005, 2006, 2007 |
| Dom | Mean diameter of dominant substrate in cm | 1.3 | 0–3.5 |
| Subdom | Mean diameter of subdominant substrate in cm | 0.42 | 0–2.31 |
| Cob.bo | Proportion of site with cobble or boulder size substrate | 0.4 | 0–1 |
| Cover.over.1 m | % of site shaded by cover >1 m above stream | 79.3 | 2.5–95 |
| Fish.den | Fish density (individuals/m ²) in a 40-m buffer around site | 0.034 | 0–0.53 |

correlation that resulted by sampling the same sites over multiple years. Due to the short time period over which we collected data and the multi-year larval stages of *D. tenebrosus*, we used a general correlation structure rather than testing less-complex correlation structures (Pinheiro and Bates 2000). We fit a series of a priori models that accounted for local habitat and then added variables that assessed basin and time-related effects. The local habitat variables consisted of the proportion of cobble or boulder, the average sizes of the dominant and subdominant substrates, and the amount of cover >1 m above a site (Table 1B). To these local habitat models, we added covariates for amount of upstream area drained, harvest unit status, sampling year, and all of the second and third order interactions (Table 1B). We did not include a variable for site elevation, because in this small basin elevation was correlated with stream size. We fit all models with and without the density of fish found in a 40 m buffer around sites (Table 1B). This resulted in 69 models for analysis (see Table S1, available online at www.onlinelibrary.com). We ranked models using AIC_c and calculated model weights (ω ; the probability a given model is the best model in the set of candidate models given the data; Burnham and Anderson 2002). We then model-averaged and calculated unconditional standard errors (Burnham and Anderson 2002).

Monte Carlo analysis.—We accounted for bias attributable to the probability of capture being less than 1 at sites with captures, but not at sites where no captures were made. We examined the potential impact of this inconsistency using a Monte Carlo analysis. From the mark–recapture analysis, we extracted regression formulas for the probability of initial capture. We used the covariate data from the sites with no captures to calculate the probability of capturing an individual (p) given presence. Using p , we calculated the probability of missing 1, 2, 3, or 4 individuals at sites with no captures. The probability of missing x individuals on all 3 surveys was $[(1-p)(1-p)(1-p)]^x$ whereas the probability of detection was $1 - [(1-p)(1-p)(1-p)]^x$. Our probability of capture at sites was fairly high ($p > 0.5$) so the probability of missing an individual in all 3 surveys in a given year was low (<0.2). The probability of failing to detect any individuals when 4 individuals were present was <0.001 .

Once we calculated probabilities that 1–4 individuals were present at sites with no captures, we compared these values to a random uniform variable. If the random uniform variable was less than the probability of 1 individual being present conditioned on no captures, we left the count of captures at the site as 0. If the random uniform variable was greater than the conditional probability of 1 individual and less than the conditional probability of 2 individuals being present, we changed the number of captures at that site from 0 to 1. This process continued for the conditional probabilities of 2, 3, and 4 individuals being present at each site with no capture. We then calculated densities from the updated counts of captures; natural log-transformed the densities, and performed the same extended linear analysis as above. We summarized the data using AIC_c and calculated ΔAIC_c and ω for each model. We repeated this process 1,000 times.

After summing weights for each model across all the iterations, we divided by 1,000 to return the weights to a 0 to 1 scale. We compared this ranking to the ranking from the initial data set to see how missing individuals might have affected our results. Because we allowed the potential for captures at all unoccupied sites, this analysis should be considered a worst-case scenario of our results to capture bias.

RESULTS

At the 100 sites sampled each year, we captured 153 *D. tenebrosus* at 56 sites in 2004, 159 individuals at 68 sites in 2005, 154 individuals at 53 sites in 2006, and 215 individuals at 70 sites in 2007. The number of captures varied at sites across years, but displayed no consistent pattern. In 2006 and 2007, the 11 sites within harvest units had 15 and 19 unique captures. Densities varied among years within stream forks, but temporal trends were similar between forks (Fig. 2).

