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Effects of anthropogenic forest stresses on the distribution and abundance of the Olympic Torrent Salamander (*Rhyacotriton olympicus*) in the Olympic National Forest and Olympic National Park

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**Effects of anthropogenic forest stresses on the distribution and abundance of the Olympic
Torrent Salamander (*Rhyacotriton olympicus*) in the Olympic National Forest and Olympic
National Park**

By

Travis Kurtz

Accepted in Partial Completion
of the Requirements for the Degree
Master of Science

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Master's Thesis

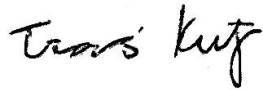
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Travis Kurtz

6/18/2020

**Effects of anthropogenic forest stresses on the distribution and abundance of the Olympic
Torrent Salamander (*Rhyacotriton olympicus*) in the Olympic National Forest and Olympic
National Park**

A Thesis
Presented to
The Faculty of
Western Washington University

In Partial Fulfillment
Of the Requirements for the Degree
Master of Science

by
Travis Kurtz
June 2020

Abstract

Salamanders worldwide are faced with habitat loss, and much of the remaining habitat is under the constant pressure of degradation. The forests of the North American Pacific Northwest are no exception. The primary anthropogenic forces impacting the stability of lotic salamander populations on the Olympic peninsula are commercial timber harvest and culverts necessitated by roads crossing streams to facilitate the removal of timber from these forests.

In this study, I conducted stream surveys on 139 headwater stream reaches in 77 streams in mature and recently harvested forests both above and below culverts on forest roads in Washington's Olympic National Forest and Olympic National Park, collecting environmental data and counting Olympic Torrent Salamanders (*Rhyacotriton olympicus*). I used an information theoretic approach to model selection to evaluate sets of candidate models for both occupancy and abundance of the salamander in streams.

Occupancy model selection showed support for models including Gradient, Turbidity, Forest Stage, and Harvest Distance as important predictors of *R. olympicus* presence at the stream-reach level. I conducted further tests on all models with a ΔAIC_c score of less than four to determine the relative impact of individual predictor variables. The abundance analysis failed on a goodness of fit test for the global model as the result of a high degree of overdispersion. Because of this failure I was unable to conduct further model selection analyses with the candidate model set. I instead conducted simple post hoc analyses to explore variables not used in the initial candidate model set.

The variables that drive occupancy all point to stream gradient as the most important factor in whether a stream reach is suitable for *R. olympicus* occupancy. Neither the candidate models nor most of the variables explored independently show a strong relationship with salamander

abundance. The presence of fish and Tailed Frogs (*Ascaphus truei*) were both significant predictors of variation in salamander abundance, as were elevation and stream flow. The lack of robust results in the abundance analysis highlights the need for further research using a different framework for questioning, possibly at a different spatial scale like Welsh and Lind (1995, 1996) or even shifting the priority from environmental factors to interspecific interactions.

This study's results provide a direction for future species management. It is clear that preserving suitable Olympic Torrent Salamander habitat requires the protection of high gradient stream reaches and the surrounding forests. The results also found no significant effect of proximity to recently harvested forests (forest age ≤ 30 years) on probability of detection, though associations with forest age may be obscured by combining all forests ages greater than 30 years. However, because occupancy analysis highlights the minimum suitable habitat needs and the abundance analysis relied on post hoc analyses, the need to understand the drivers of abundance in order to create a comprehensive species management plan persists.

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I would like to thank my advisor, Dr. John Bower, for his support, guidance, and willingness to embark on this journey with me. I also thank my other committee members, Dr. John McLaughlin and Dr. Roger Anderson for their assistance with experimental design, data analysis, and insightful critiques throughout the thesis process. I thank the Office of Research and Sponsored Programs and the Biology Department for providing the funding needed to complete this project. I also thank the Olympic National Park and Olympic National Forest for the authorization to conduct my field work within their boundaries. I give special thanks to my field assistant, Reed Henderson, for his trust and hard work in joining me in the field for the entire season.

I also want to acknowledge that the land where I conducted my research has been home to the Lower Elwha Klallam, Jamestown S’Klallam, Port Gamble S’Klallam, Skokomish, Quinault, Hoh, Quileute, and Makah Peoples since time immemorial. I want to pay respect to their continuous stewardship and knowledge of this land and its inhabitants.

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Preface

The Olympic peninsula in northwestern Washington is primarily composed of federally, state, and privately-owned forests, many of which are managed through even-aged timber harvesting practices such as clear cuts. This method of timber management, common in the Olympic National Forest, has numerous effects on forest and freshwater ecology, primarily driven by the process of harvesting timber and the creation of roads needed to extract the timber from the harvest site. Timber harvest is rare within the Olympic National Park, used only to control insects or disease, or to preserve natural or historic resources (Riddle 2019), which reduces the impacts of timber harvest and roads in the park. The Olympic National Forest and Olympic National Park are home to 13 species of native amphibians (“Amphibian and Reptile Species List” 2015), of which only four are strongly associated with the waters and immediate riparian zones of headwater streams. These four species are the Coastal Tailed Frog (*Ascaphus truei*), Cope’s Giant Salamander (*Dicamptodon copei*), Van Dyke’s Salamander (*Plethodon vandykei*), and Olympic Torrent Salamander (*Rhyacotriton olympicus*).

The Olympic Torrent Salamander (*Rhyacotriton olympicus* Gaige 1917) is a poorly studied lotic salamander species endemic to the Olympic peninsula. Torrent salamanders were first described by H.T. Gaige in 1917 as “undoubtedly represent[ing] a new species of the genus *Ranodon*,” but was later placed in the monotypic genus *Rhyacotriton*. The Olympic Salamander was originally believed to have two distinct subspecies, but in 1992 the species was split into the four currently recognized genetically distinct species due to evidence of sufficient protein variation (Stebbins and Lowe 1951, Good and Wake 1992, Petranka 1998).

Because the original species was recently split into four species, there are significant gaps in the literature on *R. olympicus* regarding its distribution, susceptibility to habitat disturbances,

and appropriate riparian zone management (Howell and Roberts 2008). In general, this species is believed to be extremely sensitive, exhibiting little tolerance for even slight variations in stream temperature or sediment content, both of which commonly result from timber harvest (Bury and Corn 1988, Hammerson 2004, Corkran and Thoms 2006, Howell and Roberts 2008). An additional threat that has been little studied is the effect of road culverts on salamander distribution and abundance. These culverts, primarily installed on roads built to allow timber harvest, can present physical barriers to salamander migration and dispersal and potentially change patterns of sediment transport and deposition.

Timber harvesting has been a significant part of the economy in Washington state since before statehood, and that long history of harvesting may have caused decline in *R. olympicus* population sizes across the geographic range of the species. Approximately 27% of the land on the Olympic peninsula is managed by federal agencies, and about 45% that federal land in the peninsula is managed by the United States Forest Service (USDA Forest Service 2012, Washington State Recreation and Conservation Office 2019). The continued practice of large-scale timber harvest leaves large parts of the Olympic National Forest vulnerable to the effects of fragmentation. Globally, 70% of forests are within one kilometer of a forest edge, and therefore subject to the effects of fragmentation which include biodiversity decreases of 13-75% (Haddad et al. 2015).

Hammerson (2004) found that the Olympic Torrent Salamander is disproportionately affected by timber harvest when compared to sympatric amphibians. Howell and Roberts (2008) opined that timber harvest is one of the primary threats to the long-term survival of *R. olympicus* and Bury and Corn (1988) suggested that most Olympic Torrent Salamander populations go extinct in the wake of clear-cutting and that recolonization is rare. Timber harvesting on the

Olympic peninsula may increase stream sedimentation (Karwan et al. 2007, Arismendi et al. 2017), and may be problematic for *R. olympicus*, because Bury and Corn (1988) found that *R. olympicus* was absent in all streams with less than 11% gradient, coincident with increased sedimentation. For the past two decades, however, forestry regulations in the Olympic National Forest have required riparian buffers (Martens et al. 2019). In the coastal forests of Washington, riparian buffers had the effect of preventing a significant increase in stream sediment after forest harvests (Jackson et al. 2001). It is likely that riparian buffer regulations in the Olympic National Forest significantly reduce stream sediment, possibly making low gradient stream reaches inhabitable for *R. olympicus*. The effects of modern tree harvesting and subsequent stream sediment changes on populations of *R. olympicus* is unknown.

Another potential cause of sedimentation in headwater streams is slash burials. In logging, slash is described as any material left on the ground after trees have been cut. Slash burials of headwater streams in Washington are more likely due to the steep topography of headwater stream sites. Based on informal surveys of timber managers, Jackson et al. (2001) inferred that slash burials are common across headwater streams with moderate to steep slopes. Slash burial in these unbuffered clear-cut streams reduces the sediment flushing, resulting in greatly reduced numbers of *A. truei* and *Dicamptodon*, perhaps due to less available microhabitat and reduced gill function (Jackson et al. 2001).

Another effect of timber harvest on headwater streams is the increase in average stream temperature (Brown and Krygier 1970, Moore et al. 2005, Pollock et al. 2009). Brown and Krygier (1970) found that for one watershed in Oregon's coast range, average monthly maximum temperatures increased by 14° F (7.78° C) one year after clear cutting. Moore et al. (2006) and Pollock et al. (2009) confirmed that clear cutting streams with no riparian buffers,

particularly small and shallow streams, resulted in significant temperature increases, and stream temperatures did not return to pre-logging temperatures until 5-10 years after logging (Moore et al. 2006). Riparian buffers in areas of clear-cut logging, however, prevent stream temperatures from significantly increasing (Brown and Krygier 1970, Moore et al. 2006). Most amphibians that inhabit these streams thrive at streams below 16° C, and few exist in streams that reach temperatures above 20° C. In Pollock's (2009) study, the mean daily maximum temperature of streams in harvested (25%-100%) plots was 14.5° C, which was 2.4° C higher than in unharvested plots. Only the plots that were 100% harvested had mean daily maximum temperatures that crossed the threshold of 16° C (Pollock et al. 2009). Such increases in stream temperature are detrimental for *R. olympicus* due to its reliance on cool aquatic habitat. In addition, it is presumed that *R. olympicus* lacks the ability to travel far enough overland to find more suitable habitat and the roads and culverts crossing these headwater streams may also be barriers (Bury and Corn 1988, Howell and Roberts 2008). Although since 1988 the Olympic National Forest has adopted passive riparian restoration measures (Martens et al. 2019), and the Olympic National Park no longer allows frequent timber harvest, the long-term harm to many populations of *R. olympicus* may have occurred prior to this time.

Riparian forests are of special importance to salamanders in the Pacific Northwest, where all 30 native species require riparian forests for reproduction and/or food acquisition (Clipp and Anderson 2014). Given the obvious benefits of protecting riparian zones, it is of concern that there is evidence that even with riparian buffers logging can negatively impact stream-dwelling amphibians. In Appalachian headwater streams with buffers of up to 30m, the available habitat for the resident populations of salamanders from the genera *Desmognathus* and *Eurycea* was reduced, such that salamanders not only were found closer to the stream, but population densities

of salamanders in the stream increased, and the average body condition of salamanders decreased (Peterman et al. 2011).

Just as timber harvest fragments forest ecosystems, culverts fragment streams. Culverts are a more economical alternative to bridges (Fragkakis et al. 2015) but have a greater impact on water quality and lotic habitat through the deposition of sediment (Wellman et al. 2000) and by creating physical barriers to animal movement (Anderson et al. 2014). Culverts are often responsible for isolating upstream and headwater habitats (Anderson et al. 2014). Although stream fragmentation by culverts is generally considered by scientists and policy makers because of its impacts on economically important fish species, culvert placement and design might be expected to have a larger impact on aquatic salamanders because they are generally not as strong of swimmers as fish (Anderson et al. 2014) and lack the ability to leap up to culverts with substantial overhangs. One study of Appalachian stream salamanders found that culverts do not have as strong of a barrier effect as initially expected, and that road effects may have more to do with a loss of riparian vegetation (Ward et al. 2008). A later study of stream-associated salamanders in the Appalachian Mountains, however, found that culverts with at least 5 cm of overhang were partial barriers, and those with 10 cm or more were full barriers to salamander passage (Anderson et al. 2014). Conflicting conclusions about the effects of culverts on salamanders underscore the importance for a study to determine how Olympic Torrent Salamander occupancy and abundance are affected by stream fragmentation due to culverts in forests on the Olympic Peninsula.

When defining habitat criteria necessary for healthy species populations, it is common to think of one set of criteria as drivers of both occupancy and abundance. However, studies of habitat correlates for two salamander species (Welsh and Lind 1995, 1996) found that the

variables that were the best predictors of salamander occupancy in a given stream reach were not the best predictors for salamander abundance in those streams. Welsh and Lind (1995, 1996) showed the need to compare multiple questions and hypotheses simultaneously, as opposed to crafting a single hypothesis from which to work. My questions are focused on addressing both timber harvest and road culverts as potential drivers of variation in *R. olympicus* occupancy and abundance in headwater streams throughout its range.

The best framework for this kind of analysis is an information theoretic approach, as described in the seminal book on the topic by Burnham and Anderson (2002). This approach steers away from the initial reporting of p-values and effect sizes and instead focuses on the use of metrics of relative empirical support such as Akaike's Information Criteria (AIC), and has adjustments that can be applied for small sample size (AIC_c) and overdispersion of data (QAIC). I will begin my analyses with this framework in order to simultaneously compare hypotheses from my research questions using scores that can be directly compared to determine which model is the "best" model, or the model that most reliably links the variation observed in the response variable to possible causes.

One primary goal of this research is to provide more reliable information about habitat use by *R. olympicus*, thus improving our ability to maintain resilient populations (Howell and Roberts 2008). The research analysis was divided into questions about habitat occupancy versus abundance. For both sets of questions I conducted model selection to determine which models best link possible causes to the patterns of presence and abundance that I observed in the field. I collected data over the course of a single field season, conducting salamander surveys and measuring abiotic environmental data from a total of 139 stream reaches in 77 different streams.

