

STREAM-BREEDING SALAMANDER USE OF HEADWATER STREAM
NETWORKS IN MANAGED FORESTS OF WESTERN WASHINGTON

by

Reed Ojala-Barbour

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This Thesis for the Master of Environmental Studies Degree

by

Reed Ojala-Barbour

has been approved for

The Evergreen State College

by

Marc P. Hayes, Ph. D.
Member of the Faculty

Date

Kevin Francis, Ph. D.
Member of the Faculty

Date

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Reed Ojala-Barbour

Stream-associated amphibians are sensitive bioindicators that occupy headwater streams across the Pacific Northwest. Much of the headwater landscape is intensively managed for timber. Forest Practices (FP) rules determine harvest prescriptions on most private lands in Washington State. Under these rules, non-fish-bearing headwater streams receive buffers on a minimum of 50% of the total stream length, including Sensitive Sites that receive 17-meter [56-foot] radius patch buffers. I evaluated the two most common Sensitive Sites, tributary junctions (TJs) and perennial initiation points (PIPs), and two additional hydrologic characteristics using an index of abundance (measured as linear density) for two stream-breeding salamander taxa: torrent salamanders (*Rhyacotriton* spp.) and giant salamanders (*Dicamptodon* spp.). I also evaluated stream order to provide context on how salamander distribution patterns overlap with harvest prescriptions. Finally, I evaluated salamander abundance in relation to two hydrologic characteristics: channel dryness as the proportion of dry stream channel and seeps including any stream channel within 15 meters [50 feet] of a seep. I used data collected in 2006 and 2007 from 17 amphibian-occupied fishless basins in managed forests in Western Washington prior to harvest.

I found that PIPs and TJs had no effect on torrent salamander abundance, and TJs had no effect on giant salamander abundance. Consistent with expectations, giant salamanders were less abundant in PIPs and first-order streams. Conversely, torrent salamander abundance had no apparent relationship to stream order. Proportion of dry channel and seeps affected for the abundance of both species. Giant and torrent salamanders showed a strong negative response to proportion of dry channel, but torrent salamanders were observed in short reaches of surface water even in predominantly dry channels. Lastly, reaches with seeps had 123% (CI: +103% to +146%) and 84% (CI: +49% to +121%) greater abundance of torrent salamanders and giant salamanders, respectively. Current rules may too narrowly define the criteria of seeps that receive protection. A study focused on the characteristics of seeps and stream channels adjacent to seeps may help refine rules to protect features most important to stream-breeding salamanders. Complimentary research is needed to understand the effectiveness of patch buffers after harvest.

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List of Acronyms

Type N – Non-fish-bearing headwater stream

FP – Forest Practices refers to forest management on most privately owned timberlands and the regulations prescribed in the Washington State Forest Practices Habitat Conservation Plan (HCP)

SAAs – Stream-associated amphibians includes tailed frogs (*Ascaphus* spp.) and torrent salamanders (*Rhyacotriton* spp.) and giant salamanders (*Dicamptodon* spp.) which are all stream-obligate amphibians

PIP – Perennial initiation point is the uppermost point of perennial surface water in a stream channel

TJ – Tributary junction or confluence of two stream tributaries

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1 INTRODUCTION

Stream-associated amphibians (SAAs) are often the dominant vertebrate upstream of fish and can be important indicators of environmental change in headwater landscapes (Welsh and Ollivier 1998). In the Pacific Northwest, three amphibian taxa, tailed frogs (*Ascaphus* spp.), torrent salamanders (*Rhyacotriton* spp.) and giant salamanders (*Dicamptodon* spp.) comprise the dominant vertebrate assemblages in non-fish-bearing (Type N) streams. Extensive management of forestland has changed the structure and function of riparian areas throughout much of the ranges of these taxa (Pan *et al.* 2011) and prompted the widespread use of riparian buffers to protect them and water quality.

Compared to their areal extent on the landscape, headwater systems are less studied than larger fish-bearing systems and they receive less protection (Richardson and Danehy 2007). Approximately 70% of total stream length in western Washington is classified as non-fish-bearing stream (Rogers and Cooke 2007). Conflicting results on the effects of timber harvest on SAAs (reviewed in Kroll 2009) underscores the importance of understanding amphibian use of stream network features and their overlap with harvest prescriptions. For example, spatial habitat use patterns at a scale relevant to management could be used to validate the appropriateness of current buffering strategies or more efficiently target key features for buffer placement and effectiveness monitoring.

