### AN ABSTRACT OF THE DISSSERTATION OF

<u>Niels Leuthold</u> for the degree of <u>Doctor of Philosophy</u> in <u>Forest Science</u> presented on <u>March 2, 2010.</u>

Title: <u>Short-term Relationship of Timber Management and Pacific Giant Salamander</u> <u>Populations, and the Response of Larval Stream Amphibian to Predators Under</u> <u>Differing Sediment Levels.</u>

Abstract approved:

John P. Hayes

Michael J. Adams

In the Pacific Northwest, multiple studies have found negative effects of timber harvest on stream amphibians, but the results have been highly variable and region-specific. In this collection of studies, I examined the short term effect of timber harvest using a field study, and used lab work to examine a potential mechanism for timber harvest effect.

Over the last 30 years forest management practices have changed substantially, yet little work examines how modern forest management relates to the abundance or density of stream amphibians. I examined the influences of contemporary forest practices on Pacific giant salamanders as part of the Hinkle Creek paired watershed study. I used a mark-recapture analysis to estimate Pacific giant salamander density at 100 1-m segments spread throughout the basin and then used extended linear models that accounted for correlation resulting from the repeated surveys at sites across years. Density was positively associated with substrate, negatively associate with upstream area drained, and had a weak positive association with fish density, but I found no evidence of an effect of harvest. A Monte Carlo analysis suggested that our results were not sensitive to missing captures at sites with no captures.

Pacific Northwest stream amphibians are often negatively associated with sedimentation, but the mechanism underlying this relationship is not clear. One hypothesized mechanism is that the reduced interstitial space that results from sedimentation increases susceptibility of amphibians to predation. I used laboratory mesocosms to test this hypothesis and examine the response of larval Pacific giant salamanders and tailed frogs to cutthroat trout and adult Pacific giant salamander presence under three different levels of sediment. I found amphibian larvae were more visible as sediment level increased and some evidence that larvae were less visible in the presence of fish. Movement decreased in the presence of cutthroat trout, though for tailed frog larvae this effect was marginally significant (p = 0.066). Larvae did not respond to presence of adult Pacific giant salamanders. These patterns are consistent with the hypothesis that sediment affects larval stream amphibians by increasing vulnerability to predation. While both species of larvae actively sought cover in

response to fish, I found little evidence that this behavior mitigates the effects of increasing sediment.

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### Short-term Relationship of Timber Management and Pacific Giant Salamander Populations, and the Response of Larval Stream Amphibian to Predators Under Differing Sediment Levels

by Niels Leuthold

### A DISSERTATION

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in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Presented March 2, 2010 Commencement June 2011 Doctor of Philosophy dissertation of <u>Niels Leuthold</u> presented on <u>March 2, 2010</u>.

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Niels Leuthold, Author

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Without the help of my field crews the Hinkle Creek portion of the study could not have been completed. Collin Grant, Jamie Conrad, Jonathan Baldwin, Benjamin Stout, Shelly Banks, Cory Earle, Neal Jander, and Travis Lewis worked long days, often under less than ideal conditions, in the back country to sample all of the sites at Hinkle Creek.

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### 1. INTRODUCTION

In the Pacific Northwest, the effects of timber harvest on stream amphibian populations have been examined in multiple studies that tend to be observational and correlative in nature, and results have varied by study and region (reviewed in DeMaynadier and Hunter 1995 and Kroll 2009). Several studies have found a negative correlation between timber harvest and stream amphibian abundance in the Pacific Northwest (Corn and Bury 1989, Murphy and Hall 1981, Stoddard and Hayes 2005, Welsh and Lind 1996, Welsh and Lind 2002), but stream amphibians can be abundant in second-growth stands (Diller and Wallace 1999, Diller and Wallace 1996, Wilkins and Peterson 2000) and site-level factors may mediate the effects of timber harvest (Welsh and Lind 2002, Raphael et al. 2002, Bull and Carter 1996).

Timber harvest is thought to affect stream amphibians through multiple routes that can generally be characterized as short-term or long-term effects (Bury and Corn 1988). Many of the short-term effects of clear-cut timber harvest appear to result from changes in energy input into the stream (Bury and Corn 1988). Increased solar input from canopy removal can raise stream temperature (Johnson and Jones 2000, Holtby 1988) and alter stream productivity (Kiffney et al. 2003). Allochthonous inputs from the stream canopy are the primary energy input to headwater streams (Vannote et al. 1980). When the canopy is removed from a stream allochthonous inputs decrease, but increased solar radiation commonly increases primary production and insect biomass (Kiffney et al. 2003, Vannote et al. 1980). These effects should decrease rapidly as the canopy reestablishes, and changes in forest management practices for clear-cut harvests that reduce the size of harvested units, require rapid replanting, retain buffers on streams, and restrict the proximity of recent harvests to one another help limit or localize the potential impacts of changes in energy input.

Long-term effects of timber harvest on stream amphibians generally result from habitat alteration, and habitat can take a relatively long time to return to preharvest condition (Bury and Corn 1988). Factors such as stream sedimentation, altered input of large wood, reduced or altered allochthonous inputs, and microclimatic changes are thought to lead to long-term effects. Some of these factors can have immediate impacts, such as sedimentation (Jackson et al. 2001), but the effects may last considerably longer (Corn and Bury 1989). Habitat alterations that produce long-term effects after timber harvest can be initiated quickly, but are sometimes mediated by other short term effects. For example, Pacific giant salamanders (*Dicamptodon tenebrosus*) sometimes increase in abundance immediately after logging, but then decline after the canopy closes (Murphy and Hall 1981, Hawkins et al. 1983). These initial increases in abundance are likely caused by increases in stream productivity, due to the increased solar radiation, but once the canopy closes population declines were seen in sites with high levels of stream embeddedness (Murphy and Hall 1981, Hawkins et al. 1983).

Stream sedimentation has been hypothesized to affect stream amphibians after timber management, though the mechanisms remain largely speculative. Several studies have found correlations between the abundance or presence of stream amphibian and substrate condition (Murphy and Hall 1981, Hawkins et al. 1983, Corn and Bury 1989, Welsh and Lind 1996, Welsh and Ollivier 1998, Diller and Wallace 1996, Diller and Wallace 1999, Dupuis and Steventon 1999, Adams and Bury 2002, Stoddard and Hayes 2005,). Sedimentation is thought to affect stream amphibians by decreasing interstitial spaces used for refuge (Bury and Corn 1988, Corn and Bury 1989). Reduction in these spaces may reduces suitable habitat and force individuals in to more open environments where they would be exposed to higher predation risks or risk from high flow events.

To better understand the short-term impacts of timber management on stream amphibians we used field work collected as part of the Hinkle Creek paired watershed study, and laboratory work examining how predators and sediment levels interact to affect stream amphibian populations. In the Hinkle Creek basin we collected 2 years of pre-harvest and 2 years of post-harvest data on populations of Pacific giant salamanders to examine 1) how timber management influenced Pacific giant salamander density; 2) habitat factors associated with salamander density; and 3) how position within the stream network related to salamander density. We used laboratory mesocosms to examine if 1) tailed frog (*Ascaphus truei*) and Pacific giant salamander larvae increased use of refuges in the presence of a predator; 2) larvae modified activity in the presence of a predator; 3) variation in larval response to a predator when cues are direct or indirect; and 4) how larval response to predator presence is affected by sediment levels.

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# 2. SHORT-TERM RESPONSE OF PACIFIC GIANT SALAMANDERS TO TIMBER HARVEST IN SOUTHWESTERN OREGON

### 2.1 Abstract

In the Pacific Northwest, amphibians inhabit forested streams ranging from barely a trickle up to larger rivers and inhabit streams as well as the surrounding forest. Many 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 do not account for differences in capture probability, which may be important if habitat condition alter capture probabilities. In addition, most of these studies have been retrospective comparisons of stands of different ages, and focus on stands that were harvested under older management practices. Over the last 30 years forest management practices have changed substantially, yet little work examines how modern forest management relates to the abundance or density of stream amphibians. We examined the influences of contemporary forest practices on Pacific giant salamanders as part of the Hinkle Creek paired watershed study. We used a mark-recapture analysis to estimate Pacific giant salamander Density at 100 1-m segments spread throughout the basin and then 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, our top model

indicated; 1) each 10 percent increase in proportion of the substrate that was small cobble or larger increased median density of Pacific giant salamanders 1.06 times, 2) each 100 hectare increase in the area drained decreased median density of Pacific giant salamander 0.93 times, and 3) increasing the fish density in the 40 m around a site by 0.01 increased median salamander density 1.02 times. Our mark-recapture analysis accounted for sampling inefficiencies at sites with captures, but sites with no captures retained densities of 0 in our extended linear analysis. At least some of these sites were likely occupied and we failed to capture individuals that were present. A Monte Carlo analysis suggested that our results were not sensitive to missing captures at some sites. We did not find evidence of a short term effect of timber harvest on the density of Pacific giant salamanders at Hinkle Creek.

### 2.2 Introduction

Stream amphibians have been identified as potentially sensitive bioindicators of forest condition (Welsh and Ollivier 1997) and, in smaller sections of stream free of anadromous fish, may compose greater than 90% of the predatory biomass (Murphy and Hall 1991). 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). In the Pacific Northwest, most of these 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, Hawkins et al. 1983, Corn and Bury 1989, Diller and Wallace 1996, Welsh and Lind 1996, Diller and Wallace 1999, 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 unconsolidated geologies (Wilkins and Peterson 2000, Diller and Wallace 1996), but a study in an unharvested preserve found stream amphibians to be relatively abundant in coastal streams on unconsolidated geologies (Adams and Bury 2002). The results of these studies appear to be at odds but could be explained by an interaction between surface geology and harvest history which neither study tested. Historical land use within a region may alter detectable habitat relationships. Several studies have found a negative relationship between presence or abundance of stream amphibians and history of 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 1999, Diller and Wallace 1996, Wilkins and Peterson 2000) and site level factors may mediate the effects of timber harvest (Welsh and Lind 2002, Raphael et al. 2002, Bull and Carter 1996).

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). Increased solar input from canopy removal can raise stream temperature (Johnson and Jones 2000, Holtby 1988) and alter stream productivity (Kiffney et al. 2003). Allochthonous input from the stream canopy is the primary energy input to headwater streams (Vannote et al. 1980). 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 rapidly as the canopy reestablishes, and changes in forest management practices for clear-cut harvests that reduce the size of units, require rapid replanting, retain buffers along streams, and restrict the proximity of recent harvests to one another help limit or localize the potential impacts of changes in energy input. The long-term effects of timber harvest are thought to be caused by habitat alteration, such as altered stream sedimentation, large wood input, allochthonus 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). Since many short-term impacts are thought to be due to changes in energy input and the Hinkle Creek basin is a relatively small, even aged stand where energy inputs across sites should be relatively even, it provides an excellent opportunity to study these short-term impacts. All of the harvest took place on fishless sections of stream, and under Oregon Forest Practice Rules stream buffers were not required (although after sampling, anadromous fish were found extended into the base

of one harvest units). The harvest up to stream bank should have maximized changes in energy input and therefore the effects on stream amphibians. This study also took place in a relatively small basin, which allowed us to look for effects of position within the network at a fine scale. Most studies have focused on stream reaches or stands (e.g. Corn and Bury 1989, Wilkins and Peterson 2000), and relatively few studies have sampled multiple locations within a stream or looked at stream amphibian's relationship to position within the stream network (but see Hunter 1998, Stoddard and Hayes 2005).

