

Understanding Amphibian Behavior:
Diel Cover Use Patterns in Alpine Lakes
With and Without Introduced Salmonids

by

Tyler Goodman

A Thesis
Submitted in partial fulfillment
of the requirements for the degree
Master of Environmental Studies
The Evergreen State College
June 2018

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This Thesis for the Master of Environmental Studies Degree

by

Tyler Goodman

has been approved for

The Evergreen State College

by

John Withey, Ph. D.
Member of the Faculty

Date

ABSTRACT

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Many of the world's amphibian species are in decline. A large portion of studies on amphibian populations in alpine environments focus on the factors that affect their success. Past research has pointed to a seemingly obvious cause of these declines: the presence of native and introduced salmonid species. While some researchers are confident in this mechanism, far fewer have examined the complete diel cycle of amphibian behavior in response to salmonid presence as well as in their absence. This study documents amphibian behavior during both day and night cycles with an emphasis on how available cover is utilized. All lakes observed in this study showed greater amphibian detectability during night observations, with variation in preferred substrate type and activity level. This study points to the possibility that amphibians are adapting to biological competition and predation within their alpine environments and may be equipped to adapt to abiotic changes. The assumption of a salmonid-caused decline may not be warranted under all circumstances as the greatest number of detected amphibians came from study sites with regularly occurring salmonid stocking. Factors such as substrate type and structure should be more seriously considered in management decisions, as should the practice of incorporating complete diel data collection to assess population trends. Determining the extent of salmonid impact allows a prioritized management effort to focus limited funds where they can provide the most benefits.

Table of Contents

List of Figures	iv
List of Tables	v
Acknowledgements	vi
Chapter 1: Introduction and Literature Review	1
Introduction	1
Literature Review: Interactions Among Amphibians, Salmonids, Biotic, and Abiotic Influences	5
History of Fish Stocking	5
Motivations for Stocking Salmonids	7
Amphibians of the Cascades	9
Opposition towards fish introduction	11
A Case for Stocking	13
Altered Amphibian Behavior	14
Gaps in Scientific Knowledge	16
Reaching Solutions	17
Chapter 2: Methods for Data Collection and Analysis	19
Study Lake Selection	19
Field Data Collection	21
Visual Encounter Survey (VES)	21
Statistical Analysis	23
Chapter 3: Results	24
Relationship Between Fish and Amphibian Abundance	28
Other Influencing Variables	29
Activity Coefficient	31

Chapter 4: Discussion and Conclusion	33
Understanding Lake Ecosystems	33
Study Limitations	37
Next Steps in Research	37
Literature Cited	38

List of Figures

Figure 1. Study Ecoregions19

Figure 2. Observations of Individual Amphibians25

Figure 3. Species Composition By Observation Period26

Figure 4. Comparison of Observed Abundance27

Figure 5. Relative Abundance By Species28

Figure 6. Activity Coefficient Comparison By Lake32

List of Tables

Table 1. Trout and Char Species Stocked in Alpine Lakes of Washington	6
Table 2. Amphibians of the Cascade Range	10
Table 3. Study Lakes with Selected Attributes	21
Table 4. Regression Relationships Between Amphibian Types	29
Table 5. Pearson's correlation	30

Acknowledgements

Although I was able to do what I love and spend time outdoors for this thesis, it would not have been possible without support from many individuals. The support of faculty, peers, friends and family was overwhelming and greatly appreciated. I would like to start by thanking my faculty reader Dr. John Withey for his tremendous support and patience through my thesis work, especially with statistical analyses. I'd also like to thank my all of my MES peers at Evergreen as they gave feedback through the developmental stages of my work. Thank you Jessica Brown and Leslie Carman for your peer-review feedback. Lastly, I'd like to thank Becca Goodman and Erik Lentz for venturing off into the unknown with me to some of the study lake sites.

Chapter 1: Introduction and Literature Review

Introduction

After the last ice age, high elevation lakes were formed as glaciers melted and left behind ice-scarred landscapes barren of macroscopic life. As ecological communities established themselves within these alpine systems, amphibians typically became the top predators in aquatic systems, as fishes were denied access due to steep gradients and natural obstacles (Bahls, 1992; Pister, 2000). Rugged terrain limited the distribution of amphibians and concentrated them around reliable sources of water. As humans explored these montane lakes and ponds, the practice of fish stocking gained popularity as it provided recreational angling opportunities in pristine settings (Pister, 2000; Landres, Meyer and Matthews, 2000). The Western North American Ranges of the Sierra Nevadas, Rockies and Cascades were the primary hotspots for such practices. Little was understood as to how alpine communities were impacted by such action and not until the mid 20th century was the impact of fish stocking considered on a management level (Miro and Ventura, 2013; Downen, 2002).

The topic of amphibian success is multi-faceted and involves many complex factors including biotic and abiotic inputs. With environmental factors rapidly changing due to climate change, it is difficult to pinpoint specific root causes for decreased amphibian success and therefore talk of correlational relationships is commonplace in alpine aquatic ecology. Amphibians are indicators of environmental health, particularly water quality and also play an important role in ecosystem health as both predators and prey (Lunghi, Manenti and Ficetola, 2015). As montane systems are relatively simple and less diverse in comparison to their lower elevation counterparts, studying more simplified

systems allows isolated analysis of variables that may aid in improving the trajectory of amphibian populations (Carpenter and Kitchell, 1993).

The Cascade Range of Washington State has largely been free from time sensitive demands to save declining amphibian species. Of the species found at higher elevations (>1200m), the Cascade frog (*Rana cascadae*) is the most impacted, listed as near threatened (NT) by the IUCN (2017). Land managers responsible for the conservation of species have not yet had to establish urgent action plans, but could benefit from a preemptive level of preparation for future needs should the species and others decline further. In order to better understand the needs of amphibian species many agencies at the federal and state levels conduct routine amphibian surveys to establish baseline data about the status of various species. North Cascades National Park (NOCA) and Mount Rainier National Park (MORA) have been leaders in Washington State with yearly surveys that incorporate citizen science for monitoring (Hoffman, Larson and Brokes, 2002; Downen, 2004). While much effort goes into these survey efforts, most of the observations occur during daylight hours. This potentially represents a problematic situation as critical decisions regarding amphibian management and the allocation of limited funding depends on the data collected. By examining half of the time period of activity within a body of water, opportunities are missed for additional data collection, which could lead to more sound representations of amphibian populations.

Relatively untouched by human development, the North-South Cascade Range is intersected by four major East-West highways that connect larger cities on either side of the range. The western side of the range receives more annual precipitation due to coastal storms and typically exhibits qualities of a temperate rainforest, whereas the east side

sees the effects of a rain shadow. The eastern slope of the Cascades is much drier and water catchments rely more heavily on stored snowpack for water flow (Downen, 2004). The alpine ecosystems on each side of the Cascade crest differ in community complexity and needs.

Environmental and Anthropogenic Influences on Amphibian Populations

Some of the most recognized contributing factors to declining amphibian populations include changes in temperature and precipitation. Amphibians rely on seasonal and permanent bodies of water for reproduction and development, which may be at risk due to climatic variation. The challenge with understanding how specific populations will be impacted and react is that each basin is uniquely influenced by factors of aspect, snowpack and elevation. A cascading effect results from these factors as faster snowmelt and more direct exposure to ultraviolet light affects growth and reproductive success (Nagl and Hofer, 1997; Sommaruga, 2001; Adams et al., 2005). Similarly, climatic variation coupled with anthropogenic carbon inputs can change water chemistry. Because of the remoteness and narrow window of seasonal accessibility, these ecosystems are grossly understood despite their relative simplicity.

Anthropogenic influences range from the above mentioned alteration of the carbon cycle and atmospheric chemistry to localized impacts of disturbance and overuse. While the impacts of historic fish stocking are still being mitigated in some alpine lakes, land managers at the state level are calling for a prioritized mindfulness of amphibians in decisions to continue these practices (Tyler et al., 2002). While controlling anthropogenic inputs to alpine systems at a global or national level are impractical, more localized

decisions that favor declining species may make a greater difference. The simple task of reducing impact through low-density stocking or even complete elimination of stocking where deemed necessary can allow opportunities for recovery where humans have overstepped in the past.