The intent is for this thesis research to improve the effectiveness of management and conservation planning and actions in the Olympic National Forest and Olympic National Park.

Chapter 1: Occupancy analysis for the Olympic Torrent Salamander (*R. olympicus*) in the Olympic National Park and National Forest

Introduction

Knowing the spatiotemporal patterns of distribution and abundance of a species and documenting the relevant ecological correlates with those patterns provides a basis for understanding the important factors allowing populations to persist. Olympic Torrent Salamanders (*Rhyacotriton olympicus*) are known to inhabit streams that exhibit a narrow range of environmental conditions in the maritime climate of the Pacific Northwest bioregion. These salamanders are occupants of late successional forests and are most commonly found in headwater streams with a narrow range of 12-14° C (Howell and Roberts 2008). They are associated with streams that are relatively clear of sediment, as they tend to utilize the space between medium and large streambed substrata as microhabitat, but the acceptable turbidity range for *R. olympicus* has not been determined (Petranka 1998, Hammerson 2004, Corkran and Thoms 2006). The ability of the governmental agencies to maintain forest streams on the Olympic peninsula that are conducive to the persistence of torrent salamanders depends on the government's forest management activities, particularly if clear cut logging and road building occur (Reeves et al. 2006).

Olympic Torrent Salamanders apparently remain in small home ranges throughout their lives, and the habitat use of by *R. olympicus* is strongly associated with stream and stream banks of headwater streams (Nussbaum and Tait 1977, Petranka 1998, Adams and Bury 2002). Hence, it is likely that variation among watersheds in how they are altered by humans will result in commensurate variation in occupancy of *R. olympicus* salamanders among streams and watersheds. Managing forest activities at the spatial scale of the watershed should allow for focused conservation efforts to maintain the habitat needs of lotic vertebrates such as *R. olympicus*. For example, watersheds act as an isolating influence for populations of cutthroat

trout, but historical connections among watersheds also influenced the patterns of isolation among populations (Loxterman and Keeley 2012). Similarly, it is likely that *R. olympicus* would also be restricted by the physical boundaries of watersheds because it is primarily restricted to the headwater streams within each watershed.

Howell and Robert's 2008 conservation assessment of *R. olympicus*, the most recent discussion of the threats facing the Olympic Torrent Salamander, emphasizes that the greatest threats of anthropogenic forest disturbance are culverts, roads, and timber harvest. Timber harvest reduces stream quality and continuity that are important for the persistence of *R. olympicus* populations. Jackson et al. (2001) observed that slash burial of headwater streams was a common phenomenon, despite timber harvesters' insistence that these burials did not happen on lands they managed. Decreases in water quality as a direct result of timber harvest are especially pronounced on streams that lack riparian buffers (Clinton 2011). Olympic Torrent Salamanders are thought to be especially sensitive to decreases in habitat quality and are not likely to repopulate streams once extirpated (Bury and Corn 1988).

Culverts likewise pose threats to habitat quality, primarily through the potential of connectivity losses from overhangs and changes to stream composition at culvert outflows and changes to downstream sediment load and substrate composition. There is evidence that road crossings of streams using culverts present a barrier to amphibian dispersal (Cushman 2005, Anderson et al. 2014). And while the impacts of roads on stream sediment are well-documented (Trombulak and Frissell 2000), the literature is conflicted on whether culverts themselves impact downstream sediment load. Wellman et al. (2000) found that culverts did impact downstream sedimentation in one southern Appalachian forest, while Arismendi et al. (2017) found that there were minimal increases following road improvement, timber harvest, and timber hauling in a

forest in northwestern Oregon. Howell and Roberts (2008) identified increased sedimentation and physical barriers from culverts as threats to *R. olympicus* microhabitat use in headwater streams.

Separating the factors that affect a species' distribution from those that may be merely coincidental often requires the simultaneous comparison of multiple questions and hypotheses. Using an information theoretic approach (Burnham and Anderson 2002) allowed me to assess multiple hypotheses and models using empirical metrics that can be compared across models to determine which model is the best for discriminating among alternative hypotheses and answering an integrative research question.

Addressing the anthropogenic threats facing *R. olympicus* populations requires answering two research questions and their associated hypotheses about age of forest stands and use of culverts. First, *how does local forest age impact the occupancy of R. olympicus in streams across its range?* In a retrospective study of forest fauna abundance in different forest management conditions, Raphael et al. (2002) found that Olympic Torrent Salamanders were more abundant in streams within older forest stands than in younger stands. Welsh and Lind (1996) also determined that Southern Torrent Salamanders (*R. variegatus*), a closely related species to *R. olympicus*, is associated with characteristics of late seral stage forests. In their 1988 study on the effects of timber harvest on stream amphibians, Bury and Corn suggested that Olympic Torrent Salamanders “probably” go extinct following clear cutting, but did not provide evidence to support their claim. Given what we know about the association between torrent salamanders and cooler, more humid forests and cold, clear streams, I expect that streams surrounded by mature forests will have significantly higher rates of occupancy by *R. olympicus* than in streams surrounded by recently harvested forests.

It is assumed that culverts may add to survival and dispersal challenges for *R. olympicus* (Howell and Roberts 2008), but that assumption is best tested by comparing presence of the salamander in stream reaches both above and below culverts. Thus, my second question: *Are the effects of culvert on salamander occupancy driven primarily by sedimentation or by the culverts acting as barriers to salamander dispersal?* On many primitive logging roads, a low-cost alternative to bridges has been to infill, but use culverts to permit stream flow. About 19.5% of watersheds studied by Anderson et al. (2014) revealed that culverts in streams reduced waterborne dispersal by salamanders more than by fish perhaps because salamanders are comparatively poor swimmers. Anderson et al. (2014) judged culverts with downstream overhang of greater than 5 cm above stream flow as partial barriers to salamander passage and culverts with a downstream overhang of greater than 10 cm to be complete barriers to upstream movement. In a study of *Dicamptodon* larvae, the largest and most powerful aquatic salamanders in northwestern streams, Sagar (2004) found that no larvae were able to pass through pipe culverts and only 2 of 2,215 larvae were able to fully pass arch culverts traveling upstream. Another effect of culverts is that sediment load is increased downstream. Wellman et al. (2000) found sediment depth and proportion of silt-clay in the sediment to be higher downstream from culverts, but in another study, Honeycutt et al. (2016) reported no effect of culverts on sediment levels in streams. It is self-evident that the effect of culverts on stream sediments may vary based on such factors as sediment types and amounts, stream rockiness, steepness and flow rate of streams and culvert design. Given what we know about how culverts act primarily as one-way barriers, I expect that variations in rates of *R. olympicus* occupancy above and below road crossings is primarily driven by the physical barriers created by culverts.

Methods

Study Area and Site Selection

The Olympic Torrent Salamander's current range extends throughout the Olympic Peninsula in Washington State (Good and Wake 1992). According to the most recent assessment by the International Union for Conservation of Nature, *R. olympicus* is found in 41% of the streams and 47% of the seeps surveyed in Olympic National Park (Hammerson 2004). I conducted field surveys with an assistant in the Olympic National Park and Olympic National Forest, which cover a combined 6,275.69 km² (1,550,756.77 acres) within the Olympic Peninsula (National Park Service 2011, USDA Forest Service 2012). We conducted surveys Monday through Wednesday 12 of the 14 weeks between June 17th and September 17th. We avoided sampling streams on private lands due to the lack of consistent land management and increased difficulty in securing access to streams on private lands. We surveyed first through third order streams (*sensu* Strahler 1957) crossed by roads within Olympic National Forest and Olympic National Park.

To test my hypotheses, we conducted stream surveys at 77 first through third order streams throughout the Olympic National Park and Olympic National Forest; survey sites are shown in **Figure B.1**. Of the sites surveyed, 25 were bordered by at least 75 meters of mature forests (30+ years) in all directions, and the other 52 sites were within 75 meters of forest harvested within the last 30 years. At each site we surveyed one stream reach, defined as any given length of a stream, upstream of the culvert and road crossing, and one reach downstream except where the downstream reach was not safely accessible; this occurred at 15 of the 77 streams, hence we surveyed 62 downstream sections and 77 upstream sections. Each sampling site contained 10 meters of perennial aquatic habitat (seep, spring, or stream channel), extending

from 50 to 60 m from the culverts. **Figure C.1** shows a generalized diagram of how I determined which stream reaches were surveyed. At each site I used a Yardage Pro rangefinder (Bushnell; Overland Park, KS) to measure 50 meters from the culvert to the upstream survey site, where my field assistant and I then used the rangefinder to mark off a 10-meter stream reach.

Physical and Chemical Measurements in Streams

In each delineated study area, we measured 1) pH with an Oakton pH Testr 20, 2) turbidity with a Hach 2100p portable turbidimeter, 3) dissolved oxygen % with a YSI Pro 20 probe, and 4) stream flow rate with a Flowtech flow meter. All stream variable measurements were taken at the center of the stream reach unless that point was not characteristic of the reach as a whole (*e.g.*, a waterfall). If the stream channel was split, we took measurements in each channel and averaged them. The fifth stream measure was a visual estimate of the prevalent and second most prevalent stream substrata for each 10 m stream transect.

Measurement of the Near-stream Forest

We also measured and recorded several ecologically relevant factors in the near-stream forest. We calculated percent canopy closure by averaging four measurements from a spherical crown densiometer: one downstream, one upstream, and one facing each bank of the stream. We also measured aspect using the compass application on an iPhone 6S. We measured the stream gradient (slope) with a Suunto digital altimeter, measuring the elevation (± 1 m) at the upper and lower ends of the 10 m section of stream then calculating stream gradient (slope) by dividing the difference in elevations by the 10 m length of the stream transect. Finally, we visually determined dominant tree type based on both quantity of trees in the vicinity of the stream and

which individual trees influenced stream shading the most. After completing the stream and forest characteristic sampling we entered the stream for salamander surveys.

Salamander Sampling

Each survey for salamanders started at the downstream end of the 10 m transect and progressed upstream. The survey areas upstream began 50 m from the culvert and extended to 60 m from the culvert; survey areas downstream began 60 m from the culvert and extended to 50 m from the culvert. Adjustments in distance of the transect from the culvert were made if the stream was impassable at a distance from the culvert less than 50m. My assistant and I conducted fixed-area aquatic searches as described by Welsh (1987) and Bury and Corn (1991) during daylight hours to determine the number of individuals at each site as well as the presence or absence of other stream-associated vertebrates and crayfish (*Pacifastacus leniusculus* Dana, 1852). We searched for salamanders in suitable habitat in accordance with the procedure described by Welsh and Lind (1996): 1) search from downstream up, 2) turn over all pebbles, cobbles, and boulders 3) sift finer substrates carefully through one's fingers, 4) sift down to the hard bottom of the streambed or to a depth of 15 cm, and 5) if a salamander is seen escaping deeper it will be pursued. We captured both adult and larval salamanders, separately recorded the counts of larvae and adults based on appearance and location of capture, and then immediately returned to the spot they were found.

Because we searched thoroughly, I assumed that the capture rate was correlated to absolute densities so that the relative densities per 10 m reach were valid for comparing abundances of *R. olympicus* among sites (Bury and Corn 1991). In their 1991 report on amphibian sampling in the Pacific Northwest, Bury and Corn stated that "hand collecting of one

10-meter long segment of stream was sufficient to determine both occurrence and relative abundance of aquatic amphibians.” They explained that this is appropriate when the goal of the study is to characterize broad patterns of variation across streams, as opposed to a more intensive study of a single stream. To quantitatively justify the 10-meter survey length, Bury and Corn (1991) calculated the probability of failing to detect a present species (P) using the following formula:

$$P = q^n$$

where “q = the proportion of 1-meter segments where the species was absent, and n = the length (m) of the survey”. Using this formula, Bury and Corn determined that there is a 3.8% chance of not finding *R. olympicus* in a 10-meter stream segment in which they are present.

GIS Analysis

The data I used for my GIS analysis were retrieved from a variety of state and federal organizations, and the International Union for Conservation of Nature (IUCN). The stream data layer was derived from the Channel Migration Potential Stream Networks dataset (2015) from the Washington State Department of Ecology. Both the National Forest System roads layer (2015) and the Timber Harvests layer (2016) were retrieved from the United States Forest Service. The current geographic range of *Rhyacotriton olympicus* was retrieved from the most recent available data on the IUCN Red List website (2004, version 3.1). HUC-8 watershed boundaries were retrieved from the National Watershed Boundary Database (2013) through the United States Geologic Survey.

After collecting my field data, I used ArcGIS Pro to extract spatial data for model analyses including whether each site was in recently harvested or mature forest, the distance in

meters from each culvert to the nearest harvested forest, the HUC-8 (8 digit hydrologic unit code) watershed each site was in, and to determine the road order for each road that contained one of my stream crossings. The road and stream data were used to find stream crossings on first to third order streams, and the logging data were used to determine which forest age category the survey areas fall under. For analysis of proximity to recently harvested forests, I used two tools. To determine whether a given road crossing was within 75 meters of a recently harvested forest I created buffers around each of the points and determined which buffers intersected with areas of recently harvested forest. To create a continuous variable of distance to harvested forest, I used the “near” tool to extract the Euclidean distance from each stream crossing to the nearest recently harvested forest.

Road order is a metric based on the stream order system (*sensu* Strahler 1957) used for approximating the level of use and other characteristics of a given road segment. The same rules for branching and increasing the order of the stream are applied to roads. The Horton-Strahler index has been used to classify relationships in a variety of branching networks including social networks (Arenas et al. 2004) and mammalian respiratory systems (Horsfield 1976). The previous use of the index for novel systems suggests it may be an appropriate tool for assessing a branching road system as well.

Statistical Analysis

I used an information-theoretic approach to investigate the relationship between candidate models and *R. olympicus* occupancy. I used R Studio (RStudio Team 2015) with R version 3.5.1 for all analyses. Before conducting any model selection, I performed a goodness of fit test on the global model to compare the observed salamander occupancy data to a theoretical binomial

distribution. A non-significant p-value ($\alpha = 0.05$) indicates that the observed data distribution does not significantly deviate from the chosen theoretical distribution.