We examined the short term effects of timber harvest on Pacific giant salamanders in a second-growth forest as part of the Hinkle Creek paired watershed study. The Hinkle Creek study is an examination of the biologic and hydrologic responses to modern timber management (Berger 2007, Kibler 2007, Zegre 2008). By collecting preharvest and postharvest data we were able to look for changes at sites within the basin over time. Our objectives were to 1) determine short-term influences of forest management on the density of Pacific giant salamanders; 2) determine local habitat factors correlated with the density of Pacific giant salamanders; and 3) determine how location within the basin affects Pacific giant salamander densities and interacts with other covariates.

#### 2.3 Study Area

Hinkle Creek is a 3<sup>rd</sup> order basin located on the western slope of the Cascade Mountains in Douglas County, Oregon, approximately 40 km northeast of the city of Roseburg (Figure 2.1). The drainage is split between the North (873 hectares) and South (1060 hectares) forks of Hinkle Creek. Elevations in the basin ranged from approximately 400 m to 1,400 m above sea level.

The Hinkle Creek basin is located in a transitional snow zone, with most precipitation occurring between fall and spring. Precipitation during the study recorded by a micro-meteorological station in the basin at 839m elevation was 1242 mm in water year (October 1 through September 30) 2004, 1300 mm in water year 2005, 1908 mm in water year 2006, and 1470 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 alders (*Alnus rubra*) with an understory of sword ferns (*Polystichum munitum*) and huckleberries (*Vaccinium parvifolium*) along the larger streams, and mainly of Douglas-fir along headwater streams. In 2001, 5 years prior to study initialization, 119 hectares of forest were clearcut harvested in three units located in the south fork basin (ca. 11% of basin area; Figure 1).

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

North Fork was left unharvested (Figure 1). Harvests occurred along fishless, headwater streams that did not require buffer strips that contain merchantable overstory conifers under Oregon Forest Practice Rules (Oregon Administrative Code 2006). Timber was largely transported along existing roads, but in 2005 3.2 km of new roads were constructed and 6.4 km of roads were reconstructed to facilitate timber transport. 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. Timber harvest, site preparation, and replanting were typical of methods used on private lands in the region. Contemporary forest management practices for clearcuts differ from those prior to the 1970s in that they limit harvest unit size and proximity to one another, require rapid forest replanting, limit activities in or near streams, and place restrictions on road placement and construction. Contemporary forest management takes place in harvest regenerated stands thus construction of few roads is required, the stands contain smaller more uniform sized trees, and timber harvest uses smaller, lighter machinery.

2.4 Methods

### 2.4.1 Study Design

We sampled streams from late June through mid-September of 2004-2007. We defined segments as the reach of stream between two major tributaries and used a geographic information system (GIS) to determine segment length. As we were interested in effects of cutthroat trout presence had on the density of Pacific giant

salamanders, we added a segment break where the fish crews determined fish distribution ended as part of a parallel study. We placed 3 sites on each segment of stream at ¼, ½, and ¾ of the mapped length of the segment, to ensure a 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 identified 92 stream segments for sampling in the basin. After we dropped headwater segments less than 500 m in length, segments that were dry upon visitation and segments that were too short to allow placement of 3 independent sites, there were 37 segments suitable for sampling. To limit potential confounding effects, we excluded data from sites that were harvested prior to study initiation. We were interested in comparing pre- and post-harvest data, so we also removed data from sites that we were unable to sample all four years. These sites were located in low order streams that were dry in some sample years. With these exclusions, we had 100 sites in our analysis; 47 in the North Fork and 53 in the South Fork. There was no timber harvest in the North fork basin, so all sites here were outside of harvest units and are considered reference sites. 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. The remaining 34 sites were outside of harvested units and were either upstream of harvest units, >500m below harvest units, or in streams that did not flow through harvest units.

We marked sites and recorded their positions with a global positioning system (GPS) unit so that the same locations could be sampled in subsequent years. In the summer following timber harvest (2006), we visited sites in harvest units one week prior to sampling and moved or cut slash when necessary to allow net placement for sampling. We moved as little slash as possible and only moved slash that interfered with net placement. Inadequate GPS precision combined with slash made it impossible to locate 2 sites, so we remeasured the stream and placed the sites at the stream distances determined from the GIS system.

Sampled reaches spanned the wetted width of the stream and were 1 m long. We initially used a site size of 1 m to optimize site occupancy for an occupancy analysis (MacKenzie et al. 2003, MacKenzie et al 2006), but after exploratory analysis we elected to use density instead of site occupancy. 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. At each site, we recorded the length and the width, at both ends of the site, and later calculated 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. 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 the place 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 placed each capture in a plastic bag, and recorded the species and stage. 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 any animals captured back into the site. Ten minutes after captures were released, or 10 minutes after the previous pass was completed if there were no captures, a different member of the crew sampled the site. We repeated this process until 3 passes were completed. Recaptures were identified by markings and animals caught for the first time on pass 2 or 3 were measured and weighed. Due to the temporary nature of the marks, we did not mark animals captured on the third pass in a year. Our use of block nets ensured closure within a year. In streams > 2 m in width, 2 surveyors sampled the site, splitting the width equally.

Prior to net placement and surveying we collected habitat data about sites. At each site we recorded site length (m), site width (m), 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 in the analysis. At each site, we split the area along the downstream boundary into 0.3 m by 0.3 m squares. We categorized the two most prevalent substrates classes (dominant and subdominant) into 12 categories (based on Cummings (1962) modification of the Wentworth Scale (Wentworth 1922)): silt/clay, fine sand (< 1 mm), coarse sand (1-2mm), gravel 1 (3-4 mm), gravel 2 (5-8 mm), gravel 3 (9-16 mm), gravel 4 (17-32 mm), pebble (33-64 mm), small cobble (65-160 mm), large cobble (161-256 mm), boulder (>256 mm), and bedrock. After converting the categories to the mid-point of the size range of the category, we calculated the average substrate size (henceforth average size dominant, average size subdominant). For these calculations we assigned sizes to categories that did not have easily definable midpoints: bedrock 0 mm, silt/clay 0.1 mm, fine sand 0.5 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 combined with observation from the field we determined the amount of upstream area drained at each site and stream order.

### 2.4.2 Analysis

We estimated abundance of Pacific giant salamanders for each site each year using a closed, single season mark-recapture model in Program MARK (White and Burnham 1999). Tailed frogs (*Ascaphus truei*) and torrent salamanders (*Rhyacotriton*  sp.) were present in the basin, but too rare for analysis (7 and 3 or fewer captures per year respectively). We used a single season approach because the marks we used were temporary and unlikely to be visible in subsequent years. We analyzed capture data using Huggins (1989) closed capture models with covariates. Due to the low number of captures at each site, we grouped all sites to allow all of the data to be used to estimate capture probabilities, but generated individual estimates of population sizes at each site. Also, we used site-level covariates in model building that allowed capture probability to vary among sites.

We fit 11 *a priori* models in MARK that we hypothesized to explain capture and recapture probabilities. The terms included in these models were the site area, mean dominant substrate size, mean subdominant substrate size, percentage large wood, percentage organic debris, and if a site was in a location that was harvested in 2005-2006. 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 look for effects of initial disturbance on capture probability, we fit the same models, but allowed the effects to vary over the 3 passes that occurred each year 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 in both parts of each model, but allowed the probabilities to vary. We fit the same models to the data from each year, and within each year we ranked models with Akaike's information criterion for small sample sizes (AIC<sub>c</sub>; Burnham and Anderson 2002). Lower AIC<sub>c</sub> values indicate a more parsimonious approximation of the data by a given model. After ranking with  $AIC_c$ , 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 ( $\Delta AIC_c$ ; Burnham and Anderson 2002). We evaluated the same set of models each year, and summed the  $\Delta AIC_c$  value for each model across all 4 years. The model with the lowest summed  $\Delta AIC_c$  was used to calculate the population estimates for each site across all years. While 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. In our models, we allowed probabilities of capture and recapture to differ, but we constrained probabilities so initial capture probability were constant among passes 1, 2, and 3 and recapture probability were constant for passes 2 and 3. Given the short time between sampling occasions it is highly unlikely that actual probabilities would vary greatly among passes. In the years when models allowing the capture and recapture probabilities to vary by pass converged, these models always had higher AIC<sub>c</sub> values than the same model where probabilities did not vary by pass often had higher AIC<sub>c</sub> than models using different variables that did

not allow these probabilities to vary by pass. For a related species, the Idaho giant salamander (*Dicamptodon aterrimus*), Sepulveda and Lowe (2009) did not find evidence that the first survey affected the probability of detection in the second survey.

To assess hypotheses about factors underlying variation in salamander densities, we fit extended linear models using restricted maximum likelihood via the gls function in S-Plus. 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 (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. To stabilize the variance of the density estimates we natural log transformed the data prior to analysis. The extended linear model accounted for the 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 Pacific giant salamanders, 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 > 1m above a site. To these local habitat models, we added covariates for the location of the site in the stream network

(amount of upstream area drained), if the site was located in or near a harvest unit, the year of sampling, and all of the 2<sup>nd</sup> and 3<sup>rd</sup> order interactions. We fit all models with and without the density of fish found in a 40 m buffer around sites (range 0 to 0.53 individuals/m<sup>2</sup>, mean = 0.034 per individuals/m<sup>2</sup>). The fish were mostly cutthroat trout (Onchorhyncus clarki), but also included a small number of steelhead trout (Oncorhynchus mykiss). The fish data were compiled from single pass electroshocker sampling of streams carried out in late summer for a parallel study (late August-September; Gresswell and Bateman unpublished data, Berger and Greswell 2009, Bateman et al. 2005). At two 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. The fish crews were able to sample these sites in 2008 and 2009, so we averaged these densities from these two years and used the average as the densities in 2006 and 2007. This resulted in a total of 69 models for analysis (Appendix 1). We ranked models using AIC<sub>c</sub>, and then calculated model weights ( $\omega$  - the probability a given model is the best model in the set of candidate models given the data; Burnham and Anderson 2002).