A Balancing Act

Making management decisions at the crossroads of conservation and recreation can be very challenging. While the focus primarily falls on obligations to protect or conserve native amphibian species, the matter also has a social side that is equally as complex. Land managers, namely the Washington Department of Fish and Wildlife, are responsible for addressing concerns on both fronts. The balance of conservation efforts and public recreation opportunity can be seen as conflicting goals. For many people, the culprits of amphibian decline are introduced salmonids. The recreation side of the responsibility requires a careful management for a quality over quantity experience. In many regards these goals can coexist, but the cases where amphibians are in greater decline could stand to use a management system that is capable of assessing the greatest threat to those species. By understanding the complete life cycle of an amphibian and all of the factors that influence its success, managers are equipped to take action where issues of amphibian decline are the most time sensitive. This thesis seeks to bridge the gap of current surveying practices by looking to other indicators of amphibian health within lake ecosystems to then organize lakes in a prioritized list of needed management action. Understanding the research that exists within this area of study helps to set the stage and evaluate management practices that are based on these findings.

Literature Review: Interactions Among Amphibians, Salmonids, Biotic, and Abiotic Influences

Setting the Scene

Globally, climate is affecting species that require specific habitat conditions necessary for breeding, rearing offspring, and acquiring food, as these conditions are changing at a pace too rapid for species to readily adapt (Carey and Alexander, 2003; Parmesan, 2006; Case et al., 2015). Amphibians across the world are of particular concern and often face many other pressures correlated with human impact and recreation (Ryan et al., 2014). One such impact that is a topic of debate is non-native salmonid fish stocking in mountain lakes. Amphibians at high elevations are susceptible to changes in the snow pack and available water for rearing and summer time habitat, and often require deeper, more permanent bodies of water (Case et al., 2015; Carey and Alexander, 2003; Taylor, 1983). In certain bodies of water trout and char species such as rainbow trout (*Oncorhynchus mykiss*), Westslope cutthroat trout (*Oncorhynchus clarki lewisi*), Coastal cutthroat trout (*Oncorhynchus clarkii clarkia*), golden trout (*Oncorhynchus mykiss aguabonita*) brook trout, (*Salvelinus fontinalis*), and arctic grayling (*Thymallus arcticus*) have been stocked for recreational fishing opportunities and have replaced amphibians as the top predators in these alpine ecosystems (Table 1; Pister, 2001). Much of the debate in the fields of ecology, conservation biology, and public land management are based on this head-to-head competition between salmonids and amphibians.

Table 1. Trout and Char Species Stocked in Alpine Lakes of Washington State (Bahls, 1992; Pister 2001; WDFW, 2018).

Common Name	Scientific Name	Status
Westslope Cutthroat Trout	<i>Oncorhynchus clarki lewisi</i>	Current
Coastal Cutthroat Trout	<i>Oncorhynchus clarki clarki</i>	Current
Rainbow Trout	<i>Oncorhynchus mykiss</i>	Current
Golden Trout	<i>Oncorhynchus aguabonita</i>	Current
Eastern Brook Trout	<i>Salvelinus fontinalis</i>	Historical
Lake (Mackinaw) Trout	<i>Salvelinus namaycush</i>	Historical
Arctic Grayling	<i>Thymallus arcticus</i>	Historical
Kokanee Salmon	<i>Onorhynchua nerka</i>	Historical

Academic literature on the topic often portrays the anti-fish perspective and calls for actions to remove salmonids in totality (Drake and Naiman, 2000). While there can be ecological value in this action in certain lakes where the impacts of fish on amphibians are greatest, this task is not feasible with limited management resources and short seasons of accessibility in remote areas. This literature review begins with an overview of the

historic motivations for fish stocking, with special attention on the Cascade Range of Washington state. Next, I will discuss prominent literature that has established an anti-stocking mentality among researchers and land managers. After this I will present counter-arguments to these viewpoints and elucidate the complex nature of alpine lake ecosystems.

Historical Motivations for Stocking Salmonid Species

Beginning in the 1800's fish stocking became common practice among loggers, trappers and outdoorsmen who visited mountain lakes and wanted recreational opportunities through sport fishing as well as opportunities for sustenance over prolonged periods of time in remote locations (Pfeifer et al., 2001). Stocking practices were very much rooted in the pursuit of catchable trout with a "singular goal to enhance sport fishing without consideration of ecological ramifications" (Pister, 2001). Since the last ice age nearly 95% of mountain lakes in the western U.S. were naturally fishless, but stocking efforts resulted in 60% of these high-elevation lakes containing trout species (Tyler et al., 1998). While most stocking activity occurred under the direction of various state departments, illegal stocking activity from unknown parties has been and remains to be an ongoing concern for land managers. Common legal methods involved airplane drops of tens of thousands of fish in hopes that a sizeable majority would survive the traumatic experience (Pfeifer et al., 2001). The most commonly utilized species was the eastern brook trout (*Salvelinus fontinalis*), now understood to have detrimental impacts on lake biota as they are successful breeders in a range of habitats (Knapp et al., 2001). Where most other trout and char species would be unsuccessful breeding, brook trout thrive and can quickly overpopulate a lake, depleting it of food sources. Without an

understanding of the life history, species characteristics, or potential impacts on habitat and native species, the practice of overstocking lakes continued for many years.

As these practices continued, the Leopold Report of 1963 and the Wilderness Act of 1964 changed the way that fish stocking was conducted within National Parks and Wilderness areas respectively (Leopold et al., 1963; Landres et al., 2001). Additionally, a decline in the quality of the fishery was detected and a re-evaluation of lake management took place and favored low impact stocking by significantly lowering the number of fish stocked in each stocking period. In some cases the impacts on native lake biota were extreme as species, namely *S. fontinalis*, consumed whatever resources were available (Pfeifer et al., 2001). Within Washington State there are many agencies involved in the preservation and restoration of ecosystems as well as providing recreational opportunities. The agency charged with this balancing act is the Washington Department of Fish and Wildlife. Efforts to provide “sustainable fishing, hunting and wildlife viewing opportunities” require adoption of new values surrounding fish stocking by being responsible stewards of managed land (WDFW, 2015).

By using best available science to assess impacts of introduced fish species on native biota, there can be responsible implementation of management practices that provide conservation of species and maintain a high lakes fishery where deemed appropriate. A major driver of continued stocking is the economic value that recreational fishing provides. Angler surveys reflect a large percentage of license-buyers that frequent high lakes for recreation, accounting for \$67 to \$70 million annually (Pfeifer et al., 2001). Changing societal values have largely influenced a shift towards a conservationist mentality as activities such as hunting and fishing have seemingly fallen secondary to the

goals of protecting biological diversity (Landres et al., 2001). Despite a changing paradigm, the economic and cultural values associated with trout and other cultivated introduced species makes decisions to end stocking programs difficult (Hartman et. al 2014).

Amphibians In Question

Amphibians that inhabit the Cascade Range include various species of frogs and salamanders, each exhibiting characteristics that have evolved over time. There are fifteen common species of frog and salamander that inhabit regions found within this study in what is considered an alpine landscape (Table 2). Each has adapted behaviors and responses to predatory threats, as well as increased competition with others of their species, or other amphibians. Historically, the literature classifies frogs as nocturnal creatures with a tendency to be most active and vocal during evening and nighttime hours. More inquestion is the behavior of salamanders and newts . With more complex life history stages there are circumstances in which adults leave a body of water for a subterranean life. Many of the individuals found to inhabit lakes and ponds long-term are gilled larvae. Larvae from each species have varying durations of life as a juvenile, based largely on elevation and snowpack. Some species take as long as two years to complete their metamorphosis into adults. Others permanently retain gills and other larval characteristics and live an aquatic lifestyle, a phenomenon known as paedomorphism (Farner and Kezer, 1953; Tyler et al., 1998b) .

Table 2. Amphibians of the Cascade Range in Washington. NT = Near Threatened, LC = Least Concern (Nussbaum et al., 1983; IUCN, 2004; IUCN, 2017).