I built 23 a priori models using 11 habitat variables to test in predicting target species occupancy within streams (**Table 1.1**).

Table 1.1. Complete list of models used in model selection analysis for salamander occupancy.

1.	Null model	13.	FS + HD
2.	Stream Number	14.	FS + Tu
3.	Forest Stage	15.	HD + Tu
4.	Harvest Distance	16.	FS + HD + Tu
5.	Road Order	17.	SD + RO
6.	Gradient	18.	FS + Gr
7.	Turbidity	19.	HD + Gr
8.	Temperature	20.	FS + HD + Gr
9.	Stream Flow	21.	FS + Gr + Tu
10.	Canopy Closure	22.	HD + Gr + Tu
11.	Dominant Tree	23.	FS + HD + Gr + Tu
12.	Stream Direction		

All variable definitions are listed in **Appendix A**. The global model was used for goodness of fit analysis, and not included in the candidate model set because that combination of variables did not represent a meaningful ecological hypothesis. I applied the AIC_c adjustment to all models in the candidate set to account for a small sample size to parameters ratio using the following equation:

$$AIC_c = 2K - 2\log(\mathcal{L}(\hat{\theta}|y)) + \frac{2K(K + 1)}{n - K - 1}$$

where $\mathcal{L}(\hat{\theta}|y)$ is the maximum value of the likelihood function of the model, K is the number of parameters used in the model, and n is the sample size. If the $n:K$ ratio is lower than 40:1 AIC_c

will provide more accurate results; additionally, if the $n:K$ ratio is high any correction from AIC_c will be negligible (Burnham and Anderson 2002). I also used generalized linear model regression analyses to examine the effect sizes for both the composite models and the individual predictor variables.

Results

We found salamanders in 42 of 77 (54.55%) streams surveyed, and 61 of 139 (43.88%) individual stream reaches surveyed. 25 of 61 (40.98%) stream reaches containing salamanders were downstream of culverts, while 36 of 61 (59.02%) were upstream of culverts. The observed detection probabilities at the stream reach level varied from 0.1176 to 0.6154 across the HUC-8 sub-basins (**Figure B.2a**). I also found varying rates of occupancy across stream gradients (**Table 1.2**).

Table 1.2. Average occupancy at each observed stream gradient.

<i>Stream Gradient % (slope)</i>	<i>Average occupancy</i>
0	0.333
10	0.173
20	0.490
30	0.790
40	0.700
50	0.800

Timber Harvest

Local forest age was one of the factors included in several of the models that showed substantial evidence for being the best model to explain variation in salamander stream occupancy. But when comparing the spread of the harvest distance data using notched boxplots, it is clear that this factor alone cannot predict salamander presence. When plotted, there is a

substantial overlap of the notches on the boxplots which represent rough 95% confidence intervals, meaning that there is no significant difference (**Figure D.2**) (McGill et al. 1978). Additional analysis of both Forest Stage and Harvest Distance as univariate logistic regression models showed nonsignificant effects on salamander presence (**Table 1.6**).

Culverts

None of the models containing factors relating to culverts (stream direction and road order) showed any evidence of predicting salamander presence. The high ΔAIC_c scores do not support the hypothesis that culverts acting as physical barriers to salamander movement impacts salamander presence in streams. The results of the logistic regression analysis for stream direction, displayed in **Figure D.3**, show that despite the increase in observed occupancy upstream of culverts, stream direction is not a significant factor in salamander occupancy.

Model Selection

Before conducting any model selection, I used the global model to determine an overall goodness of fit for the observed binomial occupancy data. The residual deviance for the global model was 116.4, and the residual degrees of freedom were 105. These inputs resulted in a p-value of 0.2103, which means that the observed *R. olympicus* occupancy did not significantly differ from the theoretical binomial distribution. The overdispersion parameter, estimated from the global model (Burnham and Anderson 2002), was 1.109. A low overdispersion parameter and a high p-value, paired with a low sample to model ratio allowed me to use the AIC_c , or second-order AIC, as an appropriate metric for comparing models in the candidate set. Next, I examined some of the top models based on their ΔAIC_c scores.

Of the 23 models included in the candidate set, seven showed at least moderate empirical support and five showed strong empirical support. The candidate model with the strongest

support for its ability to predict the presence of a salamander in a stream reach was #22, Salamander Presence ~ Harvest Distance + Gradient + Turbidity ($AIC_c=163.816$ $w_i=0.2291$). As shown below in **Table 1.3**, all models that included Gradient showed at least moderate support based on their ΔAIC_c scores of four or lower. The predictor that differentiated between the best and second-best models was turbidity. Turbidity itself had a small impact on the fit of the model.

Table 1.3. Summary statistics for all models included in the model selection analysis for salamander occupancy. Bolded models indicate $\Delta AIC_c \leq 4$.

<i>Model #</i>	<i>Predictor Variables</i>	<i>K</i>	<i>Log Likelihood</i>	<i>Deviance</i>	<i>AIC_c</i>	ΔAIC_c	<i>AIC_c Weight</i>
1	Null Model	2	-92.997	185.994	193.667	29.851	7.55E-08
2	Stream Number	2	-89.871	87.467	183.83	20.014	1.03E-05
3	Forest Stage	3	-88.797	87.639	183.771	19.955	1.06E-05
4	Harvest Distance	3	-88.519	88.103	183.216	19.400	1.40E-05
5	Road Order	5	-87.294	83.151	185.039	21.223	5.64E-06
6	Gradient	4	-79.145	96.102	164.59	0.774	0.1556
7	Turbidity	9	-85.634	91.46	178.664	14.848	0.0001
8	Temperature	3	-89.231	89.22	184.641	20.825	6.89E-06
9	Flow	3	-88.316	90.259	182.81	18.994	1.72E-05
10	Canopy Closure	3	-88.213	83.595	182.603	18.787	1.91E-05
11	Dominant Tree	18	-78.577	59.816	198.854	35.038	5.65E-09
12	Stream Direction	3	-88.285	79.395	182.748	18.932	1.77E-05
13	FS + HD	4	-88.276	87.909	184.85	21.034	6.20E-06
14	FS + Tu	10	-84.972	91.848	179.663	15.847	8.30E-05
15	HD + Tu	10	-84.613	91.881	178.945	15.129	0.0001
16	FS + HD + Tu	11	-84.507	91.891	181.093	17.277	4.06E-05
17	SD + RO	6	-85.62	74.666	183.876	20.06	1.01E-05
18	FS + Gr	5	-78.244	95.58	164.94	1.124	0.1306
19	HD + Gr	5	-77.838	96.529	164.128	0.312	0.1960
20	FS + HD + Gr	6	-77.677	96.055	165.991	2.175	0.0772
21	FS + Gr + Tu	12	-76.171	95.831	164.817	1.001	0.1389
22	HD + Gr + Tu	12	-75.67	95.805	163.816	0	0.2291
23	FS + HD + Gr + Tu	13	-75.609	95.777	166.131	2.315	0.0720

The top performing model was Salamander Presence ~ Harvest Distance + Gradient + Turbidity. It had the lowest AIC_c score of any candidate model at 163.816 and therefore a ΔAIC_c

score of 0. Models #3 (forest stage), #4 (harvest distance), and #7 (turbidity) lack a clear univariate pattern when plotted against salamander presence (**Figure D.1**).

Model Subset Analysis

After determining which models provided the greatest empirical support for the stated hypotheses, more inference was required to understand which variables were the relatively strongest predictors for salamander presence. Selecting the appropriate threshold for selecting models with “enough” empirical support was difficult, as setting the cutoff criterion at the wrong point can lead to bias in the outcomes or even exclusion of the best model from the subset (Grueber et al. 2011). I included all models with $\Delta AIC_c \leq 4$ in the model averaging (**Table 1.4**). The common variable in each of the seven candidate models is Stream Gradient (Gr). The cumulative weight (w_i) of the selected subset indicates that the cumulative probability of Stream Gradient being present in the best model is 0.9994 (99.94%). Both the weights and the ΔAIC_c scores support this pattern (**Table 1.4**). Across models, gradient shows a consistent positive relationship to increased salamander occupancy. The other variables display a high degree of uncertainty as shown by standard errors nearly equal to, or in some cases larger than, the coefficient (**Table 1.5**). Additionally, the R^2 values in **Table 1.6** indicate that all variables other than Gradient fit the data very poorly.

Table 1.4. Subset of models ($\Delta AIC_c \leq 4$) selected for further analysis. Models listed in order of increasing ΔAIC_c .

<i>Model</i>	<i>df</i>	<i>Log Likelihood</i>	<i>Log-likelihood R²</i>	<i>AIC_c</i>	<i>ΔAIC_c</i>	<i>Weight</i>
HD + Gr + Tu	5	-75.67	0.132	163.816	0.000	0.2291
HD + Gr	4	-77.84	0.155	164.128	0.312	0.196
Gr	3	-79.15	0.139	164.59	0.774	0.1556
FS + Gr + Tu	5	-76.17	0.125	164.817	1.001	0.1389
FS + Gr	4	-78.24	0.149	164.94	1.124	0.1306
FS + HD + Gr	6	-77.68	0.156	165.99	2.175	0.0772
FS + HD + Gr + Tu	13	-75.61	0.132	166.13	2.315	0.072

Table 1.5. Coefficient and standard error values for all models in selected subset, measured in change in log odds of salamander presence at the 10-meter stream reach level. Values taken from logistic regression models.

<i>Model</i>	<i>Harvest Distance</i>	<i>Gradient</i>	<i>Turbidity</i>	<i>Forest Stage</i>
HD + Gr + Tu	-0.0003 ± 0.0002	0.083 ± 0.021	-0.024 ± 0.211	-
HD + Gr	-0.0003 ± 0.0002	0.091 ± 0.021	-	-
Gr	-	0.092 ± 0.021	-	-
FS + Gr + Tu	-	0.083 ± 0.021	0.038 ± 0.153	-0.456 ± 0.412
FS + Gr	-	0.091 ± 0.021	-	-0.545 ± 0.408
FS + HD + Gr	-0.0003 ± 0.0002	0.091 ± 0.021	-	-0.241 ± 0.483
FS + HD + Gr + Tu	-0.0003 ± 0.0002	0.083 ± 0.021	0.017 ± 0.154	-0.155 ± 0.489

Table 1.6. Summary statistics for univariate fixed effects of all variables in selected subset. Coefficient and standard error measured in change in log odds of salamander presence at the 10-meter stream reach level. Bolded values indicate significant p-value ($\alpha=0.05$).

<i>Predictor</i>	<i>Coefficient ± SE</i>	<i>Log-likelihood R²</i>	<i>P-value</i>
Gradient	0.092 ± 0.021	0.132	8.7e-6
Turbidity	0.107 ± 0.112	0.005	0.36
Harvest Distance	-0.0004 ± 0.0002	0.019	0.097
Forest Stage	-0.618 ± 0.372	0.015	0.097

Discussion

Although I began this study planning to investigate anthropogenic effects on *R. olympicus* distribution, the variable with the clearest impact on salamander occupancy in headwater stream reaches was stream gradient. All models containing stream gradient showed empirical support for being the best available model, and stream gradient was the only univariate model that showed any evidence for impacting the response variable. The finding of a positive relationship between steeper streams and increased average occupancy is consistent with conclusions in other studies (Bury and Corn 1988, Adams and Bury 2002, Howell and Roberts 2008, Ward et al. 2008). However, we observed salamanders in 10 of 55 (18.18%) of the stream reaches with 0% and 10% gradients including one low-gradient stream reach containing 28 salamanders, suggesting that *R. olympicus* may have a greater tolerance for low gradient streams than stated elsewhere. Steeper stream gradient is indicative of greater flushing capacity (Bury and Corn 1988), as well as a possible absence of competition from salmonid species (Kroll et al. 2008). Both may be factors in *R. olympicus*' greater association with steeper streams but do not preclude them from streams with lower gradients. Conservations assessments by the IUCN Red List (Hammerson 2004) and the U.S. Forest Service (Howell and Roberts 2008) both make statements suggesting that lower gradient streams may not be suitable habitat for *R. olympicus*. My data are not in agreement with those statements.

The results pertaining to anthropogenic forest stresses were inconclusive. My initial hypothesis regarding local forest age was not supported by the results of the model selection and logistic regression analyses. Both Forest Stage and Harvest Distance were included in the models that showed the strongest evidence as being predictors of salamander occupancy in a stream reach. However, their p-values (0.097, 0.097) and low R^2 values (0.019, 0.015) which resulted

from univariate logistic model analysis indicated a poor fit to the salamander occupancy data (**Table 1.6**). A likely explanation for the lack of a pattern in these variables is that by measuring forest age as either recently harvested or older than 30 years, I obscured patterns between groups in the “older than 30 years” group. Forest ages greater than 30 years contain a variety of successional stages, and *R. olympicus* may exhibit different patterns of association with each of these stages. The preponderance of evidence in the existing literature points to Olympic Torrent Salamanders associating with mature, late successional forests (Bury and Corn 1988, Adams and Bury 2002, Raphael et al. 2002, Howell and Roberts 2008), yet as stated above the method of measuring forest age removes the possibility of seeing this pattern. As a result of this, their inclusion in the selected model subset may have been coincidental with the presence of Gradient in those models. My second hypothesis regarding the effects of culverts was also not supported. The best model including Stream Direction was Salamander Presence ~ Stream Direction + (1|Stream), which had a ΔAIC_c score of 18.932, indicating no empirical support for the model and excluding it from the subset of models selected for further analysis.

Turbidity, like to both Forest Stage and Harvest Distance, shows no significant impact on salamander occupancy (**Table 1.6**). It too appears to have been included in the selected model subset because it was included in models with Gradient, the strongest predictor of salamander presence. Although gradient is related to the flushing capacity of a stream reach, which in turn impacts how much sediment is present in the water of that reach, there are questions about the reliability of the use of turbidity as a surrogate for suspended sediment (Ziegler 2002). As shown in **Table 1.4**, Turbidity had a negative impact on the fit of all models it is in when compared to the analogous models without it.