Land managers deploy riparian buffers to help limit the presumed negative effects of harvest on streams (Richardson *et al.* 2012). Currently in western Washington, the vast majority of timber comes from private industrial lands (Zhou and Daniels 2018) where uplands are clearcut and some aquatic features receive no-cut buffers. Forest Practices (FP) rules dictate harvest prescriptions on approximately 9.3 million acres of private

timberland and require buffers on all fish-bearing streams and on at least 50% of Type N stream length (WFPB 2001). Within headwater basins, FP buffers target the lower portion of Type N streams to minimize impacts on downstream fish. Select stream network features, including tributary junctions (TJs) and perennial initiation points (i.e., uppermost point of perennial surface water in a stream channel; PIPs), are designated as Sensitive Sites and receive 15-meter to 17-meter [50- to 56-foot] radius patch buffers to protect wildlife habitat and mitigate water quality impacts. Land managers across ownerships have set the resource management objective of maintaining viable populations of sensitive amphibians in lands impacted by forest harvest (WADNR 1997; Molina *et al.* 2003; WADNR 2005). Despite this objective, amphibian use of features that receive Sensitive Site buffers on FP-covered lands have not been evaluated.

2 LITERATURE REVIEW

In this literature review, I synthesize key information on the physical structure of headwater stream networks, including the potential unique ecological functions of TJ and PIP Sensitive Sites for SAAs. I also provide context on forest management including the landmark Forest Practices Habitat Conservation Plan (HCP) and associated rules that dictate buffer placement. I then review conservation status, habitat associations and natural history of focal SAAs, namely giant and torrent salamanders, which rely on headwater streams in western Washington. Finally, I provide a brief overview of the amphibian sampling methodology used in the field study component of this thesis.

2.1.1 ECOLOGICAL FRAMEWORK AND PHYSICAL CHARACTERISTICS OF HEADWATER STREAMS

The spatial structure of stream networks affects physical processes and stream conditions, and organizes aquatic habitats and communities (Grant *et al.* 2007). These controls may be especially important for highly constrained organisms such as SAAs due to their reliance on aquatic habitats for reproduction and early development and because of desiccation intolerance in terrestrial stages. Physical conditions and processes that affect headwater streams are highly variable compared to their lowland counterparts (Montgomery and Buffington 1998). This inherent variability produces patchy distributions of taxa across the landscape and makes habitat associations difficult to decipher. However, even within these dynamic and complex systems, dendritic ecological networks (Grant *et al.* 2007) and hierarchical habitat classifications help frame the spatial structure of the headwater landscape and inform process that act on their biotic assemblages.

The distribution and function of spatial stream network features can help inform riparian management decisions by recognizing features and spatial patterns important to sensitive taxa. Dendritic networks are organized by nodes and branches with inherently different characteristics. Stream order descriptors enable organizing stream reaches into a hierarchy that informs stream power (Strahler 1952) and in turn organizes biotic communities (Olson and Weaver 2007). Similarly, channel-reach characteristics like surface water intermittency and the presence of unique features like channel-connected seeps alter aquatic habitats along environmental gradients. This framework highlights the unique roles of TJs and PIPS, both FP Sensitive Sites, and other important habitat characteristics for SAAs within stream networks.

2.1.2 DENDRITIC NETWORKS AND STREAM ORDER

Stream networks are composed of dendritic, or branching, structures that are hierarchically organized (Strahler 1952). As one moves up the stream network the number of branches increase in number and decrease in size (**Figure 1**). This pattern helps explain the frequency of low order Type N streams at a landscape scale, which in western Washington represent nearly 70% of the total stream length (Rogers and Cooke 2007). The spatial structure of streams coupled with reach-level channel process including inputs from hillslopes, confinement, and wood provide additional context for understanding stream features and their ecological function.