Common Name	Scientific Name	IUCN Status
Cascade Frog	<i>Rana cascadae</i>	NT
Coastal Tailed Frog	<i>Ascaphus truei</i>	LC
Pacific Tree Frog	<i>Pseudacris regilla</i>	LC
Columbia Spotted Frog	<i>Rana luteiventris</i>	LC
Red-legged Frog	<i>Rana aurora</i>	LC
Western Toad	<i>Bufo boreas boreas</i>	LC
Rough-skinned Newt	<i>Taricha granulosa</i>	LC
Ensatina	<i>Ensatina eschscholtzii</i>	LC
Cope's Giant Salamander	<i>Dicamptodon copei</i>	LC
Pacific Giant Salamander	<i>Dicamptodon tenebrosus</i>	LC
Long-toed Salamander	<i>Ambystoma macrodactylum</i>	LC
Northwestern Salamander	<i>Ambystoma gracile</i>	LC
Van Dyke's Salamander	<i>Plethodon vandykei</i>	LC
Western Red-backed Salamander	<i>Plethodon vehiculum</i>	LC

The variation among salamanders and newts in behavior is so great that there is not one widely accepted time of day to find them active. This is part of what prompted my interest in studying amphibians in alpine environments. Little work has been done to understand the full diel life history and activity of salamanders and newts in response to salmonid presence or absence. One area that the literature has covered particularly well is the defense response of amphibians, even analyzing the angle at which they flee from predators. A handful of studies look at the ability of predators to alter the behavior and use of cover by amphibians. In both lab and field experiments there are tendencies noted towards increased hiding behavior (Kenison et al., 2016; Pilliod et al., 2010; Hoffman, Larson and Brokes, 2003; Walls, 1995). The utilization of this cover is an adaptation, as amphibians were once the top predators in alpine aquatic systems. Similarly, an adaptation towards nocturnal behavior could represent an adaptation for predator avoidance.

An Alpine Scapegoat?

With the shift of societal values and scientific papers using combative language about non-native fish including “biological pollutants” (Schindler and Parker, 2001) and “alien” (Kats and Ferrer (2003); Cambray, 2003; Winandy et al., 2015), little support exists for the continued practice of salmonid fish stocking. Further attacking this practice is the assumed attitude that the presence of fish is synonymous with destruction and predation. A study by Knapp et al. (2007) in the Sierra Nevada Mountains has been

adopted as a seminal paper within the academic community, without careful consideration for the differences among species and watersheds that were studied. This study examined a declining population of the mountain yellow-legged frog as a result of shared wintering habitat under frozen high-elevation lakes as a potential “synergistic” factor with a variety of environmental influences (Vredenburg and Wake, 2004; Knapp et. al 2007). Exhibiting this unique characteristic, overwintering tadpoles are subjected to fish searching for food during the most resource poor time of the year. Fish removal efforts in affected lakes and streams proved effective initially in rebounding populations within these bodies of water (Knapp et al., 2007). While this study may prove to be of great significance in the studied lakes, it becomes problematic to assume this impact across all bodies of water and amphibian species that do not exhibit the same life history characteristics.

Similarly, another study conducted in the Sierras attributed terrestrial-aquatic links with donor and recipient systems. In fishless lakes, mayflies are abundant and substantial hatches of the insects shape distribution patterns of Gray-crowned Rosy-Finches. Initial insights into the reduced presence of Rosy-Finches around lakes with introduced trout pointed to the robbery of resources. While connections could be made between mayfly availability and fish presence or absence, it was found that additional factors such as tree cover surrounding the lake was also a determinant of Rosy-Finch presence (Epanchin 2010).

While various field-based studies draw correlations between fish presence and amphibian impacts, other efforts have been made to explore these impacts in laboratory recreations of habitat (Huang and Sih, 1990). One such study conducted by Tyler et al.

(1998) recreated various substrate and habitat cover scenarios, controlling water temperature, period of light exposure, and feeding intervals. The ratio selected by the researchers was one fish per twenty larval salamanders. The conclusions of this study pointed out that there is correlation between fish presence and amphibian use of cover. While the scientific method for testing hypotheses is a valid approach to understanding behavioral patterns, fabricating predation pressure in a laboratory setting overlooks various biotic and abiotic factors that may favor either fish or amphibian. In all cases amphibians utilized cover structure that was made available to them.

A Case For Stocking

With past mistakes recognized and scientific inquiry informing management decisions, this is the most responsible period in the history of fish stocking. Efforts by managers within the North Cascades National Park Complex (NOCA) show that a balance can exist between conservation and stocking. These examples can serve as a framework of responsible high lakes fisheries management during a time in which funds are limited for removal efforts that are rarely successful. The methods outlined in High Lakes Management documentation carefully analyze lake biota and habitat before fish are considered for stocking (Downen, 2004). Many view the pursuit of a successful high lake fishery to be connected with past approaches of vast quantities of fish, but efforts to minimize ecosystem disturbances through low-density fish stocking achieve responsible management while appealing to both conservationists and recreationalists (Downen, 2004; Pope, 2008). Stocking that once was conducted with aircraft depositing tens of thousands of fish has shifted to efforts by volunteer backpackers carrying as few as fifty fish. With a decrease in the number of fish in lakes there is a better “quality over

quantity” approach as lake biota are minimally disturbed with a low number of non-reproducing fish living for a finite period of time. Should ecological impacts be greater than initially anticipated the stocking regime can simply be halted and the fish will die off naturally (Liss et al., 2002).

Studies on amphibians at various elevations and global locales have pointed to the ability of certain species to adapt to changing conditions and environmental stressors. The North Cascades National Park Complex (NOCA) has noted such behavioral shifts as the development of the North Cascades National Park High Lakes Fishery Management plan has called for in-depth baseline surveys of lake habitat. One observation of long-toed salamander larvae shows that larger bodied (i.e. more developed, older) larvae were more prone to finding refuge in substrate than their smaller, younger siblings (Downen, 2004). Additionally, lakes that were observed during afternoon hours with few observed amphibians came to life at night, pointing to a shift in behavior towards nocturnal activity. The locations of amphibian sightings also reflected tendencies towards more shallow nearshore areas or areas with significant bottom cover (Sih et al., 1992; Downen, 2004).

Others have pointed to the ability of different life history stages of amphibians to utilize available structure and alter activity levels in response to stress (Winandy et al., 2015; Walls and Williams, 2001). Additionally, increased predation stress can cause amphibians to be selective with breeding and feeding sites, which may not be possible in isolated watersheds that lack additional ponds and lakes to which amphibians can migrate (Winandy et al., 2016).

Beyond the Adaptation Theory

While the controversy is focused on the amphibian-fish interaction, a host of other biotic and abiotic variables may be at work as either the primary forces of amphibian success or synergistic contributors to the impacts of salmonids. Returning again to NOCA, a study conducted by Tyler et al. (1998) attributed the abundance of crustacean zooplankton (e.g. copepods and gammarus) to Total Kjeldahl Nitrogen (TKN) concentrations within a lake. This in turn contributed to an increased abundance of long-toed salamanders (Tyler et al., 1998). Other impacts of trout on alpine ecosystems remove the direct conflict between amphibian and fish and look into trophic cascade impacts at lower trophic levels. Such studies look at fish predation on phytoplankton and zooplankton and other invertebrates within lake ecosystems. An Italian study conducted by Tiberti et al. (2014) examined the feeding ecology of introduced *S. fontinalis* and concluded that adult fish were more impactful on zooplankton depletion within a lake than younger fish, with more limited mouth gape (Tiberti et al., 2014).

Additional explanations exist for amphibian behavior that is viewed to have driving factors outside of predation response. A study by Pough (2007) analyzed amphibian activity in response to lighting, UVB radiation, and temperature. While weak correlations were made between use of cover in response to the intensity of lighting and use of UVB radiation, temperature variation proved to be a significant driver of cover use. Because amphibians have glandular skin that facilitates gas exchange and water transport, extreme temperature fluctuations are stressful. Pough concluded that amphibians chose shelter under benthic cover as a response to elevated temperatures and fled in search of new cover when temperatures exceeded 32 degrees C (Pough, 2007).

Another perspective comes from research from Walls and Williams (2001), Wildy et al. (1998), and Taylor (1983) who all review impacts of interspecific competition among amphibians of the order *Urodela* and *Anura*. These interactions ranged from segregation of habitat due to differences in life history traits and avoidance of competition to cannibalistic behavior influencing growth rates of juvenile amphibians. The valuable information gleaned from these studies is that given a host of potential influential variables, there are a number of explanations for the decreased success of amphibians in alpine ecosystems.