Management Implications

Knowing that stream reaches with steeper gradients are more likely to contain *R. olympicus* and knowing that my assessment of the effects of timber harvest was inconclusive, my results call for targeted stream and riparian forest management focused on protecting the steep headwater reaches most likely to contain salamanders. While manipulating stream gradient is an act that is largely beyond the scope of human intervention, the finding that steeper stream gradient is a constraint for greater average *R. olympicus* occupancy allows forest managers to target those areas, and areas directly upstream, as being of conservation priority. Management practices could include instituting larger riparian buffer zones around such areas, building on Olympic National Forest buffer practices (Martens et al. 2019). However, the existing literature is not clear on whether this is a useful management practice. Peterman et al. (2011) found that in streams with riparian buffers of widths of up to 30m the associated salamanders were less likely to utilize the riparian zone and exhibited decreased body condition compared to unharvested forests. Although, the lack of significant findings in relation to local forest age could be a result of many forest stages being lumped together in the >30 years group. If *R. olympicus* is only associated with late successional forests (Howell and Roberts 2008), then patterns of low detection probability in forests older than 30 years but younger than late successional would obscure this pattern. In this case, a more useful management option would be to disallow forest harvest near stream reaches of greater concern to allow those forests to reach an appropriate successional stage.

Another concern is the definition of “short-term” effects of logging and timber. Short term connotes a temporary deviation from established conditions. Bury and Corn (1988) define the short term as 5-10 years while Clinton (2011) reported that leaf area may regenerate by up to

68% in the first three years following harvest, but that an elevated maximum stream temperature was recorded for up to 15 years following harvest. Torrent salamanders have a larval stage of 3-4 years during which they are entirely aquatic (Nussbaum and Tait 1977, Petranka 1998), so if short-term effects persist for this entire life stage then referring to them as short term is misleading with regards to possible effects. Additionally, my study was limited to changes in occupancy at the 30-year temporal scale due to my forest stage treatment. However, if the Olympic Torrent Salamander is associated with late successional forests or is slow to repopulate stream reaches once extirpated, then 30 years may not provide enough time to see patterns of repopulation. This could either be a result of the 30-year forest not providing the necessary environmental characteristics, or because the salamanders have simply not made it back to that portion of the stream.

Research Needs

The most important line of inquiry to build upon this work will be completing a model-averaged detection probability analysis to build a stream network map that predicts Olympic Torrent Salamander occupancy at the 10-meter stream reach level. Using the subset of models selected in the previous analysis, I will be able to map the headwater stream network of the Olympic peninsula and assigned a weighted detection probability to each 10-meter stream reach to predict areas of high occupancy probability, as well as areas that have a lower detection probability than expected based on stream gradient and other characteristics. This crucial next step in the distribution analysis will be able to better explain the variation seen in my occupancy data (**Figure B.3**), as well as serve as a roadmap for improved *R. olympicus* management.

Other important studies for creating a more complete picture of *R. olympicus* distribution include a study looking at characteristics on a broader spatial scale, as were included by Welsh and Lind (1996). While gradient was a significant predictor at the reach scale, other predictors may have effects that become clear at coarser resolutions. A second avenue of inquiry should be to examine the effects of forest age, separated in a manner that can find associations with specific successional stages, on *R. olympicus* distribution. One of the major limitations of my approach to measuring forest age is the inability to look at patterns found between age groups greater than 30 years, which is crucial in determining the true effects of timber harvest and assessing patterns of association with late successional forests that are supported by the existing literature. The final path for suggested future research is a study of the dispersal abilities and tactics of *R. olympicus*. The assumption for the species is that of extreme philopatry, and very limited dispersal even within streams. However, there have been no studies focused on its ability to travel between streams or around barriers in a single stream. A change in this assumption could drastically change the hypotheses associated with the needs of *R. olympicus*, as well as its ability to select suitable habitat and leave unsuitable habitat.

Chapter 2: Abundance analysis for the Olympic Torrent Salamander (*R. olympicus*) in the Olympic National Park and Olympic National Forest

Introduction

Analyzing abundance in addition to occupancy may increase the confidence in the importance of patterns discovered during analysis of occupancy, or it may shed light on other factors that help define optimal habitat as opposed to minimum acceptable habitat. In other studies of forest salamanders, it has been shown that the factors driving variation in abundance are often different, and operating at different scales, than those driving occupancy (Welsh and Lind 1995, 1996). In these studies, occupancy was related to the minimum suitable habitat available for a species while abundance is more closely related to determining the best available habitat.

Olympic Torrent Salamanders apparently remain in small home ranges throughout their lives, and the habitat use of by *R. olympicus* is strongly associated with stream and stream banks of headwater streams (Nussbaum and Tait 1977, Petranka 1998, Adams and Bury 2002). Hence, it is likely that variation among watersheds in how they are altered by humans, will result in commensurate variation in abundance of *R. olympicus* salamanders among streams and watersheds. Managing forest activities at the spatial scale of the watershed should allow for focused efforts to maintain the habitat needs of lotic vertebrates such as *R. olympicus*. For example, watersheds act as an isolating influence for populations of cutthroat trout, but historical connections among watersheds also influenced the patterns of isolation among populations (Loxterman and Keeley 2012). Similarly, it is likely that *R. olympicus* would also be restricted by the physical boundaries of watersheds because it is primarily restricted to the headwater streams within each watershed.

Addressing the anthropogenic threats facing *R. olympicus* populations requires answering three research questions and their associated hypotheses about age of forest stands and use of culverts. *First, how does local forest age impact the abundance of R. olympicus in streams*

across its range? One study of amphibians in Olympic National Park (Adams and Bury 2002), found Olympic Torrent Salamanders had a weak relationship with increased canopy cover, a characteristic of older forests, while another study (Raphael et al. 2002) found that Torrent Salamanders were associated with older forests. Welsh and Lind (1996) determined that Southern Torrent Salamanders (*R. variegatus*), a closely related species to *R. olympicus*, are also associated with characteristics of late seral stage forests. In a study on the effects of timber harvest on stream amphibians, Bury and Corn (1988) suggest that Olympic Torrent Salamanders “probably” go extinct following clear cutting, indicating the potential for an inverse relationship between forest age and abundance. Given what we know about how timber harvest increases stream sedimentation levels, I expect that streams with close proximity to recently harvested forests will have significantly lower rates of abundance of salamanders when compared to mature forests.

It is assumed that culverts may add to survival and dispersal challenges for *R. olympicus* (Howell and Roberts 2008), but that assumption is best tested by comparing counts of the salamander in stream reaches both above and below culverts as well as comparing sediment above and below culverts. Thus, my second question: *Are the culvert effects on salamander abundance driven primarily by sedimentation or by the culverts acting as barriers to salamander dispersal?* Anderson et al (2014) found that culverts act as one-way barriers to salamander dispersal and isolated up to 20.4% of the watersheds they studied. Sagar (2004), in their study of *Dicamptodon* salamander distribution, also found that larval salamanders did not fully pass through pipe culverts when moving upstream, though some individuals did use the culverts as shelter. For reasons that have not yet been studied, Olympic Torrent Salamanders movement is predominantly upstream (Howell and Roberts 2008) which indicates that culverts may have a

substantial influence on their distribution in headwater stream reaches. Given what we know about how culverts act primarily as one-way barriers I expect that variations in average *R. olympicus* abundance above and below road crossings is primarily driven by the physical barriers created by culverts. However, culverts have also been found to increase sediment levels downstream of culverts due to the accumulation of sediment in pools that form at culvert outflows, and the subsequent flushing of that sediment during times of higher flow (Wellman et al. 2000). Olympic Torrent Salamanders require clear streams because they utilize the space between large substrata as refugia (Petranka 1998, Corkran and Thoms 2006). The lack of essential microhabitat is likely to decrease the abundance of salamanders in an affected stream reach. Given what we know about the microhabitat substrate needs of *R. olympicus*, a secondary hypothesis is that increased stream sediment levels from road crossings drives variation in *R. olympicus* abundance above and below culverts.

The literature on both culverts and timber harvest discuss changes to sediment regimes in streams (Wellman et al. 2000, Jackson et al. 2001, Clinton 2011). Because streams can frequently be under the stress of both forest harvest and culverts, I developed a third question: *How do road effects and timber harvest interact to impact R. olympicus abundance in streams?* Given what we know about the detrimental effects of both timber harvest and culverts as a result of increased sediment in the stream, I expect that these two variables will cause a decrease in the relative abundance of *R. olympicus* that cannot be explained solely by the two main effects.

Methods

Study Area and Site Selection

The Olympic Torrent Salamander's current range extends throughout the Olympic Peninsula in Washington State (Good and Wake 1992). According to the most recent assessment by the International Union for Conservation of Nature, *R. olympicus* is found in 41% of the streams and 47% of the seeps surveyed in Olympic National Park (Hammerson 2004). I conducted field surveys with an assistant in the Olympic National Park and Olympic National Forest, which cover a combined 6,275.69 km² (1,550,756.77 acres) within the Olympic Peninsula (National Park Service 2011, USDA Forest Service 2012). We conducted surveys Monday through Wednesday 12 of the 14 weeks between June 17th and September 17th. We avoided sampling streams on private lands due to the lack of consistent land management and increased difficulty in securing access to streams on private lands. We surveyed first through third order streams (*sensu* Strahler 1957) crossed by roads within Olympic National Forest and Olympic National Park.

To test my hypotheses, we conducted stream surveys at 77 first through third order streams throughout the Olympic National Park and Olympic National Forest; survey sites are shown in **Figure B.1**. Of the sites surveyed, 25 were bordered by at least 75 meters of mature forests (30+ years) in all directions, and the other 52 sites were within 75 meters of forest harvested within the last 30 years. At each site we surveyed one stream reach, defined as any given length of a stream, upstream of the culvert and road crossing, and one reach downstream except where the downstream reach was not safely accessible; this occurred at 15 of the 77 streams, hence we surveyed 62 downstream sections and 77 upstream sections. Each sampling site contained 10 meters of perennial aquatic habitat (seep, spring, or stream channel), extending

from 50 to 60 m from the culverts. **Figure C.1** shows a generalized diagram of how I determined which stream reaches were surveyed. At each site I used a Yardage Pro rangefinder (Bushnell; Overland Park, KS) to measure 50 meters from the culvert to the upstream survey site, where my field assistant and I then used the rangefinder to mark off a 10-meter stream reach.

Physical and Chemical Measurements in Streams

In each delineated study area, we measured 1) pH with an Oakton pH Testr 20, 2) turbidity with a Hach 2100p portable turbidimeter, 3) dissolved oxygen % with a YSI Pro 20 probe, and 4) stream flow rate with a Flowtech flow meter. All stream variable measurements were taken at the center of the stream reach unless that point was not characteristic of the reach as a whole (*e.g.*, a waterfall). If the stream channel was split, we took measurements in each channel and averaged them. The fifth stream measure was a visual estimate of the prevalent and second most prevalent stream substrata for each 10 m stream transect.

Measurement of the Near-stream Forest

We also measured and recorded several ecologically relevant factors in the near-stream forest. We calculated percent canopy closure by averaging four measurements from a spherical crown densiometer: one downstream, one upstream, and one facing each bank of the stream. We also measured aspect using the compass application on an iPhone 6S. We measured the stream gradient (slope) with a Suunto digital altimeter, measuring the elevation (± 1 m) at the upper and lower ends of the 10 m section of stream then calculating stream gradient (slope) by dividing the difference in elevations by the 10 m length of the stream transect. Finally, we visually determined dominant tree type based on both quantity of trees in the vicinity of the stream and

which individual trees influenced stream shading the most. After completing the stream and forest characteristic sampling we entered the stream for salamander surveys.

Salamander Sampling

Each survey for salamanders started at the downstream end of the 10 m transect and progressed upstream. The survey areas upstream began 50 m from the culvert and extended to 60 m from the culvert; survey areas downstream began 60 m from the culvert and extended to 50 m from the culvert. Adjustments in distance of the transect from the culvert were made if the stream was impassable at a distance from the culvert less than 50m. My assistant and I conducted fixed-area aquatic searches as described by Welsh (1987) and Bury and Corn (1991) during daylight hours to determine the number of individuals at each site as well as the presence or absence of other stream-associated vertebrates and crayfish (*Pacifastacus leniusculus* Dana, 1852). We searched for salamanders in suitable habitat in accordance with the procedure described by Welsh and Lind (1996): 1) search from downstream up, 2) turn over all pebbles, cobbles, and boulders 3) sift finer substrates carefully through one's fingers, 4) sift down to the hard bottom of the streambed or to a depth of 15 cm, and 5) if a salamander is seen escaping deeper it will be pursued. We captured both adult and larval salamanders, separately recorded the counts of larvae and adults based on appearance and location of capture, and then immediately returned to the spot they were found.

Because we searched thoroughly, I assumed that the capture rate was correlated to absolute densities so that the relative densities per 10 m reach were valid for comparing abundances of *R. olympicus* among sites (Bury and Corn 1991). In their 1991 report on amphibian sampling in the Pacific Northwest, Bury and Corn stated that "hand collecting of one

10-meter long segment of stream was sufficient to determine both occurrence and relative abundance of aquatic amphibians.” They explained that this is appropriate when the goal of the study is to characterize broad patterns of variation across streams, as opposed to a more intensive study of a single stream. To quantitatively justify the 10-meter survey length, Bury and Corn (1991) calculated the probability of failing to detect a present species (P) using the following formula:

$$P = q^n$$

where “q = the proportion of 1-meter segments where the species was absent, and n = the length (m) of the survey”. Using this formula, Bury and Corn determined that there is a 3.8% chance of not finding *R. olympicus* in a 10-meter stream segment in which they are present.

GIS Analysis

The data I used for my GIS analysis were retrieved from a variety of state and federal organizations, and the International Union for Conservation of Nature (IUCN). The stream data layer was derived from the Channel Migration Potential Stream Networks dataset (2015) from the Washington State Department of Ecology. Both the National Forest System roads layer (2015) and the Timber Harvests layer (2016) were retrieved from the United States Forest Service. The current geographic range of *Rhyacotriton olympicus* was retrieved from the most recent available data on the IUCN Red List website (2004, version 3.1). HUC-8 watershed boundaries were retrieved from the National Watershed Boundary Database (2013) through the United States Geologic Survey.