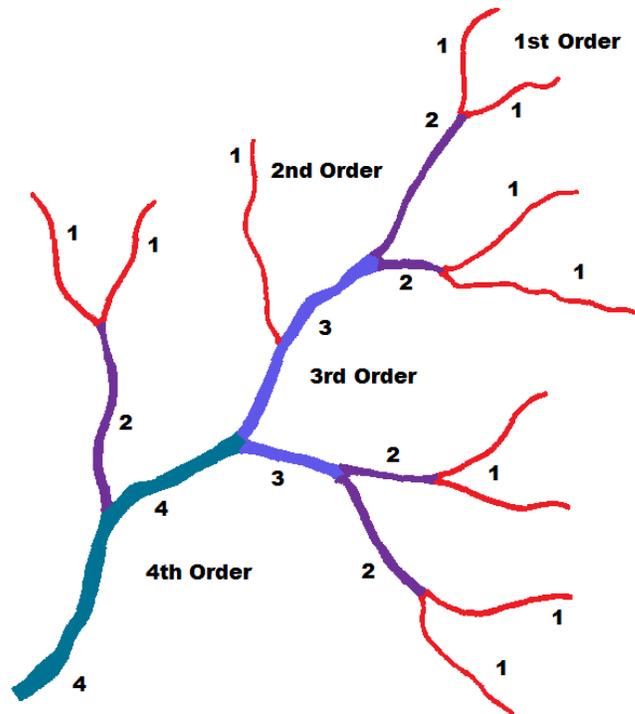


Figure 1. Dendritic stream network illustrating Strahler stream order.

Stream order allows organization of stream reaches into a hierarchy based on upstream branching complexity and informs flow conditions and a stream's potential to

sort and transport material (Strahler 1952). High flows organize stream substrates, transport wood and modify channel morphology, creating diverse habitat conditions throughout dendritic networks (Gomi *et al.* 2002). Lower-order streams (1st through 3rd order) are typically higher gradient and encompass smaller basin areas. First-order streams are often dominated by colluvial inputs that have not been sorted by flows, especially near PIPs (Montgomery and Buffington 1997). Colluvium has interstitial spaces that provide habitat for SAAs (Thompson *et al.* 2018). Downstream higher-order systems have greater potential to sort material and form step-pool morphologies that may benefit a unique set of organisms (Montgomery and Buffington 1997).

Dendritic ecological networks provide a complementary lens for understanding features in stream networks. Grant and colleagues (2007) contrast network nodes (TJs) from branches. Nodes are where tributaries merge to create a larger stream. They are transfer points, providing heterogeneity in resource distribution by linking multiple, potentially diverse tributaries. Nodes may be important features for dispersal of aquatic organisms that are restricted to the stream channel. Spatial structure is a key component of stream networks, regulating ecological processes (Grant *et al.* 2007). While micro-habitat conditions at fine scales may play an important niche-based role in structuring communities, the spatial structure of networks may be an important component for structuring species assemblages within basins.

2.1.3 AQUATIC HABITAT AND STREAM MORPHOLOGY

Stream order cannot capture the complexity of hydrologic and geomorphic processes. Different channel morphologies and processes create variable habitat

throughout headwater stream networks. For example, inputs from hillslopes have a major role in providing food and structuring habitat for biota (Richardson 1991). Wood stores sediment and can create pools and steps adding to habitat complexity. Lithology, or the parent geology, of a basin also influences hydrology (Jaeger *et al.* 2007) and species assemblages (Wilkins and Peterson 2000) in important ways.

To classify channel morphologies, Montgomery and Buffington (1997) found that a stream length of at least 10 to 20 channel widths was a useful scale to relate morphology to habitat characteristics. Step-pool systems dominate many headwater streams compared, with riffle-pool configurations in higher-order reaches (Montgomery and Buffington 1997). Step-pool systems are typically higher gradient, and fine sediment is transported downstream maintaining interstitial spaces that can be beneficial to SAAs (Welsh and Ollivier 1998). Wood and boulders trap smaller material, creating steps that further enhance habitat complexity.

Lithology is a major control on headwater systems. In western Washington, lithologies can be coarsely categorized as basalt or marine sedimentary (Jaeger *et al.* 2007). Basalt is more competent (i.e., less erodible) and produces larger cobble and gravel clast sizes than softer marine sedimentary lithologies, which produce more fine sediments. Basins underlain by marine sediment frequently have more sand. Sandy accumulations in these basins can degrade instream habitat through the filling of interstitial spaces between substrates, which can result in reduced cover for instream biota and the suffocation of eggs (Wilkins and Peterson 2000).