Gaps in Scientific Knowledge

With such variation in opinion on the topic, little progress is made pitting conservation and recreation against one another. Land managers have a two-pronged mission of conserving native species while also providing recreational opportunities for license buyers, who ultimately fund agency programs. The issue that has come about is the way in which the data is gathered to make the determinations of fish impacts and recommended management intervention. With priorities increasingly placed on conservation of native species, land managers within state and federal agencies have developed detailed land management plans that outline clear policies and criteria for surveying lakes for amphibian presence and fish impact. The gap that consistently comes to the surface of this survey data is the fact that these presence-absence surveys are largely conducted during daytime hours, disregarding amphibian activity that may take place after dark.

Half of a species' behavioral repertoire potentially goes unstudied because of existing protocol. There are many benefits to incorporating both day and night surveys for amphibian presence and activity. When we look to life history characteristics of various amphibian species we find that many frog species exhibit tendencies towards nocturnal behavior, however salamander activity is largely understudied and what little research exists on alpine species varies by life stage. My work aims to bridge this gap in knowledge by studying amphibian behavioral interactions with available habitat cover in both the presence and absence of introduced salmonid species during daytime and nighttime observational periods. While the reasons behind these protocols can be understood due to the remoteness and relatively short study period of alpine areas, understanding the complete picture within a given body of water can better inform how to use limited resources.

Historically, if daytime observations conclude that amphibian presence is low it is assumed that the population is under stress from predation. Methods for fish removal are both time intensive and expensive, so being sure of the need is critical especially with the underfunding that many agencies face. Based on studies that have anecdotally observed increased salamander activity at night and European studies of lowland salamanders and newts (Hartman and Lawler, 2014; Liss et al., 2002), I hypothesize that in instances where amphibians are exposed to increased predation stress, species will adopt nocturnal behavior to avoid predatory salmonid species. This would further point to the need for nighttime surveys as populations may not be fully represented with daytime observations.

Reaching Realistic Solutions

While the literature that specifically studies alpine environments largely disfavors the continuation of recreational fish stocking, it is unrealistic to expect a complete purge of stocked salmonids. It is clear that many view salmonids as the sole culprit to declines in amphibian populations in alpine lakes, but with increasing impacts from climate change, there is a greater need for the synthesis of values between governing agencies and the scientific community rather than the creation of a dividing fissure (Case et al., 2015). This issue is not about whether or not fish belong, but how to deal with fish that are already in place and may have detrimental impacts to amphibian species who share the same lake ecosystem. In many cases the removal of fish would prove to be advantageous for conservation as well as recreational opportunity as values are reflected in the sustainability of the activity (Aasetre and Gundersen, 2012). Through my thesis work I hope to be able to help shape and streamline the process of deciding which lakes should receive prioritized attention in an effort to improve responsible stewardship when managing native species. If we can move past placing blame and make progress towards better understanding these alpine ecosystems, the scientific community and amphibians would benefit alike.

Chapter 2: Methods For Data Collection and Analysis

Study Lake Selection

The data collection sites that I selected represent alpine lakes in three ecoregions that intersect the Washington Cascade Range, including the North Cascades, West Cascades, and East Cascades (Figure 1). These three adjacent ecoregions were selected to represent variations in annual precipitation and temperature inputs for much of the mountainous region within Washington. To select the lakes to be studied, I generated a random list of lakes based on a set of minimal criteria to ensure an equivalent probability to observe amphibians.

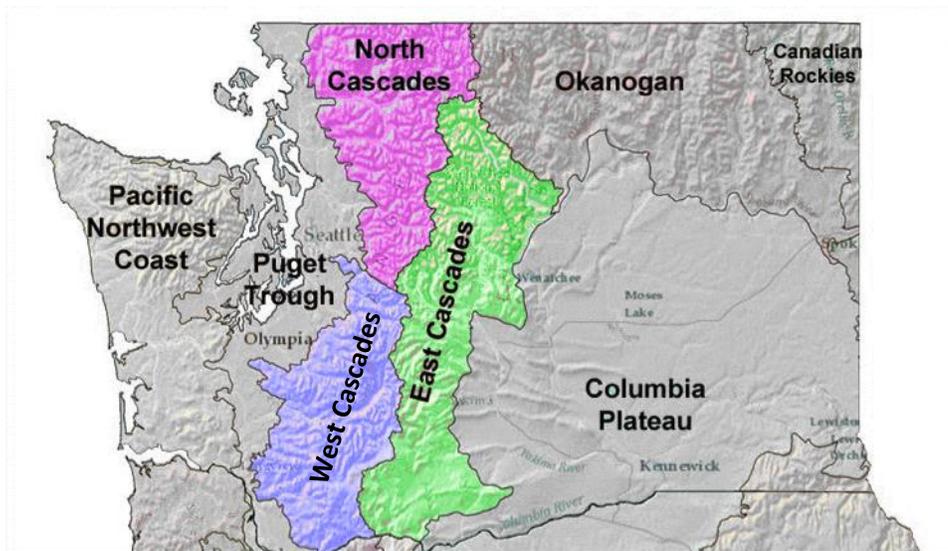


Figure 1. Ecoregions of Washington State, with the three ecoregions included in this study (North, West, and East) in color.

Criteria for selection of individual lakes included a minimum elevation of 4,000 feet (1,219 meters), overall lake depth greater than 1 meter, and accessibility on foot. By setting a lower limit on elevation, I was able to survey primarily alpine environments as aligned with the methods of other researchers in alpine studies (Case et al., 2015; Knapp

et al., 2007; Liss et al., 2002; Tyler et al., 1998). The minimum depth threshold made it more likely that the selected body of water would be permanent throughout the year and therefore suitable for amphibians and/or fishes. Lastly, accessibility was a key consideration as many of the surveyed lakes are located off trail, requiring up to three days of travel on foot.

I used a random number generator to produce a numeric value for township, range, and section, which I compared to a database of alpine lakes from the Washington Department of Fish and Wildlife (WDFW). Once a lake's coordinates matched the random number, I noted any additional permanent bodies of water within 0.5 miles of the lake, and included any such lakes in my study. I did this to maximize observation opportunities in remote locations as well as to provide a more detailed snapshot of each lake basin. I repeated this process until six lakes were selected in each ecoregion (Table 3, n=18 in total), four containing fish and two void of fish as a control (presence or absence of fish based on WDFW fish stocking archives). I noted the lake elevation, size of the lake in hectares (ha), and presence or absence of fish. In many cases the lakes generated were unnamed in mapping publications and software, therefore I coded each lake to represent its ecoregion, elevation rank, and salmonid presence (Table 3).

In addition to statistical analysis I calculated an activity coefficient to compare overall amphibian activity level within a given lake between the two observation periods. I assigned active behavior a value of "1", resting behavior a "0", and hiding behavior a "-1". The net activity values for each observation period were then divided by the number of amphibians observed during that period to obtain the activity coefficient.

Table 3. Study lakes with selected attributes. Lake Codes contain data about lake ecoregion and presence of introduced salmonids. W-West Cascades, E-East Cascades, N-North Cascades, F-Fish present, NF- No fish present. The numbers are the rank from lowest to highest elevation within each ecoregion.

Lake Code	Township-Range-Section (T-R-S)	Elevation (m)	Size (HA)
W1-F	16N-07E-32B	1405	5.0
W2-NF	06N-08E-10P	1417	1.5
W3-F	06N-08E-10E/M	1433	13.0
W4-F	06N-08E-10L/P	1448	8.0
W5-NF	13N-10E-27H	1469	0.5
W6-F	13N-10E-13Q	1554	3.7
E1-F	22N-13E-24B	1429	4.9
E2-F	13N-11E-03B	1587	12.2
E3-NF	14N-11E-34G/K	1614	7.2
E4-NF	23N-14E-27C/F	1676	1.4
E5-F	27N-15E-34F	1792	3.5
E6-F	23N-14E-27F/L	1826	1.1
N1-F	24_1/2N-11E-32Q	1408	2.8
N2-NF	24_1/2N-11E-32Q	1420	0.5
N3-F	30N-12E-04F	1533	1.5
N4-F	32N-14E-27L	1700	6.4
N5-NF	32N-14E-26B	1713	2.5
N6-F	32N-14E-26G	1814	14.7

Field Data Collection

The process for collecting field data from each of the study lakes included observing amphibians during daytime and nighttime hours. Equipment used for the observation process included a 2-meter folding ruler, GoPro camera, field notebook,

pencil, survey flag, packraft, dive mask, dive light, and headlamp. Additionally, I utilized a personal flotation device when rafting was necessary. Data collection at each lake involved a visual encounter survey as is common within organizations in Washington State management (Downen, 2014). A visual encounter survey (VES) involved one revolution around each lake, observing each individual amphibian encountered. I conducted two surveys on each lake, once during the day, and once at night within a single 24-hour period.