We accounted for bias attributable to the probability of capture being less than 1 at sites with captures, but could not make adjustments at sites where no captures were made. We examined the potential impact of this problem on our conclusion 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 survey is  $((1-p)(1-p)(1-p))^x$  while the probability of detection is  $1 - ((1-p)(1-p)(1-p))^x$ . 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 to 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 a site with no capture. For each site with no captures we drew a new number from the random uniform distribution, and the process was repeated. 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<sub>c</sub> and calculated  $\Delta AIC_c$ and  $\omega$  for each model. We repeated this process 1000 times. After summing weights for each model across all the iterations, we divided by 1000 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.

# 2.5 Results

At the 100 sites sampled each year, we captured 153 Pacific giant salamanders 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. Densities varied among years within stream forks, but temporal trends were similar between forks (Figure 2.2). 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 (Figures 2.3, 2.4, 2.5, Appendix 2). 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 (Figure 2.6; unpublished data Gresswell and Bateman, see Berger and Gresswell 2009 for methods), suggesting the changes we saw were mostly due to crew differences; particularly in 2004.

The most parsimonious mark-recapture model varied among years (Table 2.1). The model with the lowest summed  $\Delta AIC_c$  value across years included the covariates of the amount of area surveyed and if the site was in a location that was harvested in fall 2005 – spring 2006. 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  $\Delta$ AICc for the model with those variables plus mean dominant substrate size was 0.47, indicating strong support for this model. The  $\Delta$ AICc for the next most highly ranked model was >10.

The extended linear models we fit generally provided a poorer approximation of the data than did the null model (Table 2.2). Only four models had lower AIC<sub>c</sub> values than the null model which had a  $\Delta AIC_c$  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 2.2). In the four best models, there was a positive effect of a large substrate, a slightly negative effect of area drained, and a slightly positive effect of fish density on Pacific giant salamander density. The highest ranked model estimated that a 0.1 increase in the proportion of small cobble or larger size substrate increased median density of Pacific giant salamanders 1.06 times (95% CI: 1.02 - 1.10). Likewise, each 100 hectare increase in the area drained decreased median density of Pacific giant salamander 0.93 times (95 % CI 0.89 - 0.97). This model suggests that if the substrate were constant along the stream that density would be highest in the smallest streams. In reality the proportion of cobble or larger substrate decreased as stream got smaller (Figure 2.7), and peak densities occurred in

intermediate sized stream. The best model had a negative effect of increased upstream area drained, and when combined with the local substrate variable the effect was that 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 Pacific giant salamanders; in smaller headwater streams there were a greater proportion of sites with no captures, but this is not represented by the density figures (Figure 2.8). An effect of fish density was also included in the top model but the effect was small (a factor of 1.02 times for every 0.01 individuals/m<sup>2</sup> increase in fish density) and the 95% CI included 1 (0.99 – 1.03).

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 2.3). 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 low 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 it added a term for year. This model was ranked 7<sup>th</sup> in the original analysis were similar to those favored in the initial analysis where we did not account for the possibility of missing individuals at sites.

#### 2.6 Discussion

We found no support for the hypothesis that timber harvest affected density of Pacific giant salamanders in the first 2 years following harvest in this watershed. Such an effect would have been manifested as an interaction including stream basin, the location of the site relative to harvest units, or year and other variables. Our most strongly supported models included an effect of substrate size and position in the basin, consistent with other studies (Hawkins et al. 1983, Corn and Bury 1989, Murphy and Hall 1991, Hunter 1998, Welsh and Olivier 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 (Hawkins et al. 1983, Corn and Bury 1989, Murphy and Hall 1991, Stoddard and Hayes 2005). We found little relationship between other habitat variables and Pacific giant salamander 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 Pacific giant salamander 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 (Figures 2.3, 2.4, 2.5; 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 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 collect during fish sampling suggesting this is possible.

In a lab study (Chapter 3), we found a negative effect of fish presence on larval Pacific giant salamander movement and visibility. In the field data, we would expect this result to be seen as a negative effect of fish presence of Pacific giant salamander 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 aquisition. We found a positive effect of fish density on Pacific giant salamander density, but the effect size was small and the 95% confidence interval included 1. These results contradict our finding of a negative effect of fish on the visibility and movement of Pacific giant salamanders in lab experiments (Chapter 3). 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 while Pacific giant salamanders are often found in shallower waters inappropriate for fish. The weak positive correlation with fish presence in the field data does not eliminates 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 Pacific giant salamanders, the changes that have occurred in timber management practices over the last 40 years, and the relatively short time span of the study. 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. Unless the effects of timber management on Pacific giant salamanders are strong, short-term effects are likely difficult to separate from natural variation. Our study had a unique opportunity to collect both preharvest and postharvest 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 time spans of 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. Such events are not altered by timber harvest activities, but these activities might cause harvested areas to respond differently than areas not harvested.

While 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 Pacific giant salamanders. While 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.

Timber management practices have changed over the years, which make it difficult to study long term effects. Studies that have examined long term effects have examined sites where timber harvesting used older techniques that do not meet current best management practices. On Oregon private forests, management practices limit harvest unit size, require rapid replanting, limit adjacent harvest until harvested stands reach a certain height, and exclude some operations like skidding trees along stream channels or using heavy machinery near streams (Olson et al. 2007, Anonymous 2003). These changes reduce some of the potential impacts of timber harvests, such as increased sedimentation, on stream amphibians. While the forest at Hinkle Creek is a harvest regenerated stand that carries some legacy of the previous management, we were not able to detect effects of the recent timber harvest on densities of Pacific giant salamanders. Alterations from previous management may play an important role in shaping the potential impacts of current harvest practices. For example, an older timber harvest may have caused some sites in marginal habitats to become unsuitable for individuals. Even if these sites later become suitable, the organisms may not recolonize them prior to the next timber harvest. If this occurred no effect would be detected for the second timber harvest, but the older harvest would shape the potential impacts of future harvests.

## 2.7 Management Implications

Our study adds to evidence that Pacific giant salamanders are not sensitive to modern timber management. 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 Pacific giant salamanders, but long term effects and effects at other locations still need more study. While we did not examine the effect of dense slash over streams, the presence of heavy slash in the harvest units suggests a hypothesis that short-term effects of timber harvest on Pacific giant salamanders might be mitigated by heavy slash retention.

This study took place in a 3<sup>rd</sup> order basin that is approximately 19 km<sup>2</sup> 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 km<sup>2</sup> in area in the same region are unlikely to impact Pacific giant salamanders. While we caution against extrapolating these results to larger basins or basins outside of the Cascade mountain foothills near Roseburg, OR smaller basins in this area are likely to show similar results.

# TABLES

Table 2.1 Top 5 mark-recapture models for Pacific giant salamanders at Hinkle Creek, OR 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. The models are named by the covariates of capture (p) and recapture (c) probability.

Model	AICc	$\Delta$ AICc
2004		
p(In HU + area), c(In HU + area)	569.33	0.0
p(In HU + dom + area), c(In HU + dom + area).	572.56	3.2
p(In HU + subdom + area), c(In HU + subdom + area)	573.46	4.1
p(In HU + dom + subdom + area), c(In HU + dom + subdom + area)	576.22	6.8
p(.)c(.)	581.33	12.0
2005		
p(In HU), c(In HU)	606.75	0.0
p(area), c(area)	608.08	1.3
p(In HU + dom + subdom), c(In HU + dom + subdom)	609.44	2.6
p(In HU + dom + area), c(In HU + dom + area)	609.50	2.7
p(In HU + area), c(In HU + area)	610.63	3.8
2006		
p(In HU + area), c(In HU + area)	579.38	0.0
p(In HU + dom + area), c(In HU + dom + area)	580.29	0.9
p(In HU + subdom + area), c(In HU + subdom + area)	581.19	1.8
p(In HU + dom + subdom), c(In HU + dom + subdom)	581.37	2.0
p(In HU + dom + subdom + area), c(In HU + dom + subdom + area)	582.11	2.7
2007		
p(In HU + dom + subdom + LWD), c(In HU + dom + subdom + LWD)	743.07	0.0
p(In HU), c(In HU)	751.38	8.3
p(In HU + dom + area), c(In HU + dom + area)	751.82	8.7
p(In HU + dom + subdom), c(In HU + dom + subdom)	753.48	10.4
p(In HU + area), c(In HU + area)	754.36	11.2

Table 2.2 Extended linear models of Pacific giant salamander density in the Hinkle Creek Basin, OR 2004-2007. "cobble" represents the proportion of dominant and subdominant substrate classified as small cobble or larger, "upst.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 meters up and downstream of the site, and "south" was scored as a 1 is the site was in the South Fork Basin and a 0 if it was in the North Fork Basin.

	#			
Formula	param.	AIC <sub>c</sub>	$\Delta AIC_c$	$\omega$ weight
ln.density ~ upstr.area + cobble + fish.den	4	1002.43	0.00	0.311
ln.density ~ cobble	2	1003.39	0.95	0.193
ln.density ~ cobble + fish.den	3	1003.94	1.50	0.147
ln.density ~ upstr.area + cobble	3	1003.98	1.54	0.144
ln.density ~ 1	1	1004.83	2.40	0.09
ln.density ~ south + upstr.area + cobble + fish.den	5	1006.88	4.45	0.034
ln.density ~ year + upstr.area + cobble + fish.den	7	1007.50	5.06	0.025
ln.density ~ south + upstr.area + cobble	4	1008.31	5.87	0.017

Table 2.3 Summary of the Monte Carlo analysis on data from Hinkle Creek, OR 2004-2007 where sites with 0 Pacific giant salamander captures where assigned 0-4 captures based on capture probabilities. Captures were converted to densities for analysis. Extended linear models were fit to the data and the process was repeated 1000 times. Weights are scaled from 0 to 1. "cobble" represents the proportion of dominant and subdominant substrate classified as small cobble or larger, "upst.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 meters 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 ~ year + upstr.area + cobble + fish.den	0.309
ln.density ~ cobble + fish.den	0.169
ln.density ~ upstr.area + cobble + fish.den	0.128
ln.density ~ cobble	0.108
ln.density ~ south + year + upstr.area + cobble + fish.den	0.059
ln.density ~ year + upstr.area + cobble	0.057
ln.density ~ upstr.area + cobble	0.031
ln.density ~ 1	0.029
$ln.density \sim south + upstr.area + cobble + fish.den$	0.024
ln.density ~ year + upstr.area + dom + subdom + fish.den	0.014
$ln.density \sim south + year + upstr.area + cobble$	0.012
ln.density ~ upstr.area + dom + subdom + fish.den	0.010

# FIGURES

Figure 2.1 Map of sites surveyed in the Hinkle Creek Basin, OR in 2004-2007. Green dots represent sites that were we were able to sample in all 4 years and that were used in the analysis. Red dots represent sites that were excluded from sampling because they were dry or unsampleable 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 unsampleable in all 4 years.