Basalt lithology may also have bedrock flow paths in which, unlike sedimentary lithologies, discharge does not scale with drainage area. Studies conducted in the Willapa

Hills suggest that the uppermost point of flow is generally more stationary in basalt streams, compared to the downslope migration of surface water in sedimentary streams (Jaeger *et al.* 2007).

Perennial initiation points, as the uppermost point of flow are located on first-order streams by definition, and have limited power to transport sediment or scour channels. Colluvium, the gravity driven rocky inputs from adjacent hillslopes that accumulate in channels, often define these uppermost points of the channel network. A thin water-worked surface may exist, but unsorted colluvium is often stored underneath (Benda and Dunne 1997). Large cobble and wood may further limit the fluvial power of these reaches by contributing to channel roughness and reducing water velocity. One study found that only major, infrequent debris flows restructure these low-flow habitats at intervals of roughly 200 to 600 years (Kelsey 1980). The relative stability of stream habitats at the PIP may be beneficial to low flow specialist species.

Tributary junctions, or confluences, can be morphologically distinct from other reaches (Benda *et al.* 2004b), however the role of TJs in small headwater basins has not been evaluated. Morphologically significant areas occur where small tributaries join larger streams providing an additional source of sediment and wood. Benda and colleagues (2004a) found that larger tributaries had a significant geomorphic effect on the mainstem compared with smaller tributaries. They also found that confluences were effected by basin shape, network patterns, and drainage density. The geomorphic effects, when present, can increase pool depth, substrate size and depositional bars (see Benda *et al.* 2004b). Another study found that confluences can alter gradient and substrate (Frissell *et al.* 1986). Confluences can amplify local disturbances in their immediate vicinity due

to increased sediment supply (Benda *et al.* 2004a). One low-order fish study found confluences promoted wood storage and pool formation, resulting in increased salmonid rearing (Everest and Meehan 1981). Increased habitat heterogeneity associated with stream branching may provide increased diversity (Holt and Chesson 2018), but most of these studies have been focused on larger fish-bearing systems.

2.2 FOREST MANAGEMENT

Forestland covers approximately 22 million acres in Washington State and is a significant economic sector (Campbell *et al.* 2010). Private forestlands are the most intensively harvested and are the major producer of timber. Forest management has shaped the landscape through current and historic management (Pan *et al.* 2011). Harvest activities on most private lands are covered by the FP Habitat Conservation Plan and associated rules. The FP-HCP employs adaptive management to inform rule effectiveness in meeting resource objectives. Maintenance of populations of seven amphibians were selected as a metric of successful management (WADNR 2005).

Washington State forestlands fall under federal, state, and private ownership each with its respective geographic footprint, levels of production, and harvest rules. Federal lands were of greater importance prior to the early 1990s and implementation of the Northwest Forest Plan, but currently have much less timber harvest. Today, private lands contribute the majority of timber production by volume (**Figure 2**), which highlights both the economic importance and intensity of harvest activities that potentially pose a risk to sensitive organisms, their habitats, and ecological function.