Upon initiation of the survey, I recorded water temperature and began walking clockwise around the lake. Upon the observation of an individual amphibian I recorded its level of activity, which I classified as active, resting, or hiding. I observed for two minutes to note any potential changes in this activity. In addition, I recorded its position within the water column: top, mid, or bottom. After two minutes I placed a survey flag in the substrate where the amphibian was first observed and measured the distance from the shoreline. I set a maximum study radius of 5 feet from shoreline to accommodate observation on foot where possible. This is consistent with literature that questions the possible interference of observer with natural, uninterrupted behavior by wading (Rocha et al., 2014). I recorded the substrate type, which I classified as: rock, woody debris, sand, or mixed. After I completed one interval I waited until the subsequent observation period (i.e., day or night, depending on arrival time and first observation period) to conduct the second half of the survey for a given lake.

Night observations utilized additional equipment including a headlamp and dive light. The underwater camera was utilized during the day and night to record activity levels and aid in the identification of species upon later review away from the field site.

In instances where the shoreline was too steep to traverse on foot, a raft was utilized to continue observation around the complete circumference of the lake. When the shoreline was again accommodating to foot travel, I exited the raft and resumed the VES on foot. Off site, the field data was transferred to an online spreadsheet for statistical analyses.

Statistical Analysis

I used JMP software (Version 14.0.1) to perform statistical tests on my collected data, including 1-way ANOVA, multiple linear regression modeling and Chi-Squared tests of independence.. For this study I used an alpha of 0.10 to consider results as statistically significant, but take care to point out specific test results where the p-value is between .05 and .10. I used a Bonferroni correction for multiple comparisons when appropriate (Cabin and Mitchell, 2000). I generated graphs and charts to visually represent the data using Google Sheets, Microsoft Excel and Microsoft Word.

Chapter 3: Results

Relationship between Fish and Amphibian Abundance

The hypothesized results from my experiment were that there would be a distinct correlation between the presence fish and the tendency for amphibians to exhibit nocturnal behavior. I recorded a total of 756 individual amphibians from 7 species of frogs, salamanders and newts (Figure 2). Of the observations made, 239 occurred during diurnal survey periods and 517 during nocturnal surveys [Figure 3]. When examining fish presence impacts on abundance of amphibians across all lakes I began at a wide scale and worked down towards a narrower field of view to assess significance. Beginning with all amphibian abundance data, there was no difference by fish presence (lakes with vs. lakes without fish, $F_{1,16}=0.588$, $p=0.454$). I further broke abundance down into categories of “salamander/newt” ($F_{1,16}=0.3645$, $p=0.555$) and “frog” ($F_{1,16}=1.597$, $p=0.225$), which also generated non-significant results. Lastly, to examine fish impact on specific species during different times of the day I examined salamander/newt abundance during the day ($F_{1,16}=0.049$, $p=0.826$), salamander/newt abundance during the night ($F_{1,16}=0.087$, $p=0.772$), frog abundance during the day ($F_{1,16}=4.408$, $p=0.052$) and frog abundance during the night ($F_{1,16}=0.573$, $p=0.460$). Of these comparisons frog abundance during the day was the comparison with any indication of a significant difference (albeit at $0.05 < p < 0.10$) between lakes with fish vs. lakes without fish, and this significant difference disappears with a Bonferroni correction for multiple comparisons (corrected alpha = $0.10/7 = 0.0143$).

Observation Comparisons By Study Lake

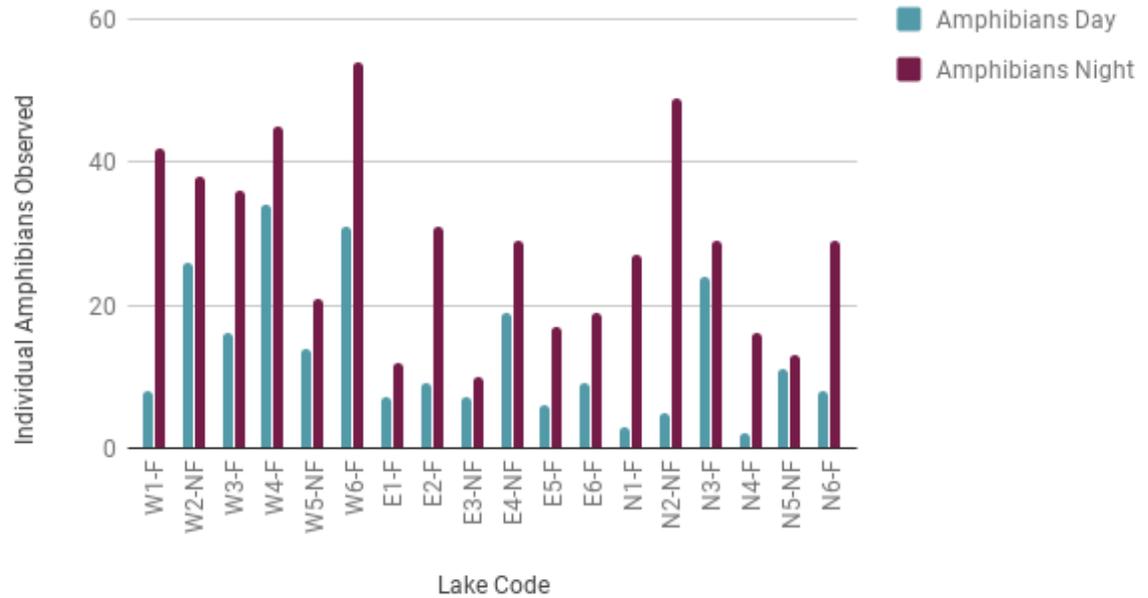
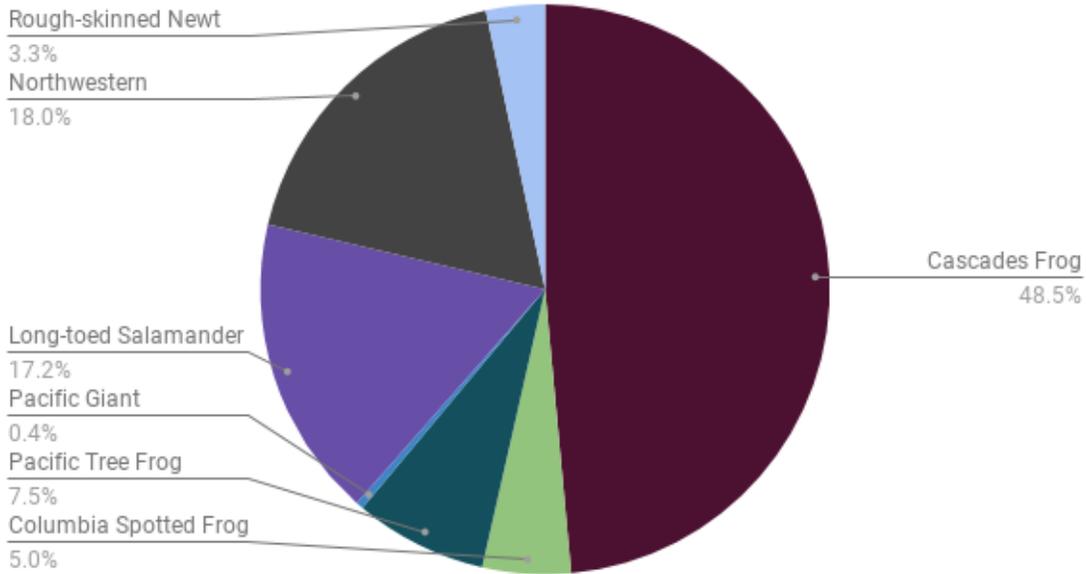


Figure 2. Observations of individual amphibians during both survey periods.