The most parsimonious mark–recapture model varied among years (Table 2). The model with the lowest summed ΔAIC_c value across years included covariates for the amount of area surveyed and harvest status. We used this model to obtain population estimates and equations that allowed us to calculate the capture probabilities used in the Monte Carlo analysis. The second-ranked model included the variables in the top model plus mean dominant substrate size and a ΔAIC_c of 0.47, indicating strong support for this model. The ΔAIC_c for all other models was >10 .

Our extended linear models generally provided a poorer approximation of the data than the null model (Table 3). The highest ranked model had a Pearson’s correlation between the predicted and observed values of 0.22 suggesting an overall poor fit of the model. Only 4 models had lower AIC_c values than the null model, which had a ΔAIC_c of 2.4. Models that incorporated the effects of year, stream fork, dominant and subdominant substrate sizes, and overhead stream cover all performed poorly. The lack of support for models that included a temporal or stream fork effect, and their interactions, is not consistent with an effect of timber harvest on salamander density (Table 3). When we averaged the models, based on AIC_c weights, only 3 variables had had

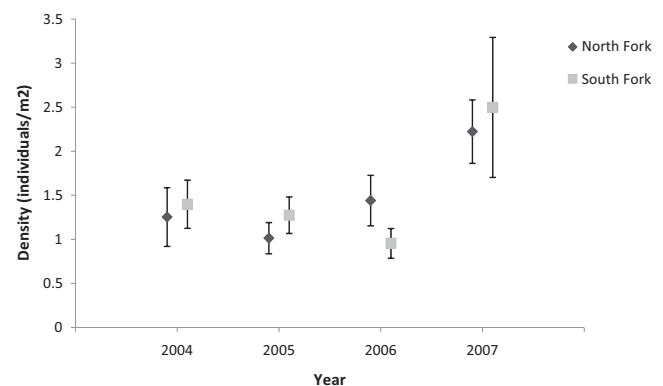


Figure 2. Mean *Dicamptodon tenebrosus* density (individuals/m²) per year by stream in the Hinkle Creek Basin, Oregon 2004–2007. Error bars equal ± 1 SE. All treatments took place in the South Fork between 2005 and 2006.

Table 2. Top 5 mark–recapture models for *Dicamptodon tenebrosus* at Hinkle Creek, Oregon 2004–2007. In HU represents sites in locations that were harvested between fall 2005 and spring 2006, dom represents the average size of the dominant substrate, subdom represents the average size of the subdominant substrate, area represents the area of the site, and LWD represent the portion of the site composed of downed large wood. We named the models by the covariates of capture (p) and recapture (c) probability. We ranked candidate models using change in Akaike’s Information Criterion (ΔAIC_c).

| Model | AIC _c | ΔAIC_c |
|--|------------------|----------------|
| 2004 | | |
| $p(\text{In HU} + \text{area}), c(\text{In HU} + \text{area})$ | 569.33 | 0.00 |
| $p(\text{In HU} + \text{dom} + \text{area}), c(\text{In HU} + \text{dom} + \text{area})$ | 572.56 | 3.23 |
| $p(\text{In HU} + \text{subdom} + \text{area}), c(\text{In HU} + \text{subdom} + \text{area})$ | 573.46 | 4.13 |
| $p(\text{In HU} + \text{dom} + \text{subdom} + \text{area}), c(\text{In HU} + \text{dom} + \text{subdom} + \text{area})$ | 576.22 | 6.89 |
| $p(\cdot), c(\cdot)$ | 581.33 | 12.00 |
| 2005 | | |
| $p(\text{In HU}), c(\text{In HU})$ | 606.75 | 0.00 |
| $p(\text{area}), c(\text{area})$ | 608.08 | 1.33 |
| $p(\text{In HU} + \text{dom} + \text{subdom}), c(\text{In HU} + \text{dom} + \text{subdom})$ | 609.44 | 2.69 |
| $p(\text{In HU} + \text{dom} + \text{area}), c(\text{In HU} + \text{dom} + \text{area})$ | 609.50 | 2.75 |
| $p(\text{In HU} + \text{area}), c(\text{In HU} + \text{area})$ | 610.63 | 3.88 |
| 2006 | | |
| $p(\text{In HU} + \text{area}), c(\text{In HU} + \text{area})$ | 579.38 | 0.00 |
| $p(\text{In HU} + \text{dom} + \text{area}), c(\text{In HU} + \text{dom} + \text{area})$ | 580.29 | 0.91 |
| $p(\text{In HU} + \text{subdom} + \text{area}), c(\text{In HU} + \text{subdom} + \text{area})$ | 581.19 | 1.81 |
| $p(\text{In HU} + \text{dom} + \text{subdom}), c(\text{In HU} + \text{dom} + \text{subdom})$ | 581.37 | 2.00 |
| $p(\text{In HU} + \text{dom} + \text{subdom} + \text{area}), c(\text{In HU} + \text{dom} + \text{subdom} + \text{area})$ | 582.11 | 2.74 |
| 2007 | | |
| $p(\text{In HU} + \text{dom} + \text{subdom} + \text{LWD}), c(\text{In HU} + \text{dom} + \text{subdom} + \text{LWD})$ | 743.07 | 0.00 |
| $p(\text{In HU}), c(\text{In HU})$ | 751.38 | 8.31 |
| $p(\text{In HU} + \text{dom} + \text{area}), c(\text{In HU} + \text{dom} + \text{area})$ | 751.82 | 8.74 |
| $p(\text{In HU} + \text{dom} + \text{subdom}), c(\text{In HU} + \text{dom} + \text{subdom})$ | 753.48 | 10.41 |
| $p(\text{In HU} + \text{area}), c(\text{In HU} + \text{area})$ | 754.36 | 11.28 |