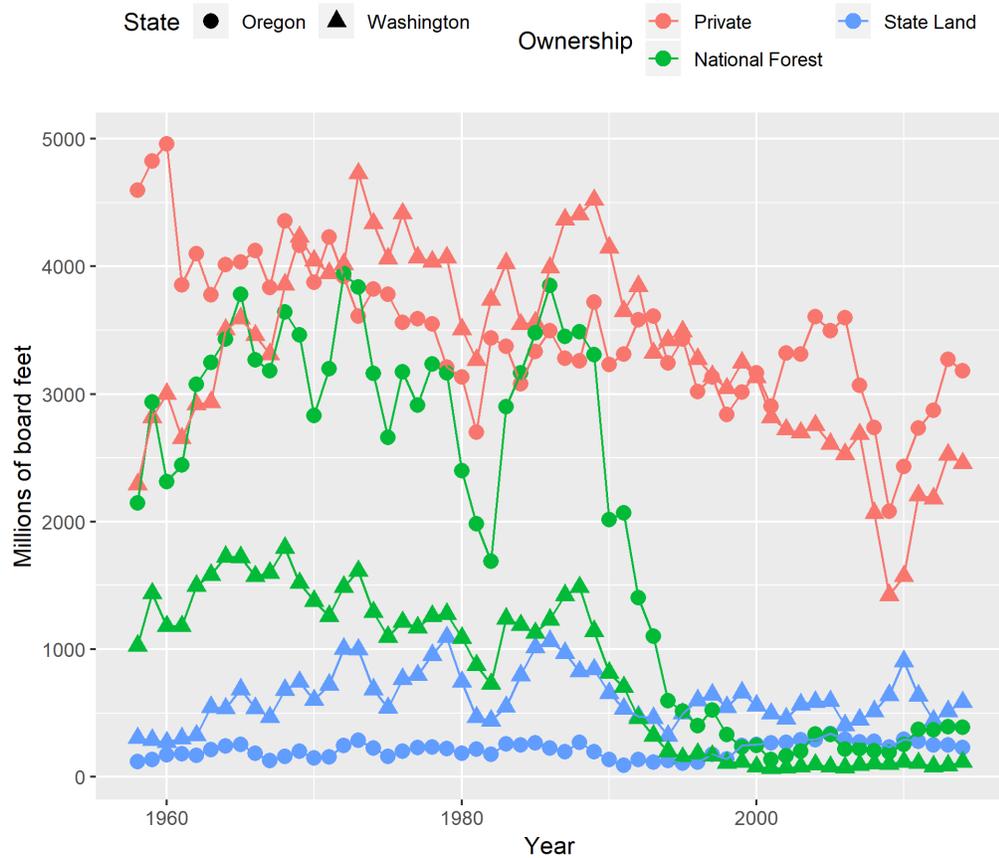


Figure 2. Timber harvest by ownership in WA and OR from 1958-2014 in millions of board feet (Source: Zhou and Daniels 2018).

2.2.1 FOREST PRACTICES HCP

The harvest-related impacts of forest management on private lands at site and landscape scales are considered in the FP-HCP and in an adaptive management framework. The creation of an adaptive management program was the result of a series of policy steps from the late 1980s to early 2000s, and led to new protections for riparian areas in managed forestland. The Forest and Fish Law and FP-HCP require that Type N streams receive buffers on a portion of stream length and set the Overall Performance Goal of supporting the long-term viability of the seven covered species of amphibians, among other objectives (WADNR 2005).

The current adaptive management program was the result of a series of policy negotiations and science-based rule making processes. First, the Timber Fish and Wildlife agreement in 1987 led to the protection of fish-bearing streams with riparian buffers to provide shade and wood to streams. However, outcomes were limited due to inadequate funding and the lack of policy representation among stakeholder groups. The listing of salmonid populations under the Endangered Species Act (ESA) and the identification of over 600 stream segments with water quality problems under the Clean Water Act prompted more protection for riparian areas. The Forest and Fish Report (USFWS 1999) was a landmark deal negotiated by the timber industry, environmental groups, tribes, and state and federal agencies, that all acknowledged the need to develop biologically sound and economically viable prescriptions with greater protection for riparian habitats in Washington. Subsequently, the Forest and Fish Law was signed in 2001 and included the protection of non-fish-bearing streams for the first time (WADNR 2005).

In 2005, the FP-HCP was finalized and became the largest programmatic HCP in the nation. It applies to approximately 9.3 million acres of private forestlands in Washington State and created a legally binding agreement to meet resource objectives. The adaptive management process uses best available science and research to inform consensus-based decisions among stakeholder groups. The HCP has multiple objectives:

- To provide compliance with the Endangered Species Act for aquatic and riparian dependent species on non-Federal forestlands;
- To restore and maintain riparian habitat to support a harvestable supply of fish;
- To meet the requirements of the Clean Water Act for water quality.

The HCP includes maintaining viable populations of three species of torrent salamander, two terrestrial woodland salamanders and two species of tailed frog.