The relative abundance of species observed varied between diurnal and nocturnal surveys as well as between lakes with and without salmonids [Figure 4]. Relative abundance was greatest in the West Cascades ecoregion (West mean=7.35; East mean = 5.46, North mean = 6.41, $F_{6,11}=3.523$, $p = 0.056$).

Daytime Species Composition



Nighttime Species Composition

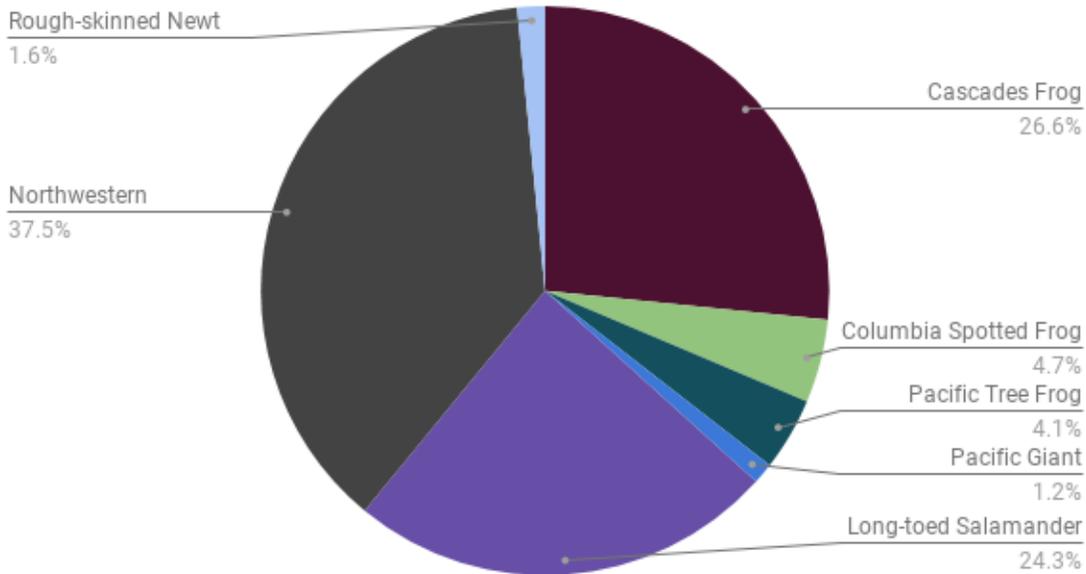


Figure 3. Species composition by observation period.

Relative Abundance of Amphibians Observed

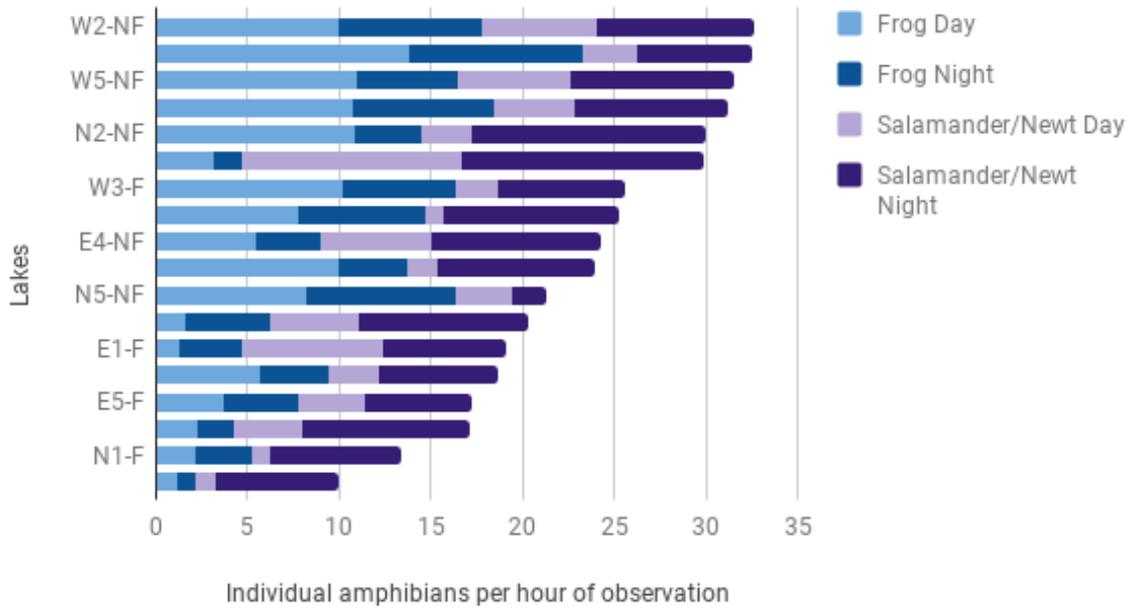
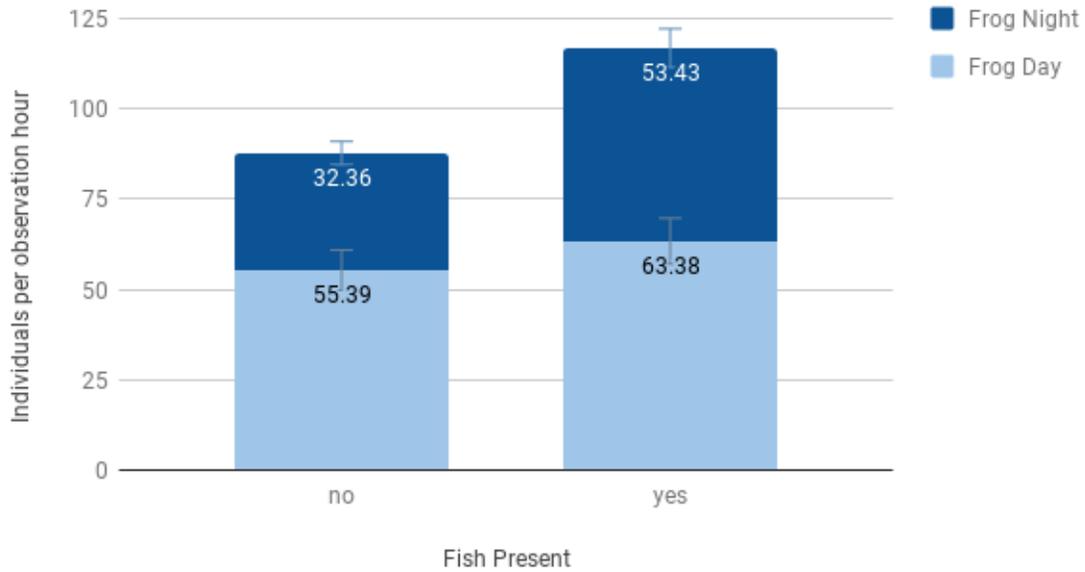


Figure 4. Aggregate Relative Abundance of All Amphibians Observed. Comparison of observed abundance of frogs and salamanders in lakes with and without salmonids. Relative abundance equals individual amphibians per hour of observation.

Frog Relative Abundance Day vs Night



Salamander/Newt Relative Abundance Day vs Night

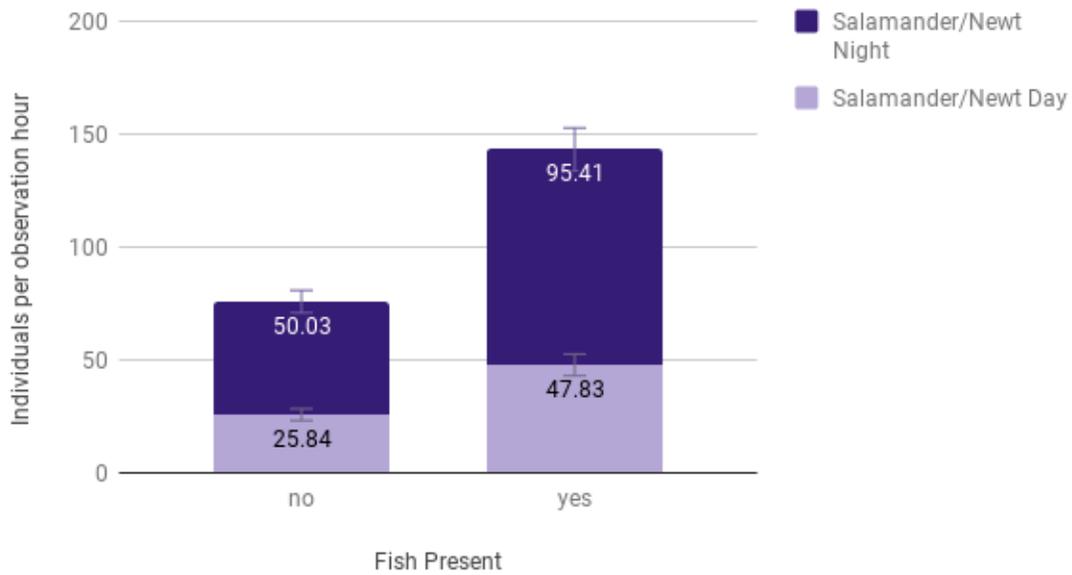


Figure 5. Relative Abundance By Species. Columns represent aggregate abundance across observation periods with individual values for each day period noted.