weights greater than 0.06. These variables were the proportion of small cobble or larger sized substrate, the amount of upstream area drained, and fish density with weights of 0.89, 0.56, and 0.52, respectively. The model based on the weighted average estimated that a 0.1 increase in the proportion of small cobble or larger size substrate increased median density of *D. tenebrosus* 1.05 times (95% CI: 0.96–1.13). Likewise, each 100 ha increase in the area drained decreased median density of *D. tenebrosus* 0.96 times (95% CI: 0.72–1.28). This suggests that if the substrate were constant along the stream, density would be highest in the smallest streams. In reality, the proportion of cobble or larger substrate decreased as streams got smaller (Fig. 3), and we observed peak densities in intermediate sized stream, although 95% CIs overlapped. The averaged model predicted a negative effect of increased upstream area drained, and when combined with the local substrate variable, peak mean densities were reached in streams that were in an intermediate position in the stream network. Density provides an incomplete picture of the

distribution of *D. tenebrosus*; in smaller headwater streams there were a greater proportion of sites with no captures, but this is not represented by the density figures (Fig. 4). There was an effect of fish density in the averaged model but the effect was small (a factor of 1.01 times for every 0.01 individuals/m² increase in fish density) and the 95% CI included 1 (0.99–1.02).

Our Monte Carlo analysis suggests that the false negatives in our data (failure to capture any salamanders at some sites where they were present) had little influence on our results (Table 4). The top model was different, although still among the top models in the original analysis, and 3 of the top 4 models were the top 3 models from the original analysis. Models with lower weights tended to vary in composition from the original analysis, but generally contained the same group of covariates. The highest ranked model in the Monte Carlo analysis was similar to the highest ranked model from the extended linear model analysis, but included a term for year. This model was ranked seventh in the original analysis

Table 3. Extended linear models of *Dicamptodon tenebrosus* density in the Hinkle Creek Basin, Oregon 2004–2007. Cobble represents the proportion of dominant and subdominant substrate classified as small cobble or larger, upstr.area represent the amount of area drained by a site, year represent the year data were collected, fish.den is the density of fish in the 20 m up and downstream of the site, and south was scored as a 1 if the site was in the South Fork Basin and a 0 if it was in the North Fork Basin. We ranked candidate models using change in Akaike’s Information Criterion (ΔAIC_c) and Akaike weight (ω).