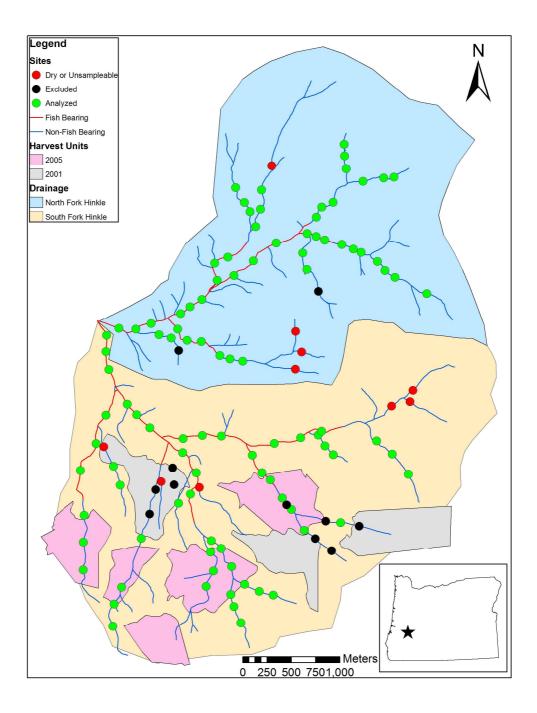


Figure 2.2 Mean Pacific giant salamander density per year by stream in the Hinkle Creek Basin, OR 2004-2007. Error bars equal  $\pm 1$  SE. All treatments took place in the South Fork between 2005 and 2006.

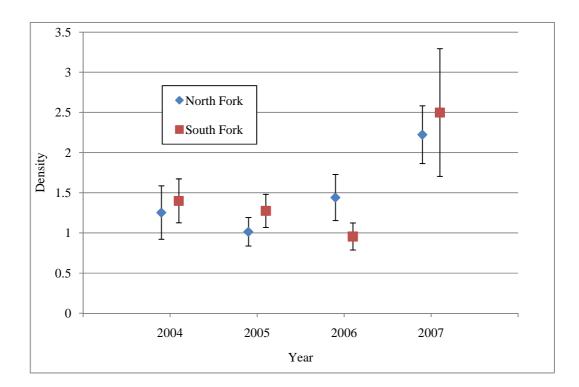


Figure 2.3 Mean proportion of substrate that was cobble or larger by site type in the Hinkle Creek Basin, OR 2004-2007. Error bars equal  $\pm 1$  SE. In the South Fork, data are presented for all sites, sites that were not near a harvest unit (Reference), sites < 500m downstream of a unit harvested fall 2005 – spring 2006 (Near HU), and sites in areas harvested in fall 2005 through spring 2006 (In HU). Data are presented for all sites combined in the North Fork.

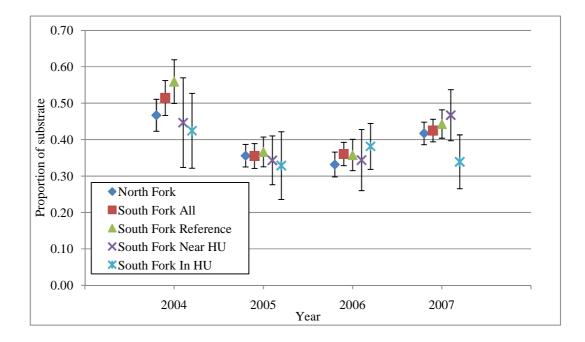


Figure 2.4 Mean dominant substrate size in each year by site type in the Hinkle Creek Basin, OR 2004-2007. Error bars equal  $\pm 1$  SE. In the South Fork, data are presented for all sites, sites that were not near a harvest unit (Reference), sites < 500m downstream of a unit harvested fall 2005 – spring 2006 (Near HU), and sites in areas harvested in fall 2005 through spring 2006 (In HU). Data are presented for all sites combined in the North Fork.

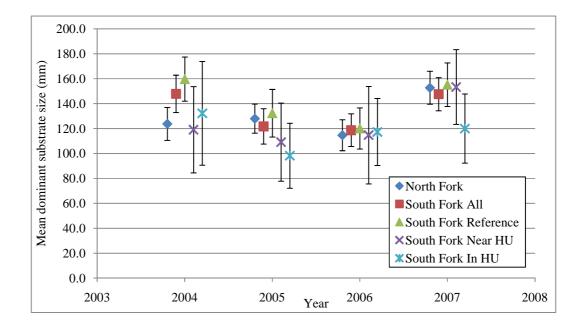


Figure 2.5 Mean sudominant substrate size in each year by site type in the Hinkle Creek Basin, OR 2004-2007. Error bars equal  $\pm 1$  SE. In the South Fork, data are presented for all sites, sites that were not near a harvest unit (Reference), sites < 500m downstream of a unit harvested fall 2005 – spring 2006 (Near HU), and sites in areas harvested in fall 2005 through spring 2006 (In HU). Data are presented for all sites combined in the North Fork.

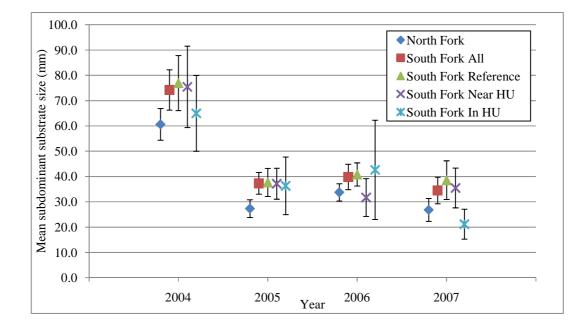


Figure 2.6 Mean proportion of substrate that was cobble or larger as estimated by fish sampling crews for fish bearing reaches of stream in the Hinkle Creek Basin, OR 2004-2007. Data presented for all fish bearing reaches of stream. Error bars equal  $\pm 1$  SE.

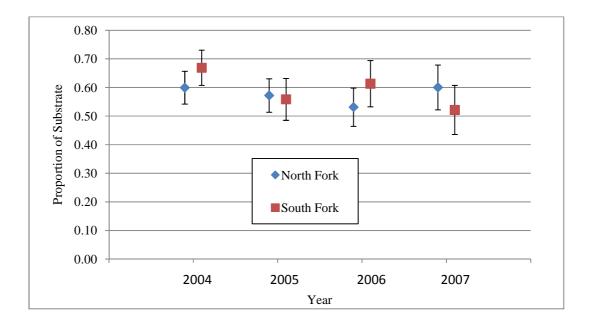


Figure 2.7 Mean proportion of substrate, by stream order, that had small cobble or larger as the dominant or subdominant substrate in the Hinkle Creek Basin, OR 2004-2007. Error bars equal  $\pm 1$  SE.

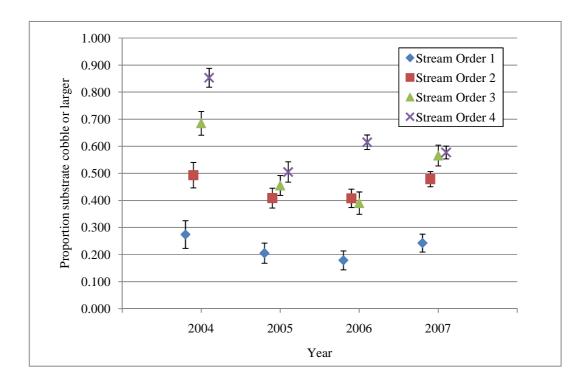
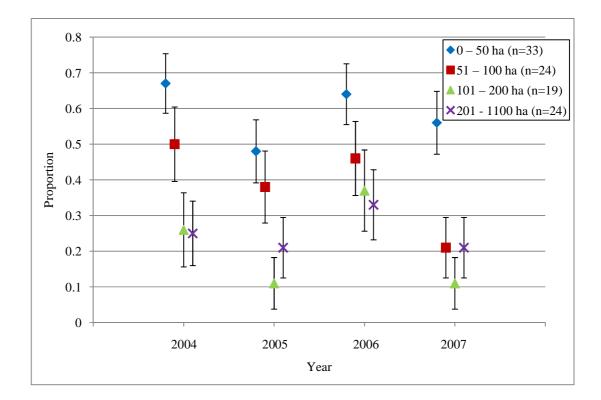


Figure 2.8 Proportion of sites with 0 Pacific giant salamander captures by upstream area drained (ha) in each year in the Hinkle Creek Basin, OR. Error bars equal  $\pm 1$  SE.



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# 3. RESPONSE OF PACIFIC GIANT SALAMANDERS AND TAILED FROGS TO THREAT OF PREDATION UNDER DIFFERING SEDIMENT LEVELS

# 3.1 Summary

Pacific Northwest stream amphibians are often negatively associated with sedimentation, but the mechanism underlying this relationship is not clear. One hypothesized mechanism is that the reduced interstitial space that results from sedimentation increases susceptibility of amphibians to predation. We used laboratory mesocosms to test this hypothesis and examine the response of larval Pacific giant salamanders and tailed frogs to cutthroat trout and adult Pacific giant salamander presence under three different levels of sediment. We found amphibian larvae were more visible as sediment level increased and some evidence that larvae were less visible in the presence of fish. Movement decreased in the presence of cutthroat trout, though for tailed frog larvae this effect was marginally significant (p = 0.066). Larvae did not respond to presence of adult Pacific giant salamanders. These patterns are consistent with the hypothesis that sediment affects larval stream amphibians by increasing vulnerability to predation. While both species of larvae actively sought cover in response to fish, we found little evidence that this behavior mitigates the effects of increasing sediment. We did not document changes in survival, but our findings suggest that cutthroat trout may be a more significant predator than Pacific Giant Salamanders and therefore that this mechanism, an increase in vulnerability to predation, might be more prevalent in reaches where fish are present.

## 3.2 Introduction

In the Pacific Northwest, several studies have examined the effects of timber harvest on stream amphibians (see DeMaynadier and Hunter 1995 and Kroll 2009 for reviews). The results of these studies vary among studies and regions, but have identified numerous factors that affect stream amphibians after timber harvest. Most of these studies did not examine the mechanism through which identified factors act. One factor hypothesized to affect stream amphibians after timber harvest is sedimentation (Bury and Corn 1988), though the underlying mechanisms for the influences of sedimentation on stream amphibians remain speculative. New procedures, called best management practices, have been implemented to limit stream sedimentation, but it is unclear how stream amphibians respond to stream sedimentation and if these practices help limit potential harvest effects.