Beyond Salmonid Influence

Using each lake's recorded elevation, average lake water temperature during sampling periods, size in hectares, ecoregion, and salmonid presence to predict overall amphibian abundance did not result in a statistically significant regression model (Table 4). When using species richness as a response variable, elevation had a significant negative influence (Table 4).

Table 4. Regression model results. Report of results with total abundance and total richness as response variables.

	Total Abundance		Total Richness	
	β (SE)	p	β (SE)	p
Elevation	-0.004 (.001)	0.391	-0.005 (0.002)	0.009*
Temperature	-0.076 (0.167)	0.657	-0.012 (0.055)	0.838
Size	-0.064 (0.161)	0.700	0.020 (0.530)	0.708
Ecoregion (N)	-0.009 (0.813)	0.992	-0.3618 (0.269)	0.205
Ecoregion (E)	-0.591 (0.874)	0.513	-0.064 (0.289)	0.829
Fish (n)_	0.266 (0.680)	0.703	-0.020 (0.931)	0.931
Adjusted R ²	-0.137		0.544	

* - denotes statistically significant value

Examining other data collected during observation periods, I compared amphibian activity level and substrate type during day and night separately. Activity level was significantly associated with substrate type, both for daytime observations ($\chi^2_6 = 27.8$, $N = 239$, $p = 0.0001$) as well as at night ($\chi^2_6 = 36.9$, $N = 517$, $p < 0.001$). Of these analyses, hiding behavior on woody debris was higher than expected (expected 8.00, deviation +9.99, cell $\chi^2 = 12.47$). Active behavior on sand was also higher than expected (expected 16.82, deviation +5.18, cell $\chi^2 = 1.59$). When examining night activity, active behavior on rock was lower than expected 50.15, deviation -25.15, cell $\chi^2 = 12.61$), and resting behavior on rock was higher than expected 71.8, deviation +23.1, cell $\chi^2 = 7.45$).

Lastly, I examined the correlation of the relative abundance at different times of the day across different groups of amphibians (Table 5).

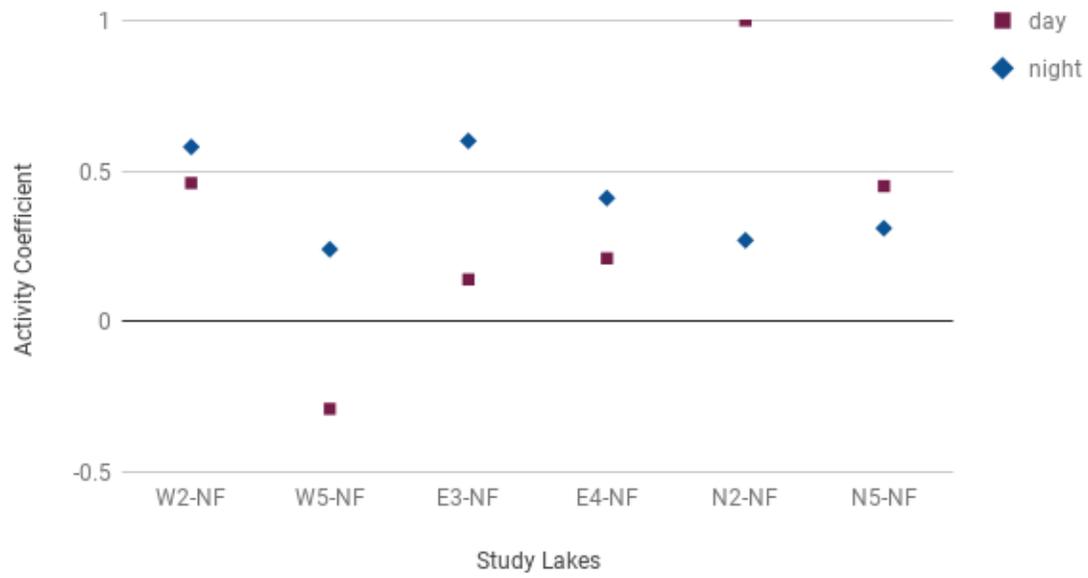
Table 5. Pearson’s correlation coefficient for Relative Abundance (Day and Night) across Amphibian Types.

	Total Abundance	Sal/Newt Day	Sal/Newt Night	Frog Day	Frog Night
Total Abundance	1.00				
Sal/Newt Day	0.645	1.00			
Sal/Newt Night	0.597	0.407	1.00		
Frog Day	0.441	-0.185	0.010	1.00	
Frog Night	0.244	-0.171	-0.371	0.752	1.00

Activity Coefficient

To examine the variability in activity from day to night with and without fish I calculated an activity coefficient to quantify the difference. Active behavior received a value of “1”, resting a “0” and hiding a “-1”, for the purpose of comparison and relatability. I compared daytime and nighttime activity levels in each lake (Figure 6). . A coefficient for both day and night was calculated in addition to the direction of movement (positive or negative) towards more or less activity at night. Overall during diurnal observations the dominant activity behavior was resting (n=139, 58.2%), followed by active (n=67, 28.0%) and hiding (n=33, 13.8%). During nocturnal observations resting was the dominant characteristic (n=288, 55.7%), followed by active (n=201, 38.9%) and hiding (n=28, 5.4%).

Activity Coefficient For Lakes Without Salmonids



Activity Coefficient For Lakes With Salmonids

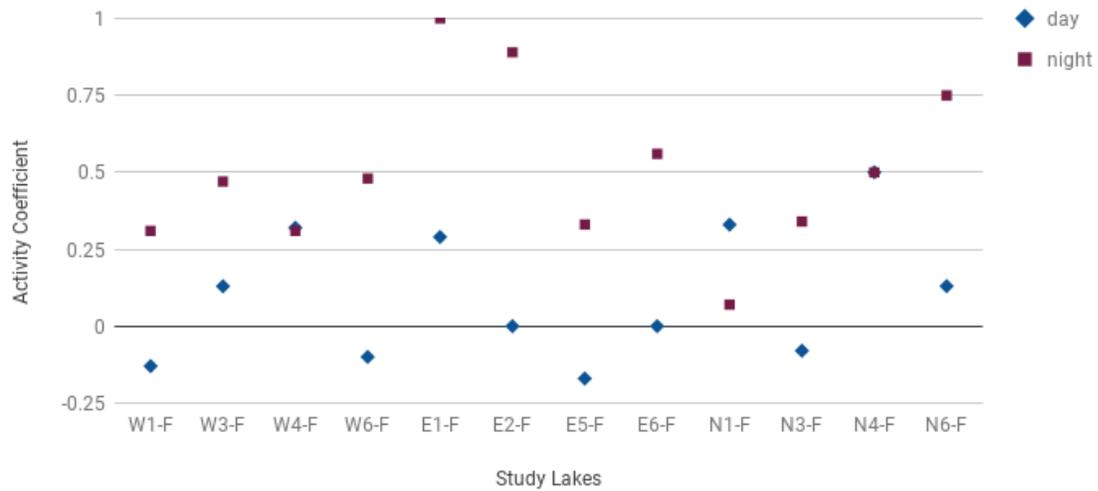


Figure 6. Activity Coefficient Comparison By Lake Between Day and Night

Chapter 4: Discussion and Conclusion

Towards a Complete Understanding

All of the lakes exhibited increased amphibian detectability at night, regardless of the presence or absence of fish. I hypothesized that there would be greater tendencies for hiding behavior in lakes with established salmonid populations due to predator prey dynamics, but this did not appear to be the case. The presence of fish did not play a significant role in predicting the presence or abundance of amphibians during daytime or nighttime hours. This finding challenges many assumptions that past researchers have based their research upon. While fish alone did not predict presence or abundance, there could be a synergistic effect at play with another variable that I did not collect during my field study. Increased detectability at night, however points to a change in how amphibians are utilizing available habitat. It is unknown whether available cover, availability of deep-water refuge, or a combination of these and other habitat structural elements play a role (Welborn, Skelly and Werner, 1996). Elevation was a significant predictor of species richness (Table 4).