The majority of private timberlands covered by the FP-HCP and associated rules are located in southwestern Washington (**Figure 3**). Small forest landowners make up a substantial portion of valley bottoms near larger fish-bearing streams while industrial timberlands tend to dominate the headwaters (Rogers and Cooke 2007).



Figure 3. Forest Practices-rules and management goals apply to most private forestland in western Washington (shown in brown). State, federal and select private lands are managed under different rules. (Source: CMER Lands, DNR; Basemap, ESRI).

2.2.2 FOREST PRACTICES HARVEST PRESCRIPTIONS IN HEADWATER BASINS

The current FP-rules require 15-m [50-ft] no-cut buffers on both sides of the stream and along at least 50% of the non-fish-bearing perennial stream network (**Figure 4**;

WFPB 2001). A primary strategy is to minimize impacts to downstream fish, so rules emphasize buffering the lower reaches of Type N waters immediately upstream of the uppermost point of fish habitat. Consequently, it is more likely that upper reaches of headwater basins will not receive buffers. This pattern led to rules calling for protection of selected Sensitive Sites in otherwise clearcut reaches of Type N streams. Specifically, 17-meter [56-foot] radius patch buffers are designated at TJs and PIPs. Rules also call for 15-meter [50-foot] radius buffers from the outer edge of saturation at seeps. Seeps located downstream of the PIP must meet specific criteria for buffers to be required, including >20% gradient and a lack of mucky substrates. Rules do not address stream intermittency (dry channel) below PIPs.

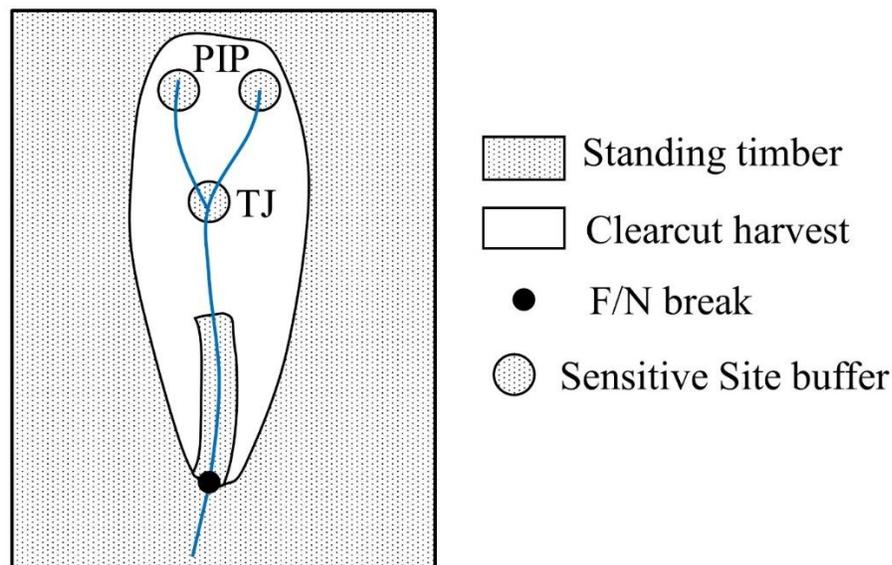


Figure 4. Schematic of harvest prescription for Type N basin. Sensitive Site buffers at Tributary Junction (TJ) and at the Perennial Initiation Point (PIP). F/N break is the uppermost point of fish habitat where fish-bearing streams become Type N.

The FP-HCP loosely explains the rationale for Sensitive Site buffers as a strategy to protect wildlife and water quality (WADNR 2005). Justification for buffering seeps

and PIPs was largely driven by a desire to protect wildlife, such as torrent salamanders, and water quality. Though the HCP does not specify rationale for buffering tributary junctions, it was motivated by the recognition that by encompassing three stream reaches it maximizes the stream length protected with the smallest buffer (T. Quinn, personal communication, Jan. 18, 2019).

Buffering strategies in the FP-HCP were intended to provide woody debris recruitment, shade, and other ecological function through retention of trees in the riparian corridor (WADNR 2005). Additionally, buffers help reduce mechanical disturbance to soil that could lead to sediment inputs. Trees closer to the water have greater function for providing shade and recruiting wood to the stream (McDade *et al.* 1990). For example, 70% of in-stream wood recruitment has source distances of 15 meters [50 feet] or less, partially explaining the rule's buffer width requirement. Similarly, buffers reduce sediment inputs by retaining riparian vegetation and limiting mechanical disturbance associated with harvest. The entire Type N stream length is protected by an Equipment Limitation Zone within 9 meters [30 feet] of both sides of the stream.