Many studies have found correlations between abundance or presence of stream amphibians and substrate condition. Some of these relationships were based on measures of fine sediment or association with related habitat measures such as small or large substrates (Diller and Wallace 1996, Welsh and Lind 1996, Welsh and Ollivier 1998, Diller and Wallace 1999, Dupuis and Steventon 1999, Adams and Bury 2002, Stoddard and Hayes 2005), but indirect linkages supply supporting evidence, such as a correlation between amphibian density and stream gradient in harvested but not in unharvested reaches, or differences in older logged and unlogged stands where sediment levels appeared to be the major physical difference (Corn and Bury 1989, Murphy and Hall 1981, Hawkins et al. 1983).

Increased sedimentation is hypothesized to affect stream amphibians by filling in interstitial spaces used for cover (Bury and Corn 1988, Corn and Bury 1989). Decreased availability of refuges could force individuals to seek shelter farther away from resources and could limit the amount of usable habitat. This in turn could increase the amount of time spent in exposed locations, and thereby increase predation risk or impacts from high flow events. Effects of sedimentation may vary with size of individuals, because increases in sedimentation are likely to reduce the abundance of large interstitial spaces more quickly than small interstitial spaces (Montgomery and Buffington 1998, Waters 1995), resulting in a greater reduction in habitat for larger individuals, especially at lower sediment levels (Lowe et al. 2004).

In New Hampshire, Lowe et al. (2004) examined the effects of sediment and the presence of brook trout (*Salvelinus fontinalis*) on spring salamanders (*Gyrinophilus porphyriticus*). In mesocosms, the presence of brook trout reduced larval spring salamander growth and survival, indicating both direct and indirect effects of the predator presence. Different sediment levels had no detectable effect, and there was no interaction between sediment and trout presence. In field surveys, Lowe et al. (2004) detected a similar pattern for larval abundance, but found adult abundance was negatively associated with sedimentation and had no relation with the presence of trout, or an interaction between trout and sedimentation. They hypothesized that larvae were able to find appropriate interstitial spaces due to their small size, but were susceptible to trout predation. Adult *G. porphyriticus* were too large to be preyed upon by trout, but sedimentation reduced the amount of larger interstitial space potentially exposing adults to non-trout predators, high flow events, or territorial interactions, and stream sedimentation may have altered food availability (Lowe et al. 2004).

Welsh and Ollivier (1998) studied stream amphibian response to a large fine sediment input that resulted from the combination of a road construction project and a large storm in Redwood National Park, California. The three species analyzed had significantly lower densities in streams affected by sediment than in other streams. The effect of sediment varied by species and it appears that tailed frog larvae (*Ascaphus truei*) were affected by factors beyond a reduction in interstitial space (Welsh and Ollivier 1998). For tailed frog larvae there was a significant interaction between habitat type and site impact, suggesting that tailed frog larvae had a negative response to sedimentation in high velocity habitats where sediment is unlikely to accumulate.

In the Pacific Northwest, many of the forested streams inhabited by tailed frogs and Pacific giant salamanders (*Dicamptodon tenebrosus*) could be subjected forest management activities. Tailed frogs are considered more sensitive to forest management due to narrow tolerances of stream temperature and negative correlation with stream sediment (Wahbe and Bunnell 2003, Corn and Bury 1989, Kelsey 1995, Bull and Carter 1996). Pacific giant salamanders are habitat generalists that may be less sensitive to temperature extremes than other species (Nussbaum et al. 1983, Bury and Corn 1988), and may respond positively to the increased stream productivity in opened reaches (Murphy and Hall 1981). After the canopies of stands adjacent to a stream have reached closure, the positive effects of stream productivity may no longer counteract any negative effects of stream sedimentation, resulting in declines (Murphy and Hall 1981, Hawkins et al. 1983).

For both species we lack an understanding of mechanisms by which stream sedimentation might reduce densities, and factors that contribute to the effect. Both species have altered behaviors in the presence of predators (Feminella and Hawkins 1994, Rundio and Olson 2003), and one possible consequence of stream sedimentation is that it may alter larval response to predator presence. Our limited understanding of the mechanisms by which stream sedimentation affects amphibians could limit our ability to develop effective mitigation methods, and to identify sites that need special protection. To effectively manage habitat for stream amphibians we need to understand how sedimentation affects them. Our objectives were to determine 1) if tailed frog and Pacific giant salamander larvae increase use of refuges in the presence of a predator; 2) if larvae modify the amount of activity in the presence of a predator; 3) if larval response to a predator varies if cues are direct or indirect; and 4) if larval response to predator presence is affected by sediment levels.

#### 3.2 Methods

3.2.1 Study Design

We tested the effects of indirect and direct predator presence on the visibility and movement of Pacific giant salamander and tailed frog larvae under 3 levels of habitat sedimentation in 6 laboratory mesocosms. We used cutthroat trout (*Onchorhyncus clarki*) and aquatic adult Pacific giant salamanders as predators. In these experiments we used a crossed design, and ran every combination of sediment level (low, medium, and high) and predator level (control, indirect [predator chemical cues only], and direct [predator in mesocosm]) for each predator and larval species. To examine indirect predator effects we set up head tanks, where all incoming water flowed through the head tanks and then into the experimental enclosures. This allowed chemical cues released by predators held in the head tank to flow into the mesocosms without the larvae viewing the predator or being exposed to predation. We used empty head tanks in the control and direct predation trials.

We conducted experiments in mesocosms that were 102 cm long by 48 cm wide. The mesocosms were 50 cm deep, but we maintained water levels at 25 cm from the tank bottom with screened (2 mm mesh) stand pipes (1.5 cm diameter). We constructed the 6 mesocosms from cell cast acrylic with Weld-On #16 adhesive and applied an aquarium safe silicone sealant over joints. We used a combination chiller/heater system along with a sump tank to maintain water temperatures in the mesocosms. Water temperature in the tanks varied between 11.5 and 14.0°C.

We used a flow-through system to supply clean, temperature controlled water to the mesocosms. Each mesocosm was supplied water that was first fed through a covered head tank. We placed the head tanks on shelves above the mesocosms, and the contents of the head tanks were not visible from the mesocosms. Water traveled the length of the mesocosm prior to draining out the opposite end at a flow rate of 1 L/min. We used a low flow rate to maximize our ability to observe predator and prey behaviors. At this flow rate the volume of the mesocosm was replaced approximately every 2 hours. We oxygenated the sump tank and each head tank using an air stone. We used full spectrum lights in the laboratory that were automatically turned on at 0600 h and off at 1800 h.

We covered the bottom of each mesocosm with 2 cm of natural sand. We used sand as the sediment because we were testing the effects of interstitial space reduction rather than a particular effect of the texture of the sediment. We added rock substrate to the mesocosms to mimic stream environments. We added 3 rocks from each of 3 size classes to each mesocosm: small cobble (65-160 mm), large cobble (161-256 mm) and boulder (>256 mm) (size classes used were based on Cummings (1962) modification of the Wentworth (1922) scale). After adding the rocks, we added 5-7 additional small cobbles to fill any resulting space so that there was ca.1 cm of space around each rock. We added sand to create 3 levels of sedimentation: low (little sediment and larvae could access the undersides of rocks; 2 l sand), medium (a moderate amount of sediment where larvae could no longer access the undersides of rocks, but could still use the space between rocks and overhangs for shelter; 8 l sand), and high (sediment covered the top of some small cobble, most overhangs, and the sediment limited the amount of cover available between rocks, but some was still available; 12 l sand) levels of sedimentation. We spread the sand as evenly as possible

across the mesocosms and removed sand from the surface of exposed substrate using brushes. For each experiment we used fresh, rinsed sand and let the mesocosms sit for a minimum of 24 hours to allow any water born sediment to settle or drain from the mesocosms. We reused some of the rock substrate between experiments, but we redistributed the reused substrate between mesocosms. We thoroughly cleaned the mesocosms, head tanks, associated plumbing, and rocks prior to each experiment. We let water flow through the mesocosms and substrate, prior to the addition of sand, for a minimum of 48 hours prior to each experiment.

For each combination of sediment and predator we ran trials in 2 mesocosms. We placed 5 larvae in each mesocosm, so a total of 10 individuals were used at each combination. We set the density of larvae used in each mesocosm at 10 individuals per  $m^2$  to mimic densities seen in the wild (Dupuis and Steventon 1999, Bury et al. 1991, Feminella and Hawkins 1994, and Richardson 2005, Hawkins et al. 1988).

We collected larval tailed frogs and Pacific giant salamander larvae and adults by hand from streams in Benton, Clatsop, Lane, and Lincoln Counties, Oregon. We obtained ten cutthroat trout from the Fall River fish hatchery (near Bend, OR). The predators and larvae were kept in flow-through tanks on the same photoperiod as the experimental mesocosms. We fed larval Pacific giant salamanders tubifex worms *ad libitum*. Aquatic adult Pacific giant salamanders were fed earthworms until 24 hours prior to experiments. Similarly, we fed cutthroat trout pelletized food until 24 hours before experiment initiation. We used unglazed ceramic tiles that we incubated in a local stream to grow periphyton to feed larval tailed frogs. Thereafter, we maintained periphyton growth with full spectrum lights in the laboratory.

At 1500 h, 1 hour prior to the start of an experiment, we placed 5 larvae of the appropriate species in each mesocosm. After 30 minutes, we added the appropriate predators to the head tanks of mesocosms that examined larval response to indirect or direct predator presence. Five minutes prior to experiment initiation, we moved predators from the head tanks to the mesocosms for the direct predator presence experiments. We ran the experiments 1600 h to 2400 h, corresponding to the period of highest activity of the species studied (Feminella and Hawkins 1994, Rundio and Olson 2003). At 1800 h the full spectrum lights turned off, and 25 watt red lights centered 1 m above each mesocosm turned on.

We recorded two metrics every 20 minutes to examine larval activity: visibility and movement. We counted the number of larvae visible from 50 cm outside the edge of the mesocosm and 30 cm above the surface of the water as a measure of visibility. To minimize observer disturbance to larvae, we made observations from behind black plastic sheets (with slits cut in them). We made observations from a position that was centered along the length of the mesocosm. At the end of each trial, all larvae were counted. A minimum of 48 hours prior to experiment initiation we uniquely marked each larva in a given trial using 1 of 5 colors of visible implant elastomer that fluoresced under the VI light (Northwest Marine Technology, Shaw Island, WA, USA). Using the VI light to identify individuals, we recorded the position of each larva in one of 136 locations based on 6 cm by 6 cm grid cells. We made every attempt to minimize disturbing the larvae, but if the larvae moved while we were attempting to record its position we used the position where we first saw the larvae to calculate the distance moved from the last observation. Observer induced movement typically occurred less than once per individual over the 25 observations in an evening. When the individual settled again we recorded its position to use as the starting point for the next distance moved measurement. Using the prior and current grid location, we calculated the distance moved. This effectively calculated the straight line distance between the centers of grid cells, and should be considered the minimum distance moved and was our metric for movement.