After collecting my field data, I used ArcGIS Pro to extract spatial data for model analyses including whether each site was in recently harvested or mature forest, the distance in

meters from each culvert to the nearest harvested forest, the HUC-8 (8 digit hydrologic unit code) watershed each site was in, and to determine the road order for each road that contained one of my stream crossings. The road and stream data were used to find stream crossings on first to third order streams, and the logging data were used to determine which forest age category the survey areas fall under. For analysis of proximity to recently harvested forests, I used two tools. To determine whether a given road crossing was within 75 meters of a recently harvested forest I created buffers around each of the points and determined which buffers intersected with areas of recently harvested forest. To create a continuous variable of distance to harvested forest, I used the “near” tool to extract the Euclidean distance from each stream crossing to the nearest recently harvested forest.

Road order is a metric based on the stream order system (*sensu* Strahler 1957) used for approximating the level of use and other characteristics of a given road segment. The same rules for branching and increasing the order of the stream are applied to roads. The Horton-Strahler index has been used to classify relationships in a variety of branching networks including social networks (Arenas et al. 2004) and mammalian respiratory systems (Horsfield 1976). The previous use of the index for novel systems suggests it may be an appropriate tool for assessing a branching road system as well.

Statistical Analysis

After collecting the data, I used R Studio (RStudio Team 2015) for global model fitting to determine which of the explanatory variables explain variation in the abundance of *R. olympicus* in streams throughout its range. The mean salamander abundance was used for a null model as a

baseline. The observed distribution of salamander abundance was compared to a theoretical Poisson distribution to determine goodness of fit.

I built 35 a priori models using 11 habitat variables to test in predicting target species occupancy within streams (**Table 2.1**).

Table 2.1. Complete list of models considered for model selection analysis for salamander abundance.

1. Null Model	13. HD + Tu	25. SD + Tu + DS1 + DS2
2. Stream	14. FS + HD + Tu	26. RO + Tu + DS1 + DS2
3. Forest Stage	15. SD + RO	27. SD + RO + Tu + DS1 + DS2
4. Road Order	16. SD + DS1	28. SD + FS
5. Harvest Distance	17. RO + DS1	29. SD + FS + SD*FS
6. Gradient	18. SD + RO + DS1	30. FS + Gr
7. Turbidity	19. SD + DS1 + DS2	31. HD + Gr
8. Dominant Substrate 1	20. RO + DS1 + DS2	32. FS + HD + Gr
9. Dominant Substrate 2	21. SD + RO + DS1 + DS2	33. FS + Gr + Tu
10. Stream Direction	22. SD + Tu + DS1	34. HD + Gr + Tu
11. FS + HD	23. RO + Tu + DS1	35. FS + HD + Gr + Tu
12. FS + Tu	24. SD + RO + Tu + DS1	

All variable definitions are listed in **Appendix A**. The global model was only used for goodness of fit analysis, and not included in the candidate model set because that combination of variables did not represent a meaningful ecological hypothesis.

Unexplored hypotheses

The analyses conducted above only represent a small subset of all possible hypotheses to explain variation in the abundance of *R. olympicus*. Based on the lack of support for any of the selected models or variables, it is possible that none of the other variables that I measured will explain a substantial amount of the variation. There are alternative hypotheses that are likely enough to warrant consideration, however they do not address the hypotheses stated in the introduction, and as such were beyond the original scope of this thesis.

One such hypothesis addresses competition with other lotic organisms such as Tailed Frogs (*Ascaphus truei*) Cope's Giant Salamanders (*Dicamptodon copei*), crayfish, and juvenile fish (Howell and Roberts 2008). Given what we know about *R. olympicus* predation and competition with other aquatic species, I expect that the presence of other aquatic vertebrates and macroinvertebrates will decrease the abundance of *R. olympicus* in streams throughout its range. I conducted rudimentary analyses of each of these four explanatory variables (*A. truei*, *D. copei*, crayfish, and fish species) to determine whether or not they appear to be a useful predictor of changes in salamander count. Another possible hypothesis relates to observed intolerance to changes in the thermal regime of stream water, including the impact this has on dissolved oxygen levels in the stream (Howell and Roberts 2008, Rounds et al. 2013). Given what we know about *R. olympicus*' preference for a low thermal range at low water temperatures, I expect that changes in stream temperature drive differences in salamander abundance between stream reaches. I conducted linear regression analyses to determine the predictive ability of each of the variables included in this hypothesis.

Unused variables

The two additional hypotheses stated above do not quite encompass all the variables that were measured that did not make it into the candidate set. Among the remaining variables are elevation, aspect, pH, stream flow, and watershed. We will conduct brief analyses of each of these in the same manner as the previous variables to explore the possibility that any of the variables could have some use as predictors of salamander abundance. As post hoc analyses, any variables that show significant relationships with variation in abundance will not be discussed later in the chapter beyond being pointed to as a research need.

Results

We identified a total of 517 (64 adults, 453 larvae) *R. olympicus*, with an average of 3.72 salamanders per 10-meter reach surveyed. The distribution of observed counts (**Figure D.4**) approximated an exponential curve, with a high number of counts between zero and five and significantly fewer in each increasing category. With a mean and standard deviation of 3.72 ± 7.20 , there was a higher degree of variability and uncertainty in the count data than could be accounted for by using the QAIC adjustment. The global model failed the goodness of fit test because the data were overdispersed when compared to a theoretical Poisson distribution, which precluded the candidate model set from further analysis. For count data using a Poisson distribution, the assumption is that the variance is equal to the mean. In this case, overdispersion means that the sample variance is greater than the mean. The overdispersion parameter, estimated from the global model (Burnham and Anderson 2002), was 4.771. According to Burnham and Anderson (2002), an overdispersion parameter above four is partly driven by an inadequate model structure that does not appropriately account for variation.

I calculated the chi-squared value based on the residual deviance (481.9) and degrees of freedom (101) and received a p-value indistinguishable from 0 in R. Under most circumstances QAIC can be used to account for overdispersion, but a p-value of 0 is so extreme that there is no reasonable belief that adjusting for overdispersion would yield legitimate results. Because the result of this test rendered my hypotheses and candidate models useless, I explored how other single predictor variables performed in explaining variation in salamander counts using univariate Poisson regressions. The variables that were not included in the prior abundance analysis were elevation, temperature, dissolved oxygen %, pH, flow, canopy closure %, and the presence of other lotic species.

Unexplored hypotheses

Because of the failure of the global abundance model, I conducted post hoc Poisson regression analyses of other predictor variables. **Figure D.5** shows the relative frequency of salamander counts in stream reaches in which each species was present. The presence of Tailed Frogs (*A. truei*) had a significant positive relationship with salamander abundance at the stream reach level. The presence of fish, both juvenile salmonids and rockfish, showed a significant negative relationship with salamander abundance. Neither the presence of *D. copei* nor the presence of crayfish showed significant relationships to salamander abundance. Summary statistics for all species presence models are shown in **Table 2.2**. It is worth noting that my sampling methods were not designed to be robust for organisms other than Olympic Torrent Salamanders. Rather, I was focused on the parts of the stream that would be considered potential habitat for *R. olympicus*; any other species found were coincidentally sharing habitat that may be used by *R. olympicus*.

Table 2.2 Summary statistics for univariate Poisson regression models of the presence of other lotic species. Coefficients measured in change in average *R. olympicus* abundance at the 10-meter stream reach level. Bold values indicate significant p-values ($\alpha=0.05$).

<i>Predictor</i>	<i>Coefficient ± SE (Salamanders/10m)</i>	<i>Log-likelihood R²</i>	<i>P-value</i>
<i>A.truei</i> presence	0.857±0.095	0.069	< 2e-16
<i>D. copei</i> presence	0.077±0.088	5.5e-4	0.38
Fish presence	-4.423±0.709	0.21	4.3e-10
Crayfish presence	-0.124±0.106	0.001	0.24

Variables related to stream temperature were all poor predictors of salamander abundance at the stream reach level. **Figure D.6** shows the lack of significant patterns for all variables relating to temperature despite small standard errors. The summary statistics also show no

significant effects and poor model fit (**Table 2.3**). The lack of statistical support for any of the listed variables suggests that the framework for question and hypothesis formation needs to be expanded to include previously unused variables.

Table 2.3. Summary statistics for univariate Poisson regression models relating to stream temperature. Coefficients measured in change in average *R. olympicus* abundance at the 10-meter stream reach level.

<i>Variable</i>	<i>Coefficient ± SE (Salamanders/10m)</i>	<i>Log-likelihood R²</i>	<i>P-value</i>
Temperature	0.012±0.024	1.6e-4	0.61
Dissolved Oxygen % (DO)	0.013±0.008	0.001	0.12
Canopy Closure %	0.003±0.007	1.6e-4	0.677

Unused variables

pH did not show significant relationships with salamander abundance when independently analyzed as univariate Poisson regressions. However, both Elevation and Stream Flow account for a small yet significant proportion of the variation in salamander abundance between stream reaches. The summary statistics in **Table 2.4** show the relationships these variables have with salamander abundance. When examining the regression plots for elevation, pH, and stream flow in **Figure D.7**, it is clear that even for the variables that have a significant effect, that effect is small.

Table 2.4. Summary statistics for univariate Poisson regressions of unused predictor variables for salamander abundance. Coefficients measured in change in average *R. olympicus* abundance at the 10-meter stream reach level. Bold values indicate significant p-values.

<i>Variables</i>	<i>Coefficient ± SE (Salamanders/10m)</i>	<i>Log-likelihood R²</i>	<i>P-value</i>
pH	-0.109±0.102	8.6e-4	0.284
Elevation	0.0007±0.0003	0.006	0.006
Stream Flow	-1.3±0.4	0.009	0.001

As shown below in **Table 2.5**, there is a substantial amount of variation in mean stream reach abundance from one sub-basin to another. **Figure B.2b** shows that the north- and south-draining sub-basins have the lowest average abundances, while the basins that drain to the east and west had higher average abundances. The patterns of variation in abundance were similar to the patterns observed for occupancy, though the basins in the east and southeast portion of *R. olympicus*' range showed different patterns of occupancy and abundance.

Table 2.5. Summary statistics of average salamander counts per 10-meter stream reach separated by HUC-8 sub-basin.

<i>Sub-basin</i>	<i>Total Salamanders</i>	<i># of Stream Reaches Surveyed</i>	<i>Average</i>
Crescent-Hoko	2	7	0.29
Dungeness-Elwha	9	17	0.53
Grays Harbor	22	9	2.44
Hoh-Quillayute	202	27	7.48
Hood Canal	89	16	5.56
Lower Chehalis	54	24	2.25
Queets-Quinault	97	26	3.73
Skokomish	42	13	3.23
Totals:	517	139	3.72

Discussion

The overdispersion of the count data prevented me from completing the model selection analysis, so I resorted to post hoc regression testing to explore the data. Burnham and Anderson (2002) acknowledge that overdispersion can be driven by biological factors such as schooling or flocking behavior, which can cause positive correlations among individuals. In the case of *R. olympicus* surveyed in the summer of 2019, there were observed influent, or “losing streams,” that may have caused concentrations of salamanders in areas of persisting water. While not the original goal of the study, the primary takeaway from the analysis in this chapter is that the none of the measured variables appear to be good predictors of variation in salamander abundance

with the possible exceptions of *A. truei* presence and fish presence. Neither the questions nor hypotheses explored in this chapter appear to have encompassed the necessary variables or scope required to answer meaningful questions surrounding variation in the abundance of *R. olympicus*. It is not unheard of for a species to have different drivers for occupancy and abundance. In a study of the Southern Torrent Salamander in northern California, Welsh and Lind (1996), the variables that were a good predictor of presence of salamanders were not a good predictor of variation in the abundance of salamanders.

Management Implications:

The current results of the abundance analysis have very limited management implications. It is clear that there are patterns of variation across the study area, however until the cause of those patterns is determined I cannot specify best management practices for this species. At best, I can say that it is not enough to solely focus on the variables that drive salamander occupancy when determining how to best manage this species. Given that the difference between occupancy and abundance is analogous to the difference between “minimum suitable” and “best available” habitat, we must not settle for preserving only the minimum suitable habitat for the Olympic Torrent Salamander when it is clear that the best available habitat is defined by other parameters.

Research Needs:

Projects that approach the questions of abundance on different scales, and perhaps from a different framework, will be important for determining the conditions that provide the optimal conditions for the survival of this species. Some approaches that I did not consider for this

project, but would be useful for further consideration of this question are evaluating environmental factors at a broader scale than was done in this project, using fewer streams and comparing differences within few streams, and comparing the interactions between *R. olympicus* and other streams vertebrates and macroinvertebrates. In their studies of the Del Norte Salamander (*Plethodon elongatus*) and Southern Torrent Salamander (*R. variegatus*) Welsh and Lind analyzed variables at a wide range of scales, from the landscape scale down to the microhabitat scale (Welsh and Lind 1995, 1996). Another approach is to select many fewer streams as a study site and sample them more intensively. There are numerous studies of headwater amphibian populations that focus their studies on relatively fewer streams (8-14) and examine the variation in counts between plots in these streams (Welsh and Ollivier 1998, Lowe and Bolger 2002, Quinn et al. 2007, Barr and Babbitt 2016).

The analysis of interspecific competition and dynamics amongst stream vertebrates is also a method that researchers have used to evaluate salamander species abundance. The current literature does not contain any studies evaluating the relationship between *R. olympicus* and *D. copei*, though Petranka (1998) does mention that *Dicamptodon* species are generally opportunistic predators that do feed on larval amphibians including conspecifics. The relationship between species is influenced by the environmental context in which it exists (Kleeberger 1984, Beachy 1994, Ennen et al. 2016), which suggests that as streams are impacted by anthropogenic stresses the relationship between *R. olympicus* and other aquatic species may also shift. Additionally, little is known about how the ontogeny of torrent salamanders impacts their abundance at the stream reach level. Possible studies in this arena include using streamside pitfall traps to assess the seasonal movement of adults between terrestrial and aquatic

environments, as well as focusing the study on larvae to eliminate any temporal patterns in adult torrent salamander abundance in the streams, such as during the breeding season.