| Formula | No. parameters | AIC _c | ΔAIC_c | ω |
|---|----------------|------------------|----------------|----------|
| $\ln(\text{density}) \sim \text{upstr.area} + \text{cobble} + \text{fish.den}$ | 4 | 1002.43 | 0.00 | 0.311 |
| $\ln(\text{density}) \sim \text{cobble}$ | 2 | 1003.39 | 0.95 | 0.193 |
| $\ln(\text{density}) \sim \text{cobble} + \text{fish.den}$ | 3 | 1003.94 | 1.50 | 0.147 |
| $\ln(\text{density}) \sim \text{upstr.area} + \text{cobble}$ | 3 | 1003.98 | 1.54 | 0.144 |
| $\ln(\text{density}) \sim 1$ | 1 | 1004.83 | 2.40 | 0.09 |
| $\ln(\text{density}) \sim \text{south} + \text{upstr.area} + \text{cobble} + \text{fish.den}$ | 5 | 1006.88 | 4.45 | 0.034 |
| $\ln(\text{density}) \sim \text{year} + \text{upstr.area} + \text{cobble} + \text{fish.den}$ | 7 | 1007.50 | 5.06 | 0.025 |
| $\ln(\text{density}) \sim \text{south} + \text{upstr.area} + \text{cobble}$ | 4 | 1008.31 | 5.87 | 0.017 |

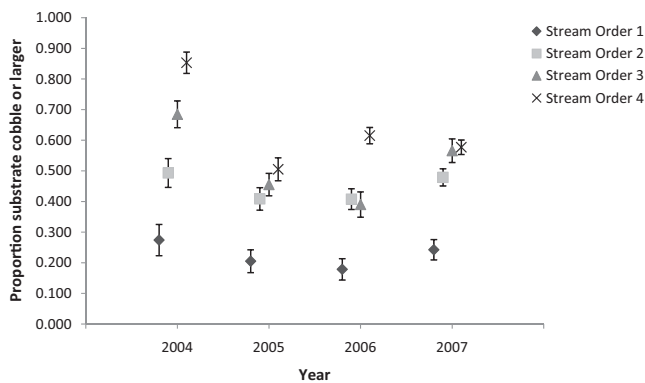


Figure 3. Mean proportion of substrate, by stream order, that had small cobble or larger as the dominant or subdominant substrate in the Hinkle Creek Basin, Oregon, 2004–2007. Error bars equal ± 1 SE.

and had a weight of 0.025. Overall, the variables favored in the Monte Carlo analysis were similar to those favored in the initial analysis where we did not account for the possibility of missing individuals at sites.

There was little difference in substrate characteristics between forks or sites in or near harvest units and those in the untreated sections of streams within years (see Table S2, available online at www.onlinelibrary.com). Within a year, sites in or near harvest units tended to have lower proportions of larger substrate and slightly smaller dominant substrate sizes compared to other sites. Between years mean substrate size and composition varied; this variation occurred at all sites suggesting similar changes across all sites or variation in how different crews classified substrate. Fish sampling crews found little change in estimated proportions of large substrate in the fish bearing streams between years (R. Gresswell and D. Bateman, unpublished data), suggesting the changes we saw were mostly due to crew differences; particularly in 2004.

DISCUSSION

We found no support for the hypothesis that clear-cut timber harvest affected density of *D. tenebrosus* in the first 2 years following harvest in this watershed. Such an effect would

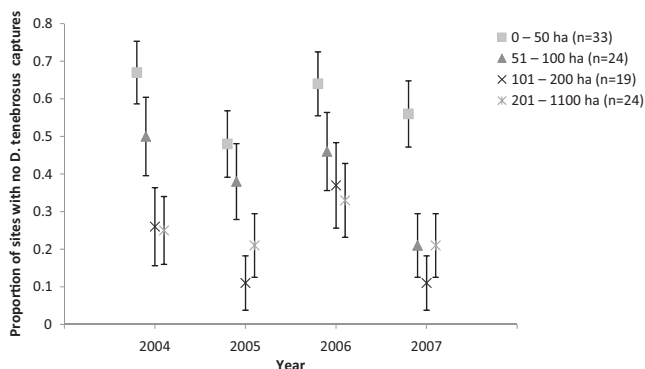


Figure 4. Proportion of sites with 0 *Dicamptodon tenebrosus* captures by upstream area drained (ha) in each year in the Hinkle Creek Basin, Oregon, 2004–2007. Error bars equal ± 1 SE.