Because larvae could hide underneath rocks at the low sediment level their position and movements could not always be assessed. We were concerned that visibility and movement measurements could miss much of the larval activity if larvae moved between the undersides of rocks. To determine if we were missing movements at the low sediment levels, we continuously observed the low sediment mesocosms for 2 15-minute periods during trials. One observation occurred between 1600 and 1800 h, while the lights were on, and the second occurred between 1900 and 2300 h.

# 3.3.2 Analysis

We summed the number of larvae visible in a mesocosm throughout the evening and divided by the total number of possible viewings (25 observations \* 5 individuals = 125) and analyzed the proportion visible using two-way ANOVAs. For each species of larvae, we treated the two mesocosms of each combination of predator

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species, predator level, and sediment level as replicates in the analysis. For this analysis there were 3 levels of sediment (low, medium, and high), and 3 levels of predator presence (control, indirect, and direct). We initially attempted to include a factor for the date of the experiment, but models failed to converge with this factor and it was removed from the analysis. Consequently, our models included effects of sediment level, predator presence, and their interaction. We evaluated the significance of terms with an F-test and  $\alpha$ =0.05.

Using the second metric, we analyzed the effects of sediment and predator presence on mean distances moved by individual larvae in a night using two-way ANOVAs. The mean was the sum of all movement distances by all individuals within a trial divided by 24 periods in which we could track movement and divided again by the 5 individuals in each mesocosm. Analysis of the movement data was complicated by the inability to track individuals at the lowest sediment level. At the low sediment level individuals could seek shelter under rocks and were often not seen for most of the evening. Due to this, we only analyzed movement under the medium and high sediment levels, where we were able to track all individuals. In the analysis, we treated the 2 mesocosms used at each combination of sediment and predator as replicates. Like the previous analysis the model we evaluated included sediment level, predator level, and their interaction. We used F-tests and  $\alpha$ =0.05 to evaluate term significance.

#### 3.4 Results

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Although we initially planned to examine the effect of direct predator presence on larval survival, survival was 100% across all replicates and species. As expected, visibility of larval salamanders and tailed frogs increased with sediment level (Fig. 3.1, 3.2). The proportion of salamander larvae visible was not related to predator treatment when an adult Pacific giant salamander was the predator, but there was a trend towards reduced visibility when a fish was the predator, especially at lower sediment levels (Fig. 3.1, Table 3.1). The main effect of predator was marginally significant (p = 0.056) when cutthroat trout was the predator (Table 3.1). The effects of treatments on tailed frog larval visibility demonstrated significant interactions between sediment level and predator treatment when either adult Pacific giant salamanders or cutthroat trout were predators (Table 3.2). Tailed frog larvae showed no consistent response to the presence of adult salamanders. The interaction is largely explained by a lack of response to sediment level in the direct predator treatment (Fig. 3.2). Tailed frog larvae decreased activity in response to fish for all treatments except the medium sediment/direct predator combination (Fig. 3.2).

Presence of adult Pacific giant salamanders did not affect movement of salamander larvae, but larvae moved shorter distances when cutthroat trout were present (Fig. 3.3, Table 3.3). Salamander response to the presence of cutthroat trout appeared to vary with sediment level (Fig. 3.3), but the interaction was not statistically significant (p = 0.157). Similarly, larval tailed frogs exhibited no change in mean movement when adult salamanders were the predator, but showed a reduction in movement that approached statistical significance when fish were the predator (p = 0.157).

0.066; Fig. 3.4, Table 3.4). Tailed frog larvae appeared to increase movement in response to cutthroat trout when sediment levels were higher (Figure 3.4).

## 3.5 Discussion

Sediment should increase the vulnerability of larvae to predators if larval positioning is a random process. If larvae actively seek cover, the expected effects of sediment are less clear. Sediment should decrease hiding opportunities but, up to a point, larvae may be able to seek out and exploit limited cover. In our experiments, larval amphibians appeared to hide from fish but not from adult salamanders. While increased sediment increased visibility of larvae, we cannot conclude that the ability of larval amphibians to actively find cover diminished with increasing sediment levels. Such an effect would be seen as an interaction with a decreasing difference in visibility between the control and predator treatments as sediment levels increase. The data suggest such a pattern for larval salamanders (Fig. 3.1), but the predator effects and the interaction were not statistically significant (Table 3.1). The nature of the interaction reduces the main effect of the predator treatment on visibility leading to its marginal significance despite a strong trend in the low sediment treatment. Tailed frog larvae did not show a diminished ability to actively seek cover as sediment level increased. Their visibility with a fish in the head tank was consistently lower than in the control, but the differences were uniform among sediment levels (Fig. 3.2). When fish were present in the mesocosm with the frog larvae, the pattern differed. The visibility of frog larvae was greater in medium sediment than at low sediment, and

visibility was approximately the same or slightly lower at medium and high sediment. This pattern might have resulted if harassment by fish increased the visibility of the frog larvae. Such a process might lead to inconsistent patterns of visibility relative to sediment. If visibility to predators is related to the visibility of larvae to observers in our experiment, these patterns suggest that increasing sediment will increase the vulnerability of larvae to visually oriented predators. It is less clear whether larvae can mitigate this effect by actively seeking cover. Visibility was always greater with higher sediment but there was some evidence that tailed frog larvae limited visibility by seeking shelter when a predator was present. Moreover, while there was a clear pattern in the data suggesting that salamander larvae behaviorally mitigate the effects of sediment (Fig. 3.1), we cannot statistically reject the null hypothesis that the effect of predator does not vary among sediment levels.

Larvae would be expected to reduce activity in the presence of a predator that they can detect to reduce predation risk. Increased activity can draw the attention of a visually oriented predator, and movement may place the larvae in direct contact with the predator. For Pacific giant salamander larvae, average movement was unaffected by sediment or adult Pacific giant salamander predators, but larvae decreased mean movement in response to direct and indirect cutthroat trout presence. While there was not any predation in the direct effects experiments, the indirect effects experiments showed similar decreases in activity in response to trout as was found in the direct effect mesocosms. This highlights that larvae had a similar response to cutthroat presence, whether or not they were able to see the predator and suggests the response was to chemical cues released by the predators. There is a weak suggestion of increased salamander movement in the high sediment mesocosms when trout were in the mesocosm (Fig. 3.3), which could be caused by trout chasing larvae. The reduced availability of refuge in these mesocosms may force larvae to search for better cover when they encountered a cutthroat trout. While adult Pacific giant salamanders can be cannibalistic, a response to conspecifics was not seen and may not be practical given that they often live in the same streams.

Movement of larval tailed frogs was lower in the direct or indirect presence of cutthroat trout than in the control, but this effect was marginally significant (p = 0.066). This pattern is consistent with findings of Feminella and Hawkins (1994) that showed decreased activity due to cutthroat trout presence. While tailed frog larvae responded to presence of cutthroat trout, there was little evidence that increasing sediment levels altered this response. There is a weak suggestion that tailed frog larvae increased movement at the higher sediment level (Fig 3.4), but this interaction was not significant. The lack of effect of adult Pacific giant salamander presence on movement of tailed frogs contrasts previous findings indicating a negative impact of indirect adult salamander presence on tailed frog activity (Feminella and Hawkins 1994). A few factors might contribute to this difference. Feminella and Hawkins (1994) used larval tailed frog densities that were an order of magnitude greater than ours. High densities may cause larvae to be more active, and a response to a predator might be heightened if they detect any movement, even of conspecifics, near them. Their experiment occurred in shallower channels with higher flow rates where the

percentage of larvae visible was used to measure activity (Feminella and Hawkins 1994). In a higher flow the turbulent water provides hiding spaces and may limit salamander access to these areas. Due to the higher flow rate individuals could remain active on submerged rocks while not being visible due to the turbulent water.

Tailed frog larvae tend to occur in fast flowing riffles and Pacific giant salamanders are often associated with slower flowing waters (Welsh and Lind 2002, Welsh and Ollivier 1998), so habitat segregation might provide a mechanism for individuals to occupy similar locations, while limiting direct interaction. Under these circumstances, reaction to chemical cues from the predator could be detrimental because the species are unlikely to be in direct contact. This might explain why we did not see an effect of adult salamander presence on tailed frog larvae. Due to depth and low flow rates, our mesocosms reflected a more pool-like environment that tailed frog larvae are less likely to inhabit.

During our experiments we did not observe any predation of either larval species. Other studies have shown that these larval species are palatable to cutthroat trout and adult Pacific giant salamanders (Rundio and Olson 2003, Feminella and Hawkins 1994). While we did not feed predators for 24 hours prior to experiments, this may not have been enough time for them to become hungry once again. Given their overlapping distributions, the behavioral response of Pacific giant salamander and tailed frog larvae to the presence of cutthroat trout suggests that this is a predator they face in the wild and to which they have developed defenses. The responses to

indirect exposure to cutthroat trout show that larval species respond to chemical cues released by the trout.

One potential concern is that, at low sediment treatments, larvae could move among the undersides of rocks between observation intervals without the observer seeing any changes in position or visibility. We attempted to see if larvae were active in low sediment mesocosms between observations by watching each mesocosm for 2 15 minute periods. During these observations, we used a higher vantage point to allow us to better spot any movement in the 15 minute period. We saw very few movements during these observations, suggesting that we were not missing large amount of activity in the low sediment mesocosms. We did not observe larvae actively burrowing into the sand, suggesting that this was not a technique they used to seek refuge.

We conducted these trials in laboratory mesocosms that had limited variation in habitat, but also create situations that are unlikely to be found in the wild. In our lower flow experiments, the interactive effect of sediment level and predator level on larval tailed frog visibility may be due to the fact that tailed frog larvae have sucker like mouth part and can attach to the surface of objects (Nussbaum et al. 1983). Tailed frog larvae frequently used mesocosm walls or locations that provided a clear view of the surrounding area. This meant they were visible, but in a more natural setting the margins of the water are likely to be rock or wood rather than acrylic, which may act as camouflage and turbulent water may add to this effect. This would likely boost larval tailed frog visibility in our trials, but the effect should have been consistent among mesocosms. These locations also might provide larvae with a view of any approaching predators

We found that stream sedimentation increased larval amphibian visibility, but that both the direct and indirect presence of predatory cutthroat trout tended to cause a decrease in the proportion of individuals observable. We also found that larval amphibians reduced their activity levels in the presence of trout. As evidenced by decreased visibility in the presence of trout, we found that both species increased use of refuges when trout were present. The increased refuge use was most apparent at lower sediment levels and did not appear to counter the effects of increasing sediment level. At the highest sediment level, the reduction in available interstitial space was large enough to make refuge-seeking difficult. When a trout was the predator, the larvae reduced their activity, possibly causing them to rest in places that did not provide suitable refuge. Neither species of larvae exhibited changes in visibility or activity in response to the presence of adult Pacific giant salamander. This suggests that cutthroat trout may have a stronger effect on larval survival and abundance than do adult salamanders. If this is true, tailed frog and Pacific giant salamander larvae may be more vulnerable to the effects of sedimentation in fish-bearing reaches of stream which, under Oregon and federal regulations, already receive greater protection from timber management practices through the use of streamside retention buffers.