Summary

I explored the relationships between the distribution and abundance of *R. olympicus*, and environmental variables related to anthropogenic changes to the composition and continuity of headwater streams in the Olympic National Forest and National Park. I gathered the field data to answer these questions with an assistant during the summer of 2019 from streams throughout the Olympic National Park and National Forest. The questions, and resulting hypotheses, shaped the candidate model sets used for the statistical analyses.

The occupancy analysis included 23 models, all of which used Salamander Presence as the response variable and a binomial distribution. I used an information theoretic approach to model selection and compared AIC_c scores for the set of candidate models. The single model with the most empirical support included Gradient, Turbidity, and Harvest Distance as the fixed predictor variables and Stream as the random variable. Other models that showed moderate or greater empirical support were mostly other combinations of the variables stated above. The other variable included in model subset analysis due to its presence in models with ΔAIC_c scores below four was Forest Stage, which is a categorical classification of Harvest Distance using a cutoff radius of 75 meters. The only bivariate model that showed substantial likelihood of being the best model was Gradient and Stream. Gradient separated itself from all other variables as the variable most likely to influence the average occupancy of salamanders across sub-basins both by its inclusion in all models in the subset, and as the only significant predictor in the univariate logistic regression analyses. Forest Stage and Harvest Distance appeared to have similar amounts of influence on the models based on log-likelihood R^2 values.

I was unable to continue with the abundance analysis beyond a goodness of fit test because the global abundance failed due to overdispersion. I explored many of the other

variables that I measured during the field season, treating them as a simple linear regression and looking for any highly influential or significant explanatory variables. The results of these tests pointed towards interactions with other aquatic species (*A. truei*, fish species) as significant predictors of salamander abundance. I suggested potential shifts in questioning framework to hopefully yield meaningful abundance results to complement the findings from the occupancy analysis.

The occupancy results emphasized that the minimum suitable habitat for Olympic Torrent Salamanders is based largely on Stream Gradient. Although Stream Gradient, Harvest Distance and Forest Stage, and Turbidity were all present in the subset of models independently analyzed, only Stream Gradient account for a significant amount of the variation in salamander occupancy when analyzed as a univariate logistic regression. Possible explanations for why Stream Gradient is the most important driver of salamander occupancy in this study include the flushing capacity associated with steeper streams, absence of salmonid competitors from higher gradient streams, or other factors yet to be considered. The existing literature widely states that this species prefers mature forests and is not likely to be present in streams with low gradients. Salamanders were present in 18.18% of stream reaches with gradients of 10% or lower that I surveyed. However, because my forest age measurement was separated into forests that are recently harvested (≤ 30 years), and all other ages, any patterns of association with late successional forests were obscured. Thus, distribution patterns in various forest ages should be studied more closely. My results also show a need for further inquiry into patterns of *R. olympicus* abundance throughout its range in order to learn what constitutes the best available habitat.

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Appendix A: Variable Definitions

Table A.1. Variable names, definitions, and brief explanations of how the values were calculated.

Canopy Closure %	The percent canopy closure determined by an average of four canopy closure readings taken from the approximate midpoint of a given 10-meter stream reach, facing upstream, downstream, left bank, and right bank using a spherical crown densiometer (Lemmon 1956).
Dominant Substrate 1	The dominant streambed substrate in a given 10-meter stream reach as determined by a visual estimate.
Dominant Substrate 2	The sub-dominant streambed substrate in a given 10-meter stream reach as determined by a visual estimate.
Dominant Tree	The dominant tree species surrounding a given 10-meter stream reach both in quantity and in responsibility for shading the stream reach, as determined by visual count and estimation.
Forest Stage	A two-level factor (mature, recently harvested) based on whether or not the forest within a 75-meter radius from the road crossing has been harvested in the past 30 years.
Harvest Distance	Euclidean distance from a road crossing to the nearest recently harvested forest patch, determined using the ArcGIS Pro “Near” tool.

Road Order	A categorical factor used as a proxy for approximate road use. This factor is determined using the same branching rules as the Strahler stream order.
Salamander Count	The total number of Olympic Torrent Salamanders, adult or larvae, found in a given 10-meter stream reach.
Salamander Presence	Whether or not an Olympic Torrent Salamander was found in a given 10-meter stream reach.
Stream Direction	Whether a given 10-meter stream reach is upstream or downstream from the culvert.
Stream Gradient	The difference in elevation between the top and bottom of a given 10-meter stream reach, multiplied by 10 to determine percent gradient.
Turbidity	The turbidity score, measured in NTU (Nephelometric Turbidity Units) for the water in a given 10-meter stream reach.

Appendix B: Maps

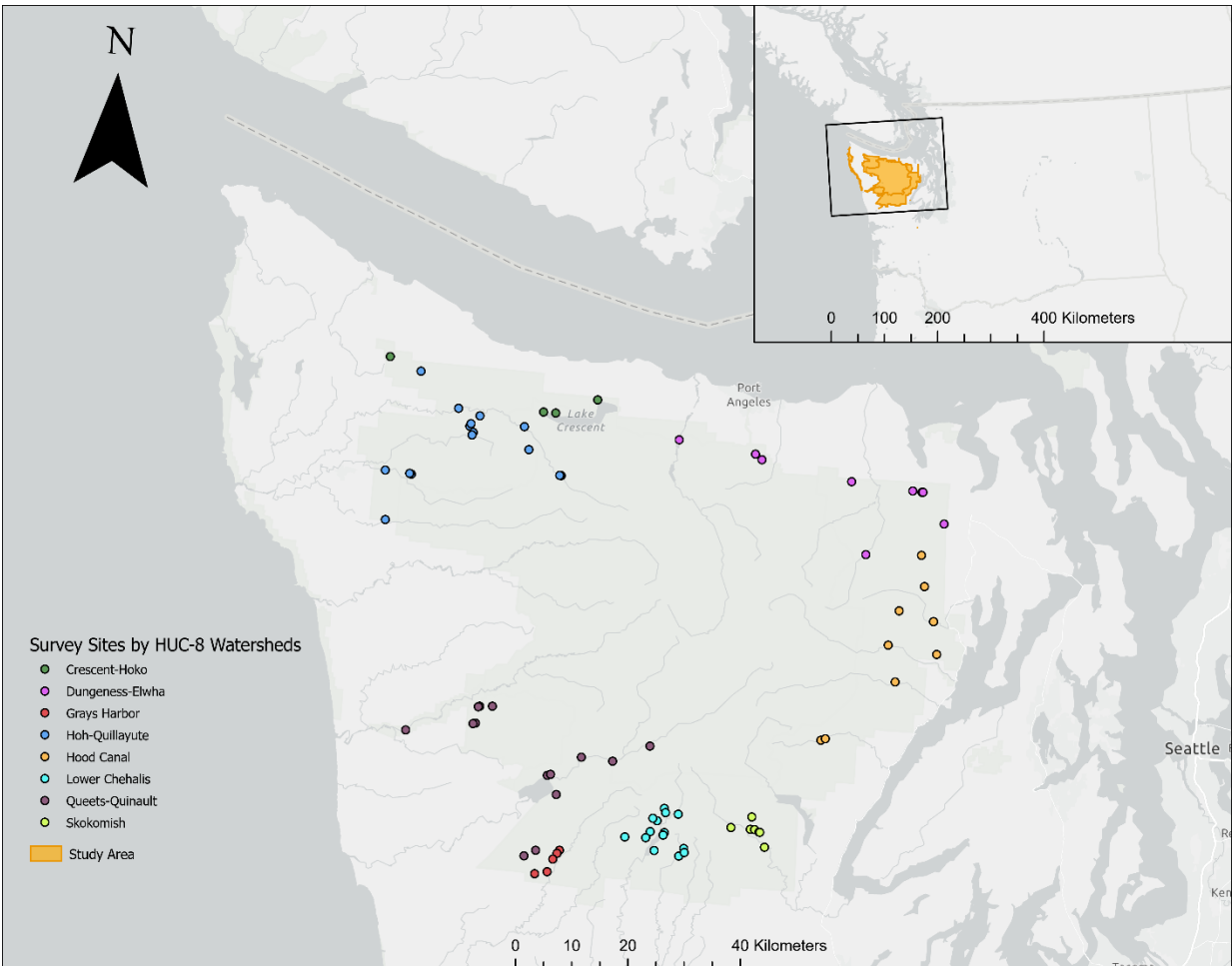


Figure B.1. Study sites with inset map of study area in Washington state. Study sites are displayed by HUC-8 sub-basin according to color.

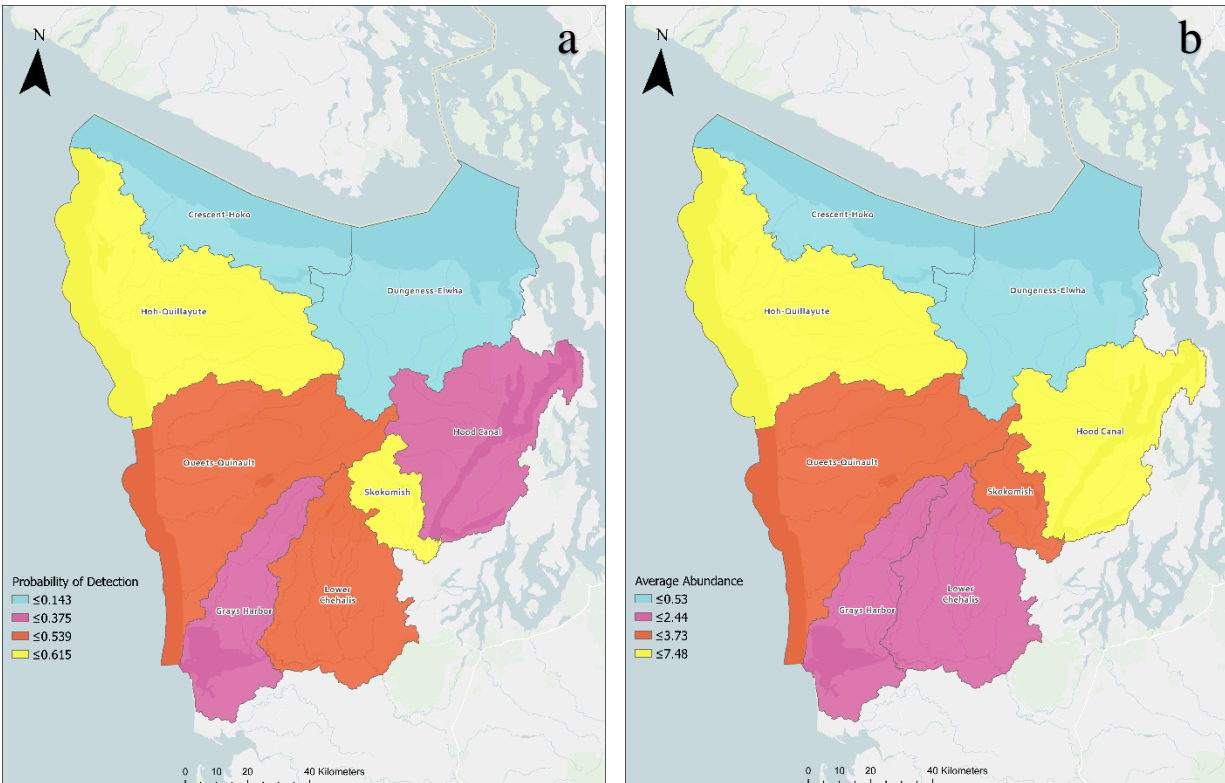


Figure B.2. Maps comparing the average *R. olympicus* occupancy (a) and abundance (b) for 10-meter stream reaches in each HUC-8 sub-basin surveyed.

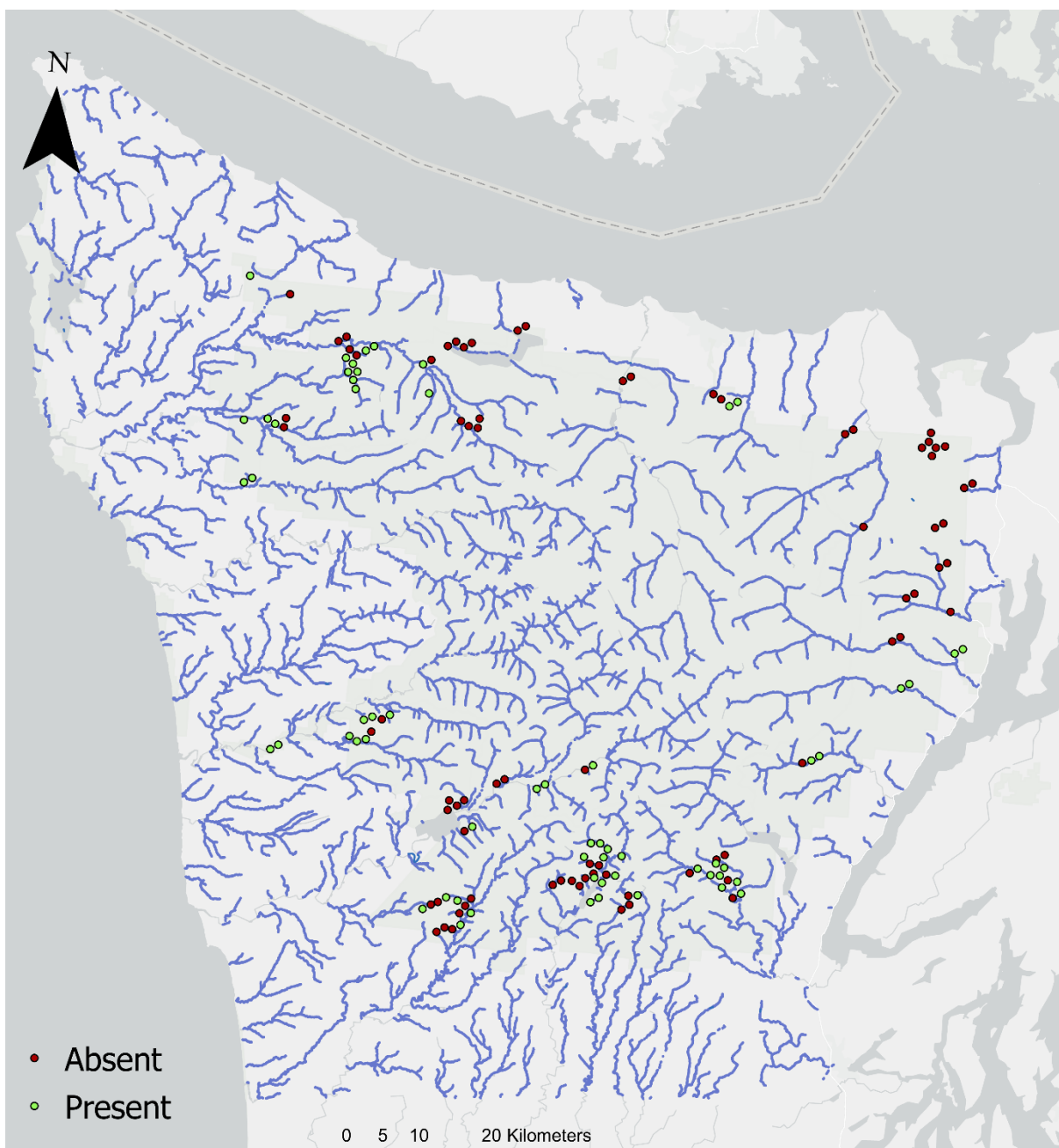


Figure B.3. Survey sites overlaid onto suitable stream network as determined by Channel Migration Potential data layer (Washington State Department of Ecology 2015). Survey sites in locations lacking streams were determined using an alternative data source. Sites where salamanders were detected are marked green, while sites without salamanders are marked red.