The Chi-Squared tests of independence that I conducted point to significant correlations between activity level and substrate type and could play a greater role in the predictability of amphibian behavior than predator prey dynamics alone. This changes in expected versus observed behavior generally point towards more cautious behavior during daytime hours and increased activity and exposure during nighttime observations. This could potentially be linked to community composition as larval salamanders may avoid larger salamanders and frogs. This correlation is represented during both daytime

and nighttime observation periods through Pearson's correlation coefficient (Table 5), which displays negative correlations of frog presence on salamander detectability.

Without a complete story as to why amphibian activity level fluctuates across lakes, I calculated an activity coefficient to help bring a better understanding of lakes that experience that greatest diel swings in activity level. Figure 6 displays the comparative activity coefficients by lake during daytime and nighttime observations. The coefficient is a measurement of the net activity per individual observed and can serve as a snapshot of general activity level for a given time of day. The activity coefficient gains power as observations are repeated over time to gain a more complete picture of amphibian activity. By looking at the variation from day to night, extreme swings may warrant additional study to understand the factors influencing the change. Land managers can then begin to understand if these fluctuations come from direct predator threat, or another biotic or abiotic factor within the lake environment. There is not currently a detection system in place for managers to identify priority lakes with amphibian populations in the greatest need. The snapshot provided through the activity coefficient could potentially lead to more efficient management practices and use of funding.

While fish alone did not predict presence or abundance, there could be a synergistic effect at play with another variable that I did not collect during my field study. Some potential explanations from the literature for variation in amphibian activity include factors not considered in this study, such as shoreline vegetation and habitat, non-aquatic predators, and other abiotic factors. Shoreline vegetation can create respite from hot summer sun and can cool water temperature in the immediate vicinity of the shoreline (Hossack et al., 2013; Warren and Buttner, 2008). This could be a factor in drawing

amphibians up from greater depths and become more detectable during daytime hours. Other landscape disturbance such as avalanche activity can alter shoreline vegetation structure and disturb surrounding trees and vegetation on a micro or macro scale.

Ultraviolet exposure at high elevations may also affect the use of cover by amphibians throughout the day (McCaffery and Maxell, 2010). Thinner atmosphere at higher elevations can cause prolonged exposure to potentially deadly UV-B rays (Hatch and Blaustein, 2000). Larval stage frogs and amphibians may be especially vulnerable to UV radiation, explaining the finding that larvae were most active at night. Winter severity also plays a role in the level of exposure to ultraviolet radiation. More severe winters provide a longer lasting snowpack that reflects UV light and protects frogs and salamanders under the ice (Blaustein, 2000; McCaffery and Maxell, 2010). The rearing timeframe for larvae begins in early summer and a longer lasting snowpack allows larvae to get a head start on development without harmful UV rays penetrating the shallow water that they typically occupy.

Non-aquatic predators deserve consideration as an influence on amphibian behavior, due to the fact that many of the observed salamanders were in larval form and an easy target for many predators. There are relatively few large predatory birds that frequent alpine lakes, aside from ospreys and eagles. However, the spread of the American dipper into higher elevations due to climate change can also be considered. Normally seen as a riparian bird at lower elevations and even the ocean, this bird would be a prime suspect for the role of diminishing the vulnerable larval stage salamanders and tadpoles (Garwood et al., 2009). Another threat of predation that is frequently overlooked as an explanation for behavior is that of inter and intra species predation by other

amphibians. Within the salamander community, cannibalism is common occurrence as individuals eliminate competition for valuable food sources (Wildy et al., 1998; Walls, 1995). Lastly, the lunar phase could play a role in activity level due to the fact that when there is increased lunar light, salmonids are able to continue to search for food in conditions that normally offer safety for amphibians and other lake inhabitants.

Additional considerations for what could be seen as confident behavior would need to be made when specifically analyzing individual species. The Northwestern salamander displays combative behavior when threatened, as does the Rough-skinned newt that is armed with a powerful neurotoxin. The increased activity displayed by these species alone could be less of a holistic representation of amphibian species as a whole. While none of the observed species are currently listed as threatened or endangered, there could potentially be valuable data collected for future struggles, which are sure to come. The umbrella approach to studying species favors some and is a disservice to others. Ideally a study specific to each species would be conducted, but due to the widely understudied nature of alpine species aquatic interactions and behavior, it isn't plausible in many circumstances.

The uniform tendency for nocturnal behavior is likely to be more than just a life history characteristic for some of the amphibians that were observed in this study (Kenison et al., 2016; Pearson and Goater, 2009). Another possible explanation for this is that food sources have diel migration patterns. The tendency to find an amphibian at the top or bottom may be a factor linked to its own hunting strategies and less of an action based in self-preservation. A study conducted by Dolmen (1983) initially examined this diel movement of species through the water column as prey and microhabitat benefits

changed with temperature and consumption needs. Another consideration linked to food is competition with salmonid species for phytoplankton and zooplankton that inhabit the lake (Parker et al., 2001).

Potential changes to analysis

If I were to continue or adapt this study I would narrow my scope to fewer lakes and focus on the repeatability of the data to examine long-term trends that occur in a given lake. With continued observation of one location, the external variables may become more evident. This is one of the main challenges that researchers face in the field today as studies may take several years for these variables to emerge. Lake basins are very diverse and there are a lot of factors that can synergistically affect behavior of biota. Additionally, by studying all amphibians present I was introducing the factor of potential immigration and emigration of species between bodies of water. By solely focusing on the larval stage salamanders and tadpoles, there would be fewer influences and the study could purely examine the seasonally permanent inhabitants of the lake.

Future implications and next steps

Responsible management action is required to be able to meet the dual mission of state agencies in Washington State to conserve native species and provide recreational opportunity for citizens. The fish stocking practices of the past changed because of a recognition that overpopulation was destructive to both native biota and a healthy fishery. Without careful management of both goals, tensions are likely to rise between supports of each side. Some value the right to recreate on public land while others value preservation of species at nearly any cost. While there is clearly variation among alpine lakes, there

will also be varied need for intervention and active management by land managers (Whittaker, Willis and Field, 2001). It is an implausible feat to move to one extreme or another of the spectrum of involvement (Fellers et al, 2008). All future decisions will likely be based on how to accommodate and consider the other side. Another danger of this duality of purpose is creating a division among people that care for the outdoors and need to support one another. With limited funding for projects and research another benefit that is underutilized is the incorporation of citizen science and volunteer efforts.

Conclusion

The discussion on threatened and declining amphibian species in alpine lakes is often accompanied by mention of introduced salmonid species. The logical step for many is to place responsibility on the misdeeds of ill-managed alpine fisheries of the past. While predation will occur when a predator is introduced into an ecosystem, the extent of that blame is not fully understood and often involves other variables that may have synergistic effects on the outcome. My work finds strong correlations between substrate type and the behavior displayed by amphibians. The interactions that take place in aquatic environments by nature are less observed than ecological interactions on land. Coupled with the remote locations of these lakes, researcher accessibility is limited and therefore little is known about the complete diel cycle of interactions and behaviors that take place. My hope is to initiate conversations that examine how field research is conducted with a larger emphasis on nocturnal observations. The aquatic environment, through substrate and other physical cover, provides physical protection for many amphibian species and is a necessary buffer in battling climate change and other changing biotic and abiotic factors. As managers are able to understand the relationship that exists between

amphibians and their natural environment, there can be a more thoughtful allocation of resources to assist populations that face these challenges without ability to adapt or adjust. By understanding the diurnal and nocturnal patterns of movement within the environment managers can better meet the challenge of conserving biodiversity and managing established fisheries that aid in funding such actions.

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