Table 3.1 Results of ANOVAs on the effects of predator presence and sediment level on larval Pacific giant salamander visibility. Predator had 3 levels of direct, indirect, or no predator presence. Sediment level also had 3 levels of low, medium or high.

	df	SS	MS	F	р
Pacific giant salamander					
Predator	2	0.009	0.004	0.98	0.412
Sediment level	2	0.687	0.344	78.84	< 0.0001
Predator x sediment level	4	0.044	0.011	2.54	0.113
Error	9	0.039	0.004		
Cut-throat trout					
Predator	2	0.133	0.067	4.05	0.056
Sediment level	2	1.938	0.969	58.90	< 0.0001
Predator x sediment level	4	0.088	0.022	1.34	0.327
Error	9	0.148	0.016		

	df	SS	MS	F	р
Pacific giant salamander					
Predator	2	0.348	0.174	9.85	0.005
Sediment level	2	0.948	0.474	26.85	0.0002
Predator x sediment level	4	0.289	0.072	4.09	0.037
Error	9	0.159	0.018		
Cut-throat trout					
Predator	2	0.080	0.040	1.80	0.220
Sediment level	2	0.965	0.483	21.74	0.0004
Predator x sediment level	4	0.428	0.107	4.82	0.024
Error	9	0.200	0.022		

Table 3.2Results of ANOVAs on the effects of predator presence and sedimentlevel on larval tailed frog visibility. Predator had 3 levels of direct, indirect, or nopredator presence. Sediment level also had 3 levels of low, medium or high.

Table 3.3 Results of ANOVAs on the effects of predator presence and sediment level on mean larval Pacific giant salamander movement. Predator had 3 levels of direct, indirect, or no predator presence. Sediment level had 2 levels of medium or high.

	df	SS	MS	F	р
Pacific giant salamander					
Predator	2	0.166	0.083	0.19	0.834
Sediment level	1	0.232	0.232	0.52	0.497
Predator x sediment level	2	0.144	0.072	0.16	0.854
Error	6	2.666	0.444		
Cut-throat trout					
Predator	2	1.785	0.892	8.58	0.0174
Sediment level	1	0.011	0.011	0.11	0.756
Predator x sediment level	2	0.532	0.266	2.56	0.157
Error	6	0.624	0.104		

	df	SS	MS	F	р
Pacific giant salamander					
Predator	2	2.807	1.404	0.62	0.569
Sediment level	1	1.051	1.051	0.46	0.521
Predator x sediment level	2	0.252	0.126	0.06	0.946
Error	6	13.574	2.262		
Cut-throat trout					
Predator	2	9.879	4.940	4.44	0.066
Sediment level	1	0.228	0.228	0.20	0.667
Predator x sediment level	2	0.583	0.292	0.26	0.778
Error	6	6.675	1.112		

Table 3.4Results of ANOVAs on the effects of predator presence and sedimentlevel on mean larval tailed frog movement. Predator had 3 levels of direct, indirect, orno predator presence. Sediment level had 2 levels of medium or high.

Figure 3.1 Mean larval Pacific giant salamander (DITE) visibility under different sediment and predator treatments with a) adult Pacific giant salamanders, and b) cutthroat trout (CT) as the predator. Error bars equal  $\pm 1$  SE. Predator had 3 levels: direct (in mesocosm – in MC), indirect (in head tank – in HT), or no predator presence (control). Sediment level had 3 levels: low, medium or high.

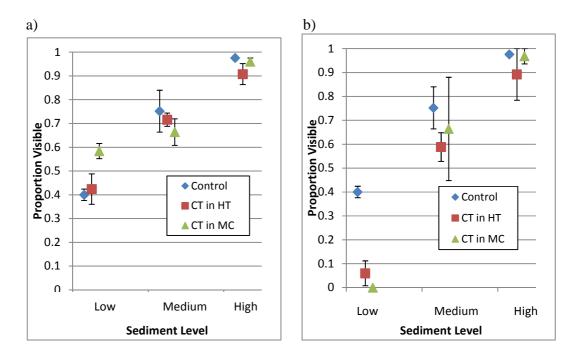


Figure 3.2 Mean larval tailed frog (ASTR) visibility under different sediment and predator treatments with a) adult Pacific giant salamanders (DITE), and b) cutthroat trout (CT) as the predator. Error bars equal  $\pm 1$  SE. Predator had 3 levels: direct (in mesocosm – in MC), indirect (in head tank – in HT), or no predator presence (control). Sediment level had 3 levels: low, medium or high.

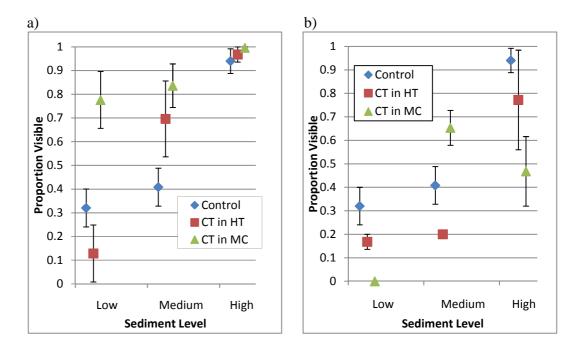


Figure 3.3 Mean larval Pacific giant salamander (DITE) movement under different sediment and predator treatments with a) adult Pacific giant salamander and b) cutthroat trout (CT) as the predator. Movement distances are based on grid cells that were 6 cm x by 6 cm. Error bars equal  $\pm 1$  SE. Predator had 3 levels: direct (in mesocosm – in MC), indirect (in head tank – in HT), or no predator presence (control). Sediment level had 2 levels: medium or high.

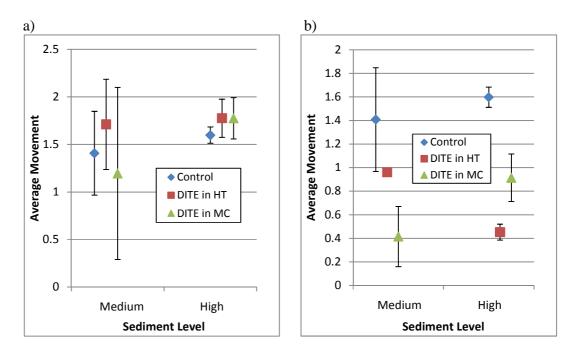
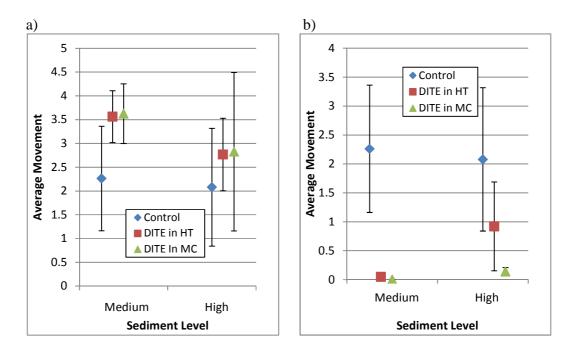


Figure 3.4 Mean larval tailed frog (ASTR) movement under different sediment and predator treatments with a) adult Pacific giant salamander (DITE), and b) cutthroat trout (CT) as the predator. Movement distances are based on grid cells that were 6 cm x by 6 cm. Error bars equal  $\pm 1$  SE. Predator had 3 levels: direct (in mesocosm – in MC), indirect (in head tank – in HT), or no predator presence (control). Sediment level had 2 levels: medium or high.



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# 4. SYNTHESIS AND CONCLUSIONS

The studies presented here add to our knowledge of the relationship between timber management and Pacific giant salamanders (*Dicamptodon tenebrosus*), and our understanding of how stream amphibians respond to presence of predators under differing levels of sediment.

In Chapter 2 we used analytical techniques that help account for inefficiencies in our sample methods at sites with captures. We found no evidence of effects of timber harvest on Pacific giant salamanders in the Hinkle Creek drainage, but salamander densities were positively related to stream substrate size, negatively related to increases in the amount of upstream area, and weakly positively related to the density of fish found in the 40 m of stream around a site. This study took place in a limited geographic range and future studies should examine areas outside the Hinkle Creek basin. Our research was part of a paired watershed study, where the number of treated units was limited. For the hydrological portion of the study, each storm system can be treated as a data point, but for the salamanders data points at each site were logistically limited to yearly data. To maintain a reasonable sample size this meant that we had several sites within each harvest unit. To identify regional trends, future studies should examine a larger geographic range and include larger number of treatment units. Our analysis methods did not account for sampling inefficiencies at sites with no captures. If a site had 0 captures it was treated as having a density of 0, even though there was a chance that we failed to detect any present individuals on all three passes within a year. To examine the impact of this we used a Monte Carlo analysis to probabilistically assign captures to sites where none occurred. This method gave all sites the possibility of being occupied, potentially overstating the impact of this bias. In the Monte Carlo analysis we found that the highest ranked models remained similar, but models ranked lower by  $AIC_e$  tended to shift. Although the top model included a year effect, there was no interaction and hence no evidence of a harvest effect. There has recently been concern about prior studies that did not accounted for differences in capture efficiencies between sites (Kroll 2009). Previous result should be viewed cautiously, but their findings should not be entirely discounted either. This could be done by considering the observed magnitude of effects, evaluating the likely effects of inefficient sampling methods, and considering the results from multiple studies.

The spatial density of sites in our study was higher than has been used in other studies. Stoddard and Hayes (2005) and Hunter (1998) are among the few studies on stream amphibians where multiple sites were sampled within a basin and on a given stream. In our study we sampled 100 sites in a  $3^{rd}$  order basin that was ~2000 hectares in area. This gave us an interesting opportunity to examine spatial patterns. The summed Pacific giant salamander densities, at sites sampled in all 4 years appears similar between stream forks (Appendix 3, Appendix 4). Sites with the highest

densities across all 4 years tended to occur in non-fish bearing section of stream, often near the end of anadromous fish. The map also suggests that sites on 1<sup>st</sup> order segments of stream showed more variability between sites than those on higher order segments. Variability among sites is better visualized by examining the coefficient of variation (CV) of the density at each site (Appendix 5). Many of the 1<sup>st</sup> order streams had CVs of 2, which appears to be due to a mathematical anomaly. At these sites Pacific giant salamanders were captured in only 1 of the 4 years sampled. Regardless of the density reported, as long as the density was 0 in the other 3 years the CV was always 2. This leads to a case where the sites with the highest CVs are not necessarily the sites with the highest variability. Excluding these points, which are spread relatively evenly between basins (10 and 7 in the North and South Fork basins respectively), the CVs have a remarkably similar distribution between basins (Appendix 6). Due to the small size of sites, ~ 1m in length, variation that occurred over kilometers may have been swamped by variation due to fine scale habitat. Using larger sample sites, or grouping our sites over segments or catchments might reveal variation across larger scales (i.e. kilometers) that we did not detect.