Appendix C: Field Survey Diagram



Figure C.1. Diagram showing the general configuration of a field site. The culvert stream passage was noted using GPS coordinates. Upstream and downstream survey sites were found by traveling 50 meters from the culvert in each direction and demarcating a 10-meter stream reach for variable and salamander sampling. Map data: Google, 2020.

Appendix D: Univariate Plots

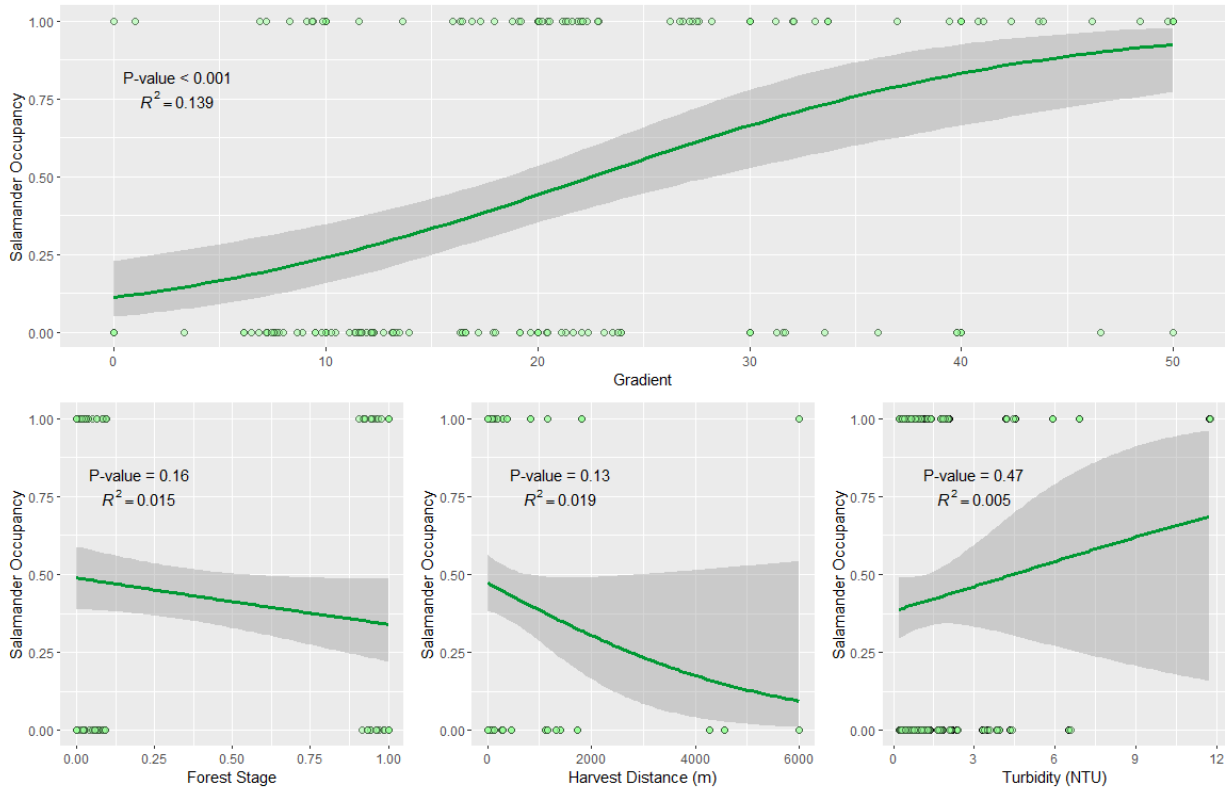


Figure D.1. Univariate logistic regression plots for probability of detection plotted against all four variables included in the selected subset of models with standard errors in dark grey. Points were displaced horizontally to hide points masked by stacking. P-values and log-likelihood R^2 values taken from univariate models.

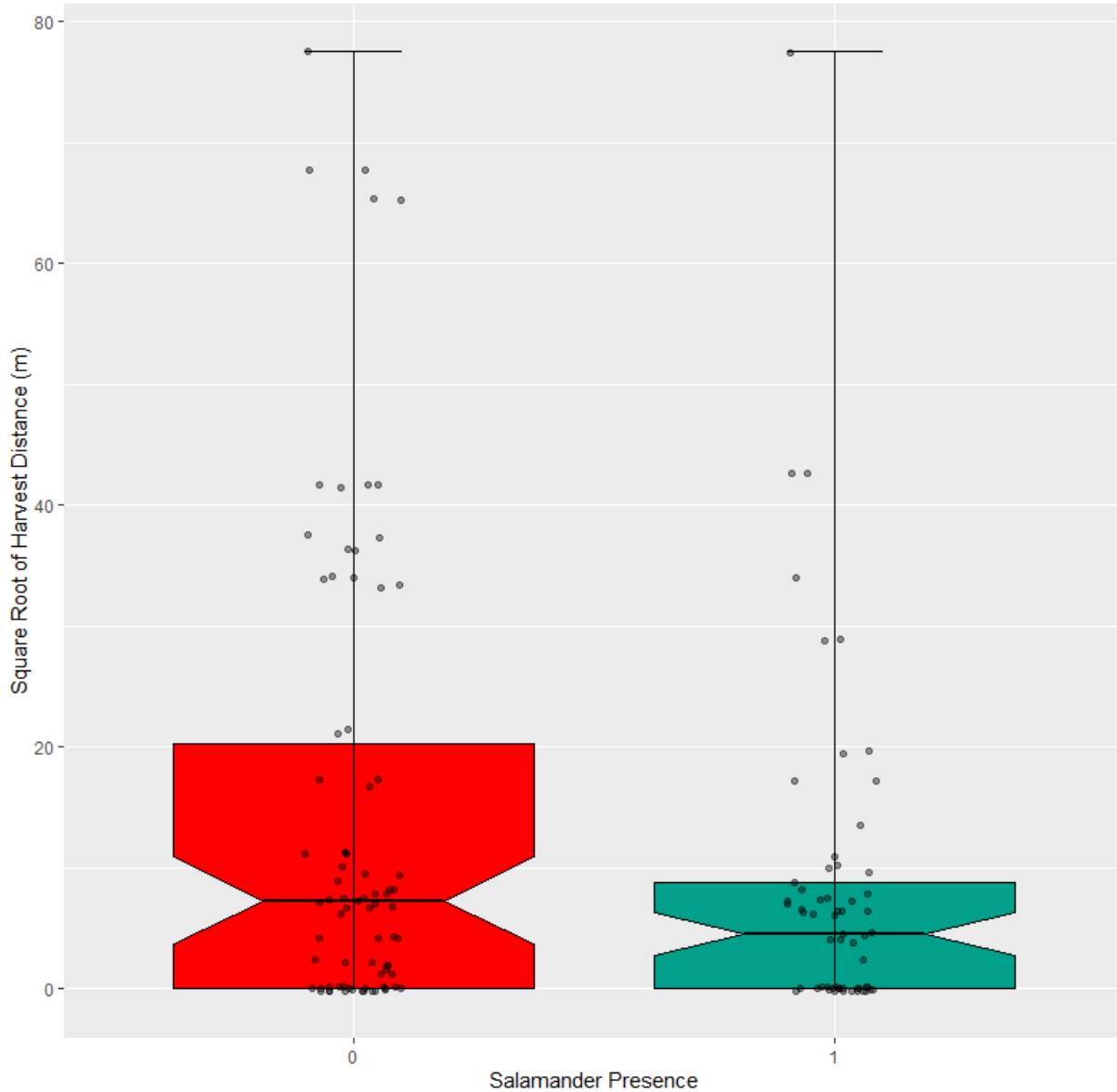


Figure D.2. Boxplot showing harvest distance salamander presence (0,1). Harvest distance transformed using square root to compress the spread of data while maintaining the relative distance of points. Jittered points overlaid onto plot for ease of interpretation.

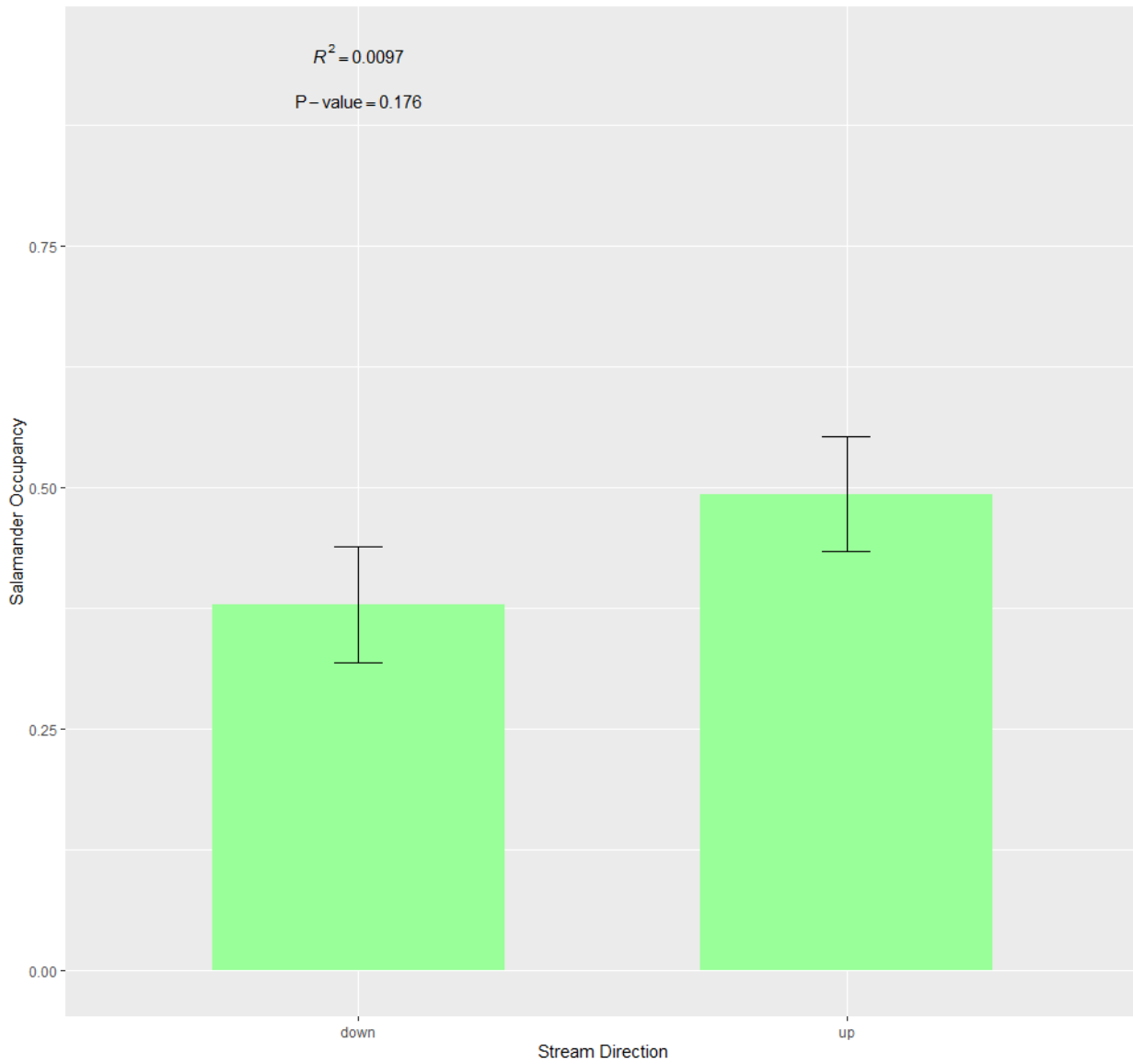


Figure D.3. Bar plot of probability of detection \pm standard error by stream direction. P-value and log-likelihood R^2 taken from univariate logistic regression model.