The disturbance associated with harvest has the potential to impact aquatic organisms through increases in sediment, stream temperature, and other habitat alterations (Richardson and Béraud 2014). Conversely, canopy closure occurring from roughly 30 to 100 years after harvest in plantations allows less light to penetrate than in old-growth forests and can suppress productivity (Kaylor *et al.* 2017). The effects of timber harvest and intensively managed single-age plantations are complex and largely outside the scope of this research. I expressly focus on addressing knowledge gaps associated with amphibian use of sites that receive buffers in headwater streams.

2.3 STREAM-BREEDING AMPHIBIANS

Stream-associated amphibians breed in flowing aquatic habitats and are an important component of headwater stream food webs and an indicator of environmental change. In the Pacific Northwest, torrent salamanders, giant salamanders and Coastal Tailed Frogs comprise the instream-breeding assemblage of amphibians. They are often the dominant predator in old-growth headwater streams (Bury *et al.* 1991) and can dominate total vertebrate biomass (Bury 1983). Their lifecycle's reliance on aquatic habitat makes them indicators of environmental change (Welsh and Ollivier 1998). Stream-associated amphibians breed in cold, flowing streams (Bury 2008), making them distinct from most amphibians that breed in stillwater habitats such as ponds and wetlands and often move larger distances. SAA larval stages metamorphose into terrestrial forms, which can disperse overland but their water-dependent physiology is generally thought to keep them in relatively close proximity to streams (Nijhuis and Kaplan 1998).

The distribution of SAAs across the landscape are patchy and not fully understood. SAAs generally are associated with coarse substrates more commonly found in basaltic lithologies, although they can also be found in basins with marine sedimentary lithologies (Wilkins and Peterson 2000). Coarse inorganic substrates provide important cover for larval salamanders and are used as grazing surfaces by Coastal Tailed Frog larvae. Amphibian's reliance on cool and moist conditions make them vulnerable to environmental impacts like logging by making them more vulnerable to desiccation and the impacts of sedimentation (Bury and Corn 1988).

2.3.1 CONSERVATION STATUS OF FOCAL TAXA

Federal and state fish and wildlife agencies as well as land management plans have designated different conservation statuses to the different species of SAA. Even with a lack consensus, the general pattern seems to be that torrent salamanders are of higher concern than giant salamanders (**Table 1**).

Conservation assessments of the Columbia Torrent Salamander (*R. kezeri*) highlight the species small global range and its overlap with intensively managed forestland. Cascades Torrent Salamander is also thought to be sensitive due to forest management, road-related sedimentation and isolated populations. Olympic Torrent Salamander (*R. olympicus*), endemic to Washington State, has the smallest global range, but assessments highlight the protected status of many of the occurrence points, perhaps justifying its lower designation. All species of torrent salamander are thought to be vulnerable to climate change because of sensitivity to temperature and limited dispersal ability (WDFW, 2015).

Table 1. Conservation status of focal SAA taxa.

Taxonomic group	Species	Federal Status	State Status ¹	Forest Practices HCP	USFS and BLM WA - Management Status
Torrent salamander	Columbia Torrent Salamander (<i>Rhyacotriton kezeri</i>)	Under Review	Candidate	Covered	
	Cascade Torrent Salamander (<i>Rhyacotriton cascadae</i>)	Under Review	Monitor	Covered	Sensitive
	Olympic Torrent Salamander (<i>Rhyacotriton olympicus</i>)		Monitor	Covered	Sensitive
Giant salamander	Cope's Giant Salamander (<i>Dicamptodon copei</i>) Pacific Giant Salamander (<i>Dicamptodon tenebrosus</i>)		Monitor		Sensitive