Table 4. Summary of the Monte Carlo analysis on data from Hinkle Creek, Oregon 2004–2007 where sites with 0 *Dicamptodon tenebrosus* captures were assigned 0–4 captures based on capture probabilities. We converted captures to densities for analysis. We fit extended linear models to the data and the process was repeated 1,000 times. We scaled Akaike weights (ω) from 0 to 1. Cobble represents the proportion of dominant and subdominant substrate classified as small cobble or larger, upstr.area represent the amount of area drained by a site, year represent the year data were collected, fish.den is the density of fish in the 20 m up and downstream of the site, south was scored as a 1 if the site was in the South Fork Basin and a 0 if it was in the North Fork Basin, and dom and subdom represent the mean size of the dominant and subdominant substrate at a site.

| Formula | ω |
|--|----------|
| $\ln.density \sim year + upstr.area + cobble + fish.den$ | 0.309 |
| $\ln.density \sim cobble + fish.den$ | 0.169 |
| $\ln.density \sim upstr.area + cobble + fish.den$ | 0.128 |
| $\ln.density \sim cobble$ | 0.108 |
| $\ln.density \sim south + year + upstr.area + cobble + fish.den$ | 0.059 |
| $\ln.density \sim year + upstr.area + cobble$ | 0.057 |
| $\ln.density \sim upstr.area + cobble$ | 0.031 |
| $\ln.density \sim 1$ | 0.029 |
| $\ln.density \sim south + upstr.area + cobble + fish.den$ | 0.024 |
| $\ln.density \sim year + upstr.area + dom + subdom + fish.den$ | 0.014 |
| $\ln.density \sim south + year + upstr.area + cobble$ | 0.012 |
| $\ln.density \sim upstr.area + dom + subdom + fish.den$ | 0.010 |

have been manifested as an interaction including stream basin, the location of the site relative to harvest units, or year and other variables. Model-averaging concluded that there was an effect of substrate size and position in the basin, consistent with other studies (Murphy and Hall 1981, Corn and Bury 1989, Hunter 1998, Welsh and Ollivier 1998, Stoddard and Hayes 2005), but not effects of year or basin. In the Monte Carlo analysis, a year effect was present in the top model, but there were no interactions with year. This suggests that years differed from one another, but not in response to harvest. Our finding of a relationship with substrate is consistent with previous work that found a positive association with larger substrate (Welsh and Ollivier 1998) or negative associations with fine substrate (Murphy and Hall 1981, Hawkins et al. 1983, Corn and Bury 1989, Stoddard and Hayes 2005). We found little relationship between other habitat variables and *D. tenebrosus* density, reflecting the wide habitat tolerances of this species (Nussbaum et al. 1983, Bury and Corn 1988) and the limited variation in habitat throughout Hinkle Creek basin.

Our data are consistent with Welsh and Lind's (2002) finding that *D. tenebrosus* abundance is best described by in-stream habitat features and is less effectively modeled by larger scale variables. After accounting for local habitat, we examined basin level effects by looking for effects of stream fork and position in the stream network (upstream area drained). A site's position within the stream network was confounded with the local substrate, where the lowest order streams tended to have low proportions of cobble or larger substrate. So the effect of position seemed to reflect a shift in substrate composition rather than an effect of position itself.

In contrast with previous work, we did not observe changes in stream substrate after timber management (Jackson et al. 2001). Jackson et al. (2001) found that the amount of fine

sediment increased in streams traversing stands harvested without buffers due to increased sediment trapping by the accumulated slash. In our study, timber harvest shifted the position of overhead cover from >1 m over the stream to <1 m, but it did not appear to alter the substrate composition. This difference might reflect a difference in regions and stream power. As the accumulated slash breaks down, it is possible that change in stream substrate may occur. It is possible that we did not observe temporal changes in substrate due to crew variation. We observed sizeable variation in our substrate data between years, but these changes were not seen in data collected during fish sampling, suggesting this is possible.

In a laboratory study (Leuthold 2010), we found a negative effect of fish presence on larval *D. tenebrosus* movement and visibility. In the field data, we would expect this result to be seen as a negative effect of fish presence on *D. tenebrosus* density. A reduction in movement should decrease a salamander's ability to seek food and find shelter, leading to increased predation and a decrease in resource acquisition. We found a positive effect of fish density on *D. tenebrosus* density, but the effect size was small and the 95% confidence interval included 1. In our laboratory experiments, fish were held in the same mesocosms as the larvae or in head tanks where all the water flowed across the fish into the mesocosm. In the field study, the fish data were the density from the surrounding 40 m of stream and were not collected at the same time as our surveys for salamanders. In the wild, fish tend to inhabit pools whereas *D. tenebrosus* are often found in shallower waters inappropriate for fish. The weak positive correlation with fish presence in the field data does not eliminate the possibility of a negative effect of fish presence, but we did not find evidence of a negative effect.