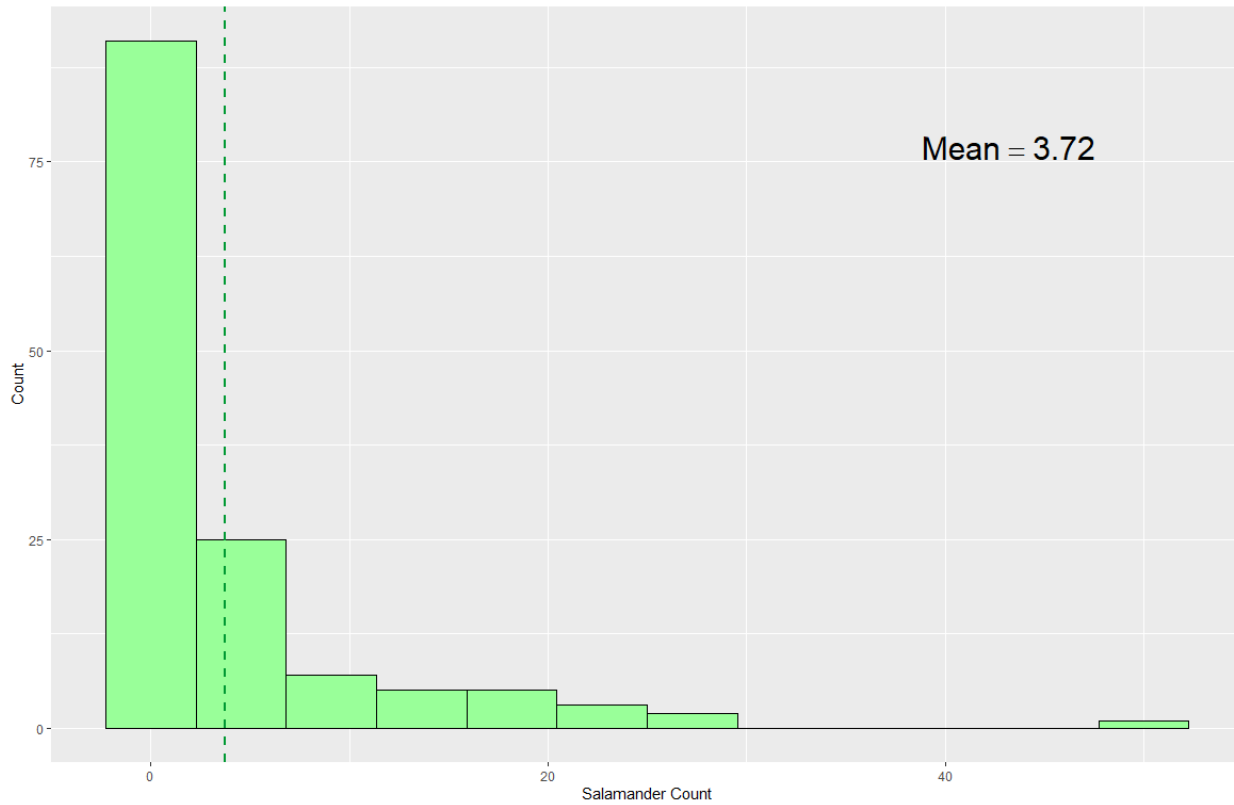


Figure D.4. Distribution of observed salamander counts for *R. olympicus* in 10-meter stream reaches. Dark green dashed vertical line marks the global mean of salamander counts.

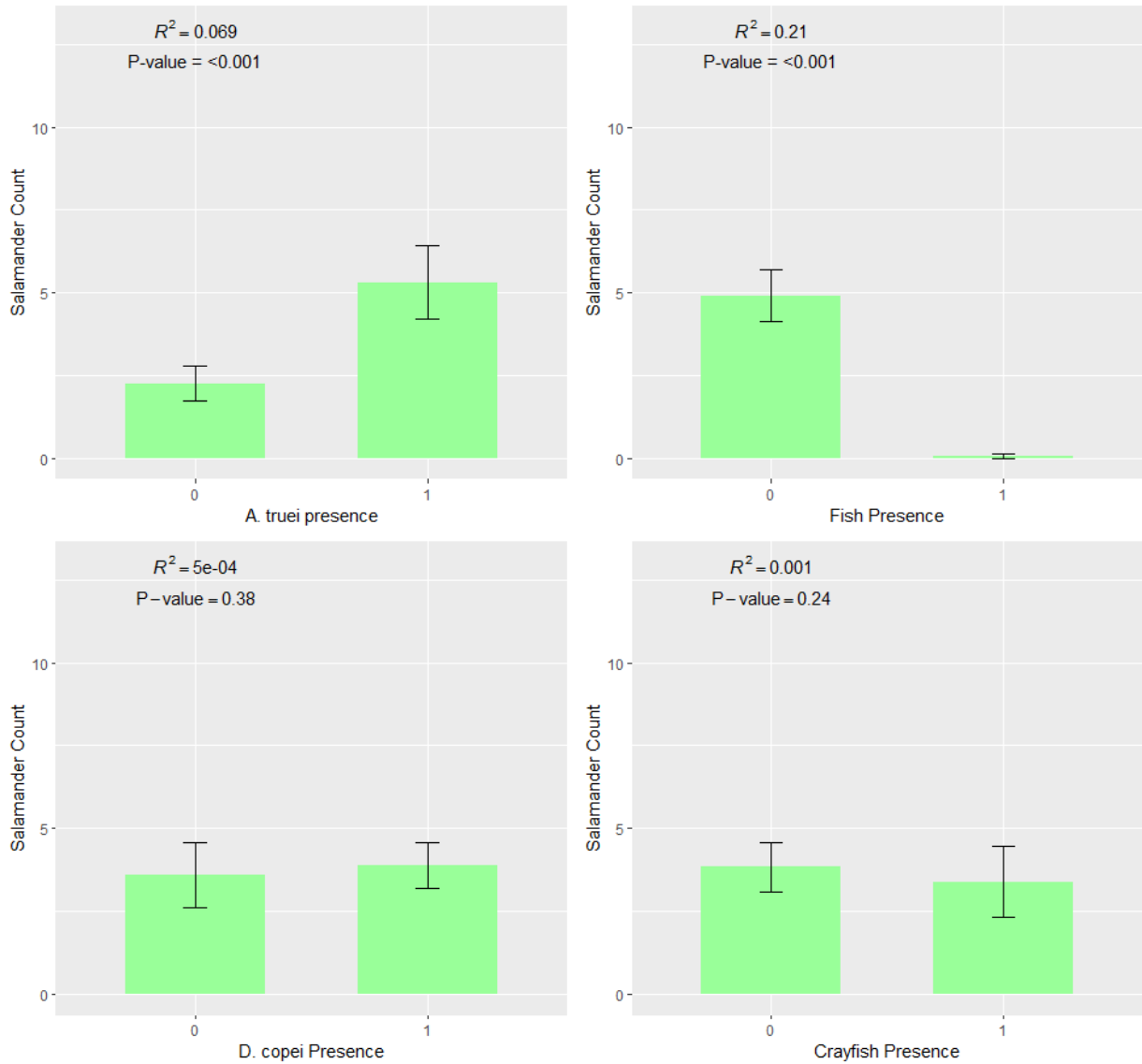


Figure D.5. Bar plots of average salamander count \pm standard error for Poisson regressions of salamander count against other species present in streams. P-values and log-likelihood R^2 values taken from univariate models.

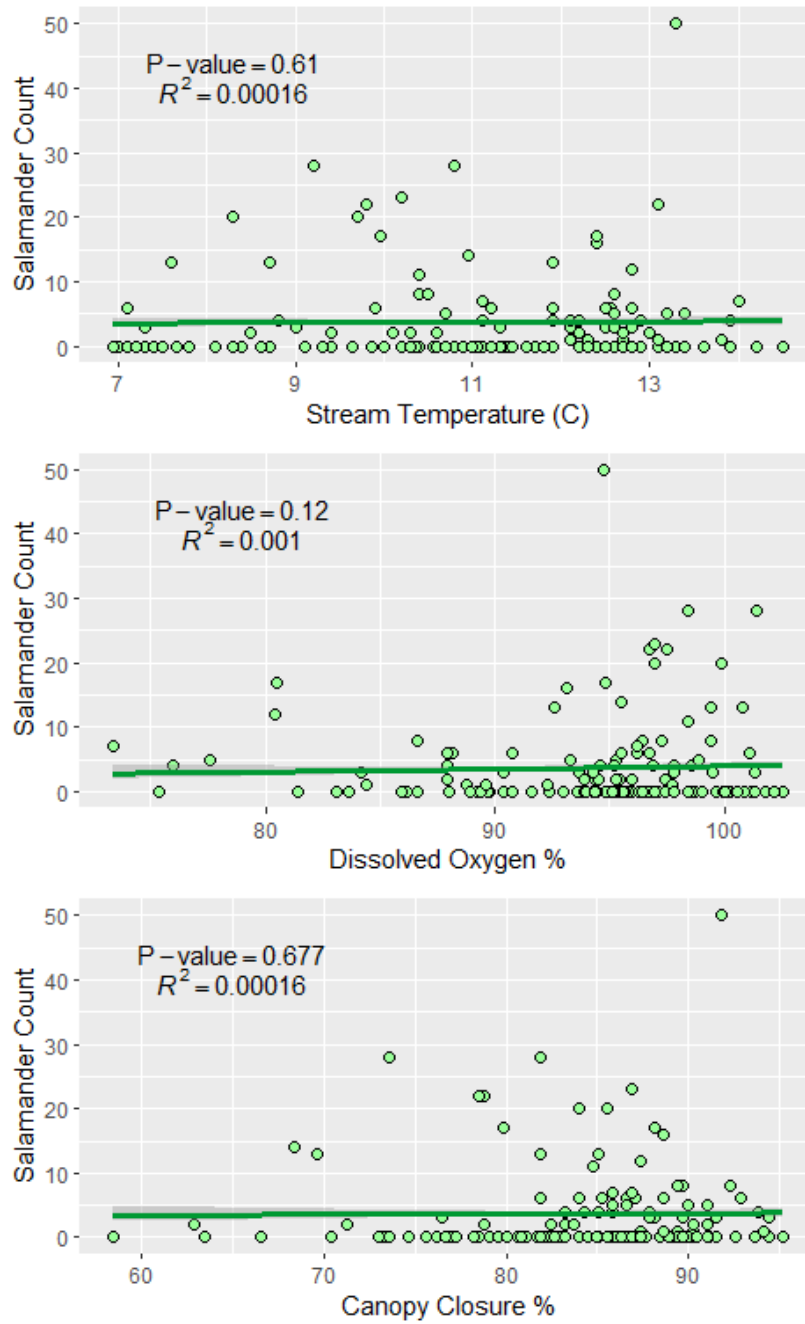


Figure D.6. Poisson regression scatterplots for stream temperature and directly related variables with model standard error shown in dark grey. P-values and log-likelihood R^2 values taken from univariate models.

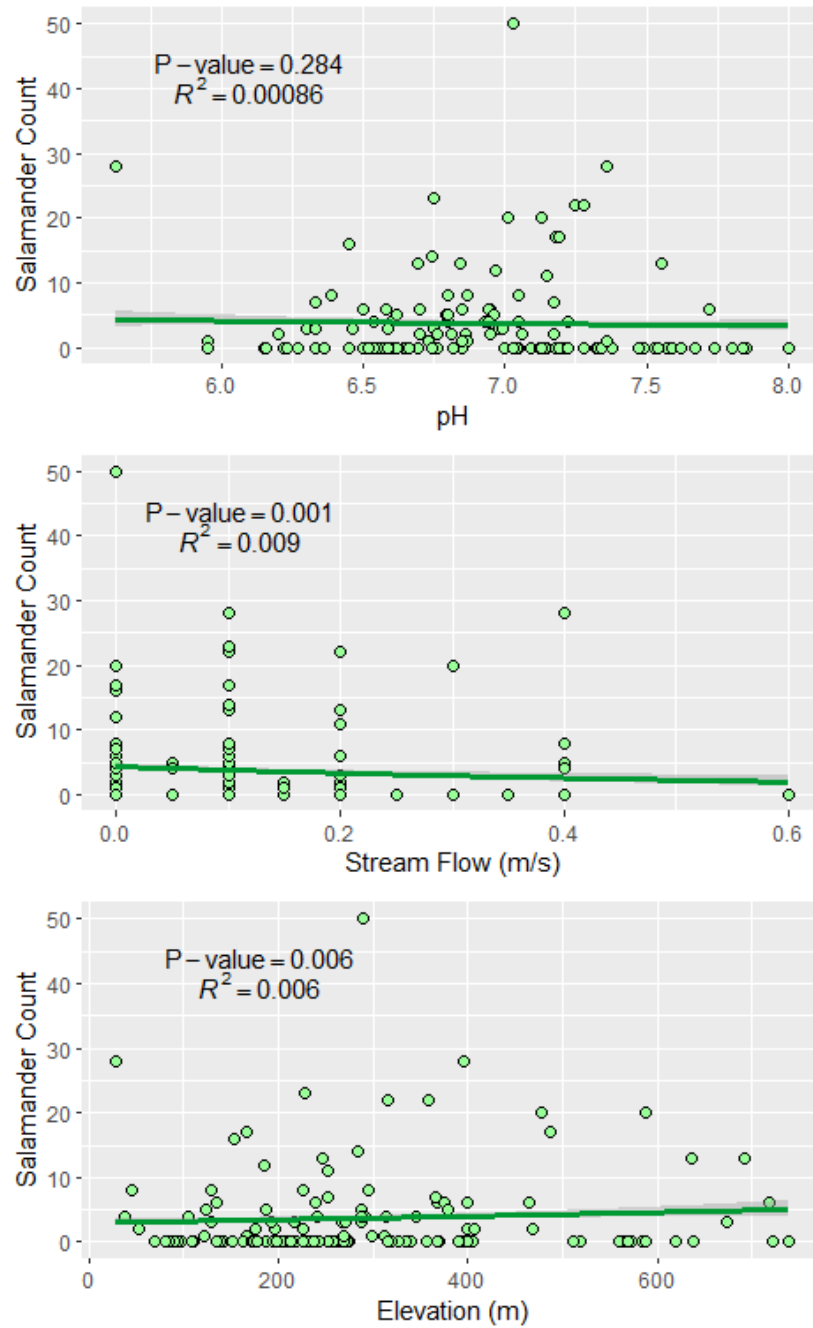


Figure D.7. Poisson regression scatterplots for the remaining unused continuous predictor variables with model standard error shown in dark grey. P-values and log-likelihood R^2 values taken from univariate models.