In Chapter 3 we found that Pacific giant salamander and tailed frog (*Ascaphus truei*) larvae were increasingly visible as sediment levels increased and we found a trend towards decreased visibility in the presence of cutthroat trout (*Onchorhyncus clarki*). Larval movement decreased in the presence of fish but neither species showed a response to predatory adult Pacific giant salamanders. The response of larvae to fish was similar under direct (fish in mesocosm) and indirect (fish in head tank) predator

treatments, suggesting that the larvae responded to visual and chemical cues. The concentration of chemical cues needed is unclear, but shows that larvae respond to fish predators that are not visible and could respond to fish that are not in their immediate vicinity. We found that larvae sought cover when fish were present, but that this behavior was unlikely to reduce predation risk as sediment levels increased. Our work is consistent with the hypothesis that sedimentation increases larval exposure to predation, and that the greatest risks might be seen in fish bearing reaches of stream.

Lowe et al. (2002) found stage specific effect of sediment and fish presence on spring salamanders (*Gyrinophilus porphyriticus*). Smaller salamanders were vulnerable to fish presence but not sedimentation, while larger salamanders were vulnerable to sedimentation but not fish presence. This difference was attributed to the larger individuals being too large for the fish to consume, but being more susceptible to sedimentation as it tends to reduce the larger interstitial spaces first (Lowe et al. 2002). While we did not examine larger prey species, such an effect might be possible. Future work examining the effects of sedimentation on stream amphibians should examine effects at different stages of life. Of course, such work is complicated by species that may or may not stay in streams as adults.

In both our field and laboratory studies we found an effect of fish, but the effects varied between the studies. In the field study the effect of fish density on Pacific giant salamander density was weakly positive and the 95% confidence interval include no effect, while in the lab cutthroat trout presence negatively affected Pacific giant salamander visibility and movement. These findings appear to be at odds with one another. One critical difference is that the lab work was looking at larval behavior, while the field work looked at densities. While one would expect that decreases in movement would translate to a reduction in body condition it is not clear that this would relate to a density decrease if sediment levels stay approximately constant.

In our field work, fish density represents the density in the 40 m of stream around a site, while amphibian sample site were 1 m in length. In addition the fish and amphibian sampling occurred at different times. While the fish density should give a representation of the fish in the area around a site, it may not accurately represent the number of fish in close contact with the salamanders. In our lab work fish were held in the same microcosm as the larvae, or in a head tank where all the water flowed across the fish and into the mesocosm. This meant that measures such as habitat segregation, which prey might use to avoid predators, could not be used in our experiments. Ideally the sizes of both sites would be equal to give a better of predation risk amphibians experience within a site. This would limit issues with local variation overwhelming larger scale variation, if present, and should better represent the predation risks experienced by salamanders.

Perhaps the most important finding of this study was the lack of a change in stream sediment after timber management. This was true for the data we collected as well as the data collected by the fish crew using somewhat different methods (Gresswell and Bateman unpublished data). Older forest harvest practices and associated activities such as road building are commonly associated with stream sedimentation (Meehan 1991, Reid 1993, Waters 1995), but the practices used at Hinkle Creek appear to improve on previous procedures. The lab work showed a potential route through which sediment could impact larval stream amphibians, but we did not see changes in stream sediment or salamander populations in relation to timber harvest at Hinkle Creek. It is important to remember that sediment measurement is difficult and it is possible we did not detect fine changes in stream sediment levels. In addition, this study took place in a small geographic range, over a short time period, on land managed by a single company, and only involved Pacific giant salamanders. Variations in the interpretation and implementation of best management practices are possible and may vary by company. Species such as torrent salamanders (Rhyacotriton sp.) and tailed frogs may be more sensitive to alterations from timber harvest, especially alterations to stream temperature or microclimate (Olson et al. 2007). With all that said, what people want to know is if current timber harvest practices are sufficient to protect stream amphibians. While a single study cannot provide a definitive answer to this question, our data suggest that the timber harvest practices used at Hinkle Creek were adequate to protect Pacific giant salamanders.

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# **APPENDICES**

Appendix 1 List of models of Pacific giant salamander densities in Hinkle Creek Basin, OR 2004-2007 examined using extended linear modeling.

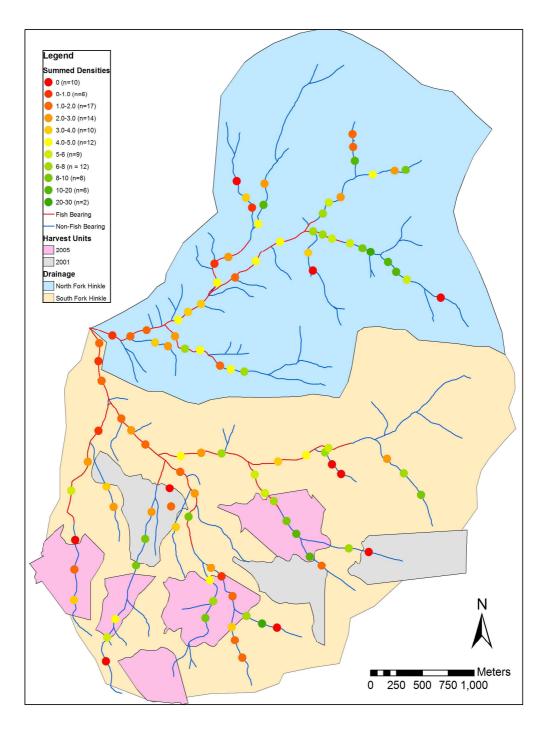
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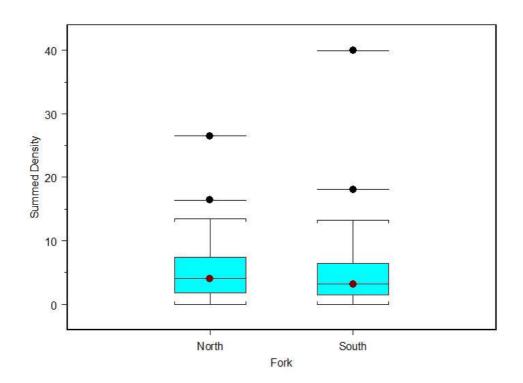
Appendix 2 Mean substrate data by site. In the South Fork, data are presented for all sites, sites that were not near a harvest unit (Reference), sites < 500m downstream of a unit harvested fall 2005 – spring 2006 (Near HU), and sites in areas harvested in fall 2005 through spring 2006 (In HU). Data are presented for all sites combined in the North Fork.

	North Fork	South Fork						
		All	Reference	Near HU	In HU			
Mean pr	oportion cobbl							
2004	0.47 (0.044)	0.51 (0.048)	0.56 (0.060)	0.45 (0.123)	0.42 (0.103)			
2005	0.36 (0.031)	0.35 (0.034)	0.37 (0.041)	0.34 (0.067)	0.33 (0.093)			
2006	0.33 (0.034)	0.36 (0.032)	0.36 (0.043)	0.34 (0.084)	0.38 (0.063)			
2007	0.42 (0.031)	0.42 (0.031)	0.44 (0.039)	0.47 (0.070)	0.34 (0.074)			
Mean siz	Mean size of dominant substrate in mm (SE)							
2004	123.7 (13.2)	147.9 (15.0)	159.7 (17.7)	119.1 (34.6)	132.2 (41.6)			
2005	128.0 (11.7)	121.7 (14.2)	132.3 (19.1)	109.1 (31.3)	98.2 (26.1)			
2006	114.6 (12.4)	118.7 (13.1)	120.1 (16.5)	114.7 (39.1)	117.3 (26.9)			
2007	152.8 (13.2)	147.6 (13.3)	155.2 (17.5)	153.3 (30.0)	120.0 (27.7)			
Mean size of subdom substrate in mm (SE)								
2004	60.6 (6.26)	74.2 (7.96)	76.9 (10.9)	75.4 (16.1)	65.0 (15.0)			
2005	27.3 (3.53)	37.3 (4.31)	37.7 (5.54)	37.1 (6.11)	36.3 (11.4)			
2006	33.7 (3.43)	39.8 (5.00)	40.8 (4.56)	31.7 (7.45)	42.6 (19.6)			
2007	26.8 (4.54)	34.5 (5.24)	38.6 (7.65)	35.5 (7.85)	21.2 (5.89)			

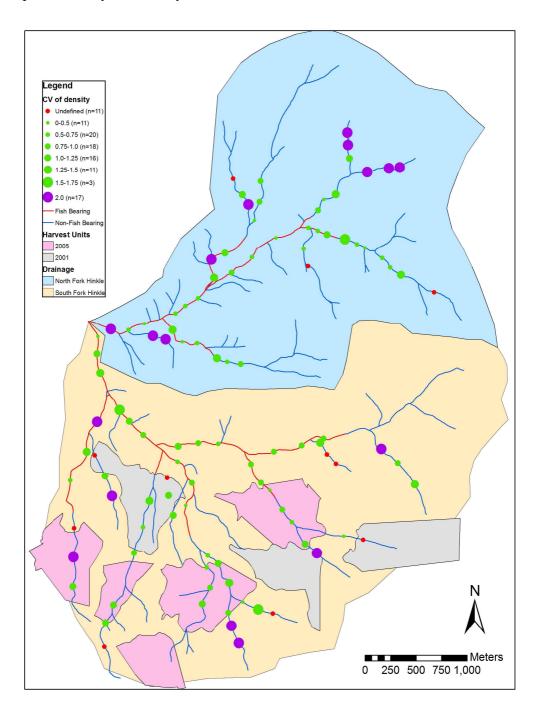
Appendix 3 Summed Pacific giant salamanders density at sites sampled in 2004-2007 in the Hinkle Creek Basin, OR.



Appendix 4 Box plots of the summed Pacific giant salamander density at sites sampled in 2004-2007 in the North and South Forks of Hinkle Creek, OR.



Appendix 5 Coefficient of variation (CV) of Pacific giant salamander density at sites sampled in 2004-2007 in the Hinkle Creek Basin, OR. Site with no captures in all 4 years have an undefined CV. Due to a mathematical anomaly, sites where there were captures in only 1 of the 4 years have a CV of 2.



Appendix 6 Box plots of coefficients of variation (CV) of density of Pacific giant salamanders at site sampled in 2004-2007 in the North and South Forks of Hinkle Creek, OR. Sites with undefined CVs and CVs that equaled 2 due to a mathematical anomaly were removed from the analysis.