2.3.2 TORRENT SALAMANDERS

Torrent salamanders (*Rhyacotriton* spp.) are habitat specialists associated with the uppermost reaches of cool headwater streams in moist conifer forests (Olson and Weaver 2007). Torrent salamanders are headwater obligates using shallow, low-flow habitats with rocky substrates often near springs, seeps and in splash zone (Nussbaum and Tait 1977). Three similar species of torrent salamanders exist in western Washington and do not co-occur (Good and Wake 1992; **Figure 6**) . The Olympic Torrent Salamander, endemic to Washington State, occurs only on the Olympic Peninsula and are known from sites between 33 and 1200 m above mean sea level. The Columbia Torrent Salamander is

¹ State Status ranked by risk: Endangered, Threatened, Sensitive, Candidate, Monitor

distributed in the coast range of southwestern Washington and northwestern Oregon. The Cascade Torrent Salamander is found from the western slope of the Cascades south of Mount Rainier to Lane County in Oregon (Good and Wake 1992).

The torrent salamander life cycle is closely linked to low-flow stream habitats, such as seeps (Nussbaum 1969). All species in the group appear to occupy similar niches with instream breeding and larval development (Thompson *et al.* 2018). They oviposit individual unattached eggs in the interstitial spaces of gravel and cobble. Since the eggs are unattached, they are at risk of scour and thus require habitats protected from scour. Perennial initiation points and other small channel-connected seeps provide this specialized habitat where a consistent trickle of cool water maintains necessary thermal conditions without risking exposure to high velocity water (Nussbaum 1969; Russell *et al.* 2004). Additional observation suggests that young larval torrent salamanders are abundant in seep habitats (Welsh and Lind 1996). Adult post-metamorphic individuals lose their gills, but maintain a close association with moist substrates and are desiccation intolerant (Ray 1958).

At broad spatial scales, torrent salamanders are headwater obligates and are associated with the smallest and steepest streams. For example, Columbia Torrent Salamander occupancy increased with increasing stream gradient and decreasing basin area (Wilkins and Peterson 2000). Studies of the Cascade Torrent Salamander have found a similar pattern (Hunter 1998; Olson and Weaver 2007). Similarly, the Olympic Torrent Salamander is associated with higher gradient reaches (Adams and Bury 2002; Bisson *et al.* 2002). Lastly, the Southern Torrent Salamander, which falls outside of my study area, also appears to be positively correlated with stream gradient (Diller and Wallace 1996;

Olson and Weaver 2007; Kroll *et al.* 2008). All torrent salamanders are desiccation intolerant and frequently associated with seeps and small streams. I group all species of torrent salamander as one taxonomic unit in analysis.

At the micro-habitat scale, torrent salamanders prefer riffles, seeps and splash zones (Cudmore and Bury 2014). Wilkins and Peterson (2000) found that surveys that included the upstream limits of channelized flow almost always encountered torrent salamanders with decreasing abundance until the first tributary junction. Another notable trait is their apparent lack of mobility; Cascade Torrent Salamanders were found to move an average of only 2.4 meters during a three-month period, making them one of the most sedentary amphibians (Nijhuis and Kaplan 1998). Additionally, in a mark-recapture study, Nussbaum and Tait (1977) found 70% of animals remained in the same 2-m plot during repeated visits at two to three week intervals between June and October. Torrents salamander use of seeps for oviposition sites and their lack of movement suggests the importance of specific locations to their population viability, however further evaluation of movement and dispersal distances is warranted.



Figure 5. Distribution of torrent salamanders (*Rhyacotriton* spp.) species in WA (Sources: Species distributions, WDFW; CMER Lands, DNR; Basemap, ESRI).

2.3.3 GIANT SALAMANDERS

Giant salamanders (*Dicamptodon* spp.) are generalists species compared to torrent salamanders as they occupy a range of small to mid-sized streams in the Pacific Northwest. Western Washington has two similar species of giant salamander: Cope's and Coastal Giant Salamanders. Cope's Giant Salamander has a more restricted range than Coastal Giant Salamander (**Figure 6**). Cope's Giant Salamander is distributed across the Coast Range and Cascade Range in western Washington South of Mount Rainier and in northern Oregon (Foster and Olson 2014). It is found at elevations from sea level to 1593 m. Coastal Giant Salamanders occurs from northern California to extreme southwestern British Columbia at elevations from sea level to 1830 m. In Washington, Pacific Giant Salamander ranges throughout the