The finding of no support for an effect of timber harvest and limited habitat correlates was not entirely unexpected given the generalist nature of *D. tenebrosus*, the changes that have occurred in timber management practices over the last 40 years, and the relatively short duration of the study. Though, a study at the northern end of the salamanders range, found a negative effect of timber management on *D. tenebrosus* genetic diversity and heterozygosity in clear-cut stands suggesting the clear-cuts were associated with population declines at those sites (Curtis and Taylor 2003). Changes in management practices that limit harvest unit size, require replanting, and limit activity near streams are likely to limit the impacts of management of stream systems. Previous stream amphibian studies typically report stand age but generally do not mention the details of forest management such as stand extent, or proximity of adjacent harvest (Corn and Bury 1989; Diller and Wallace 1996, 1999; Wilkins and Peterson 2000). Assuming the harvest met legal requirements when completed, they would have generally been larger cuts, used heavier machinery, and used techniques such as broadcast burning and natural regeneration that are not typically used in modern forestry. Unfortunately, the lack of details makes it difficult to compare results, but unless the effects of modern timber management on *D. tenebrosus* are strong, short-term effects are

likely difficult to separate from natural variation in the study area.

Our study had a unique opportunity to collect both pre- and post-harvest data in a manner that allowed us to estimate capture probabilities, but was limited to 4 years. In previous studies, the detected effects of timber harvest or stand age on Pacific Northwest stream amphibians have typically occurred over decades (Corn and Bury 1989, Ashton et al. 2006), although short-term effects have been detected (Murphy and Hall 1981, Murphy et al. 1981). In those studies, it was not possible to sample sites pre- and post-harvest so the authors substituted space for time and compared sites in stands of different ages. Leaving aside concerns about differences in stands, the effects seen might change as the stands grow. Over a longer time span the stands are more likely to experience severe weather or other stochastic events, and these chance events might cause harvested areas to respond differently than areas not harvested.

Although our data provides a pre- versus post-harvest comparison, limiting concerns about site or stand differences, it leaves questions about longer term impacts unanswered. For example, there was a large amount of slash left over the streams that buffered them from the expected increases in maximum stream temperature, although the daily variation in stream temperature increased due to the minimum temperature decreasing (Kibbler 2007). The slash may have also had other effects, such as slowing flows during peak discharges and limiting any increases in energy input into the streams. Over time, the slash will decay and this may alter any effects of the timber harvests on the stream systems. Murphy et al. (1981) found that short term increases in primary productivity resulting from canopy removal, could either override or mask the potential impacts of increased stream sedimentation on a variety of aquatic organism, including *D. tenebrosus*. Although this may have occurred, the heavy slash more likely limited primary productivity, and it is possible that a longer term effect might be seen as the slash breaks down.

MANAGEMENT IMPLICATIONS

Our study adds to evidence that larval *D. tenebrosus* are not sensitive to modern timber management immediately following treatment. Modern forest practices such as limiting harvest unit size, limiting the proximity of harvest units to one another until replanted trees have reached the free to grow stage, and improved road construction standards may be sufficient to limit short term effects of timber harvest on larval *D. tenebrosus*, but long-term effects and effects at other locations still need more study. Although we did not examine the effect of slash density over streams, the presence of heavy slash in the harvest units suggests a hypothesis that short-term effects of timber harvest on *D. tenebrosus* might be mitigated by heavy slash retention.

This study took place in a third order basin that is approximately 19 km² in area located in the Cascade mountain foothills of southwest Oregon. In a strict sense these results only apply to the Hinkle Creek basin, but they suggest

timber harvest along non-fish bearing streams in basins approximately 20 km² in area in the same region are unlikely to impact *D. tenebrosus* larvae over the short-term. Our data do not address the effects that timber harvest may have on terrestrial adults or longer term effects that might result from changes in dispersal.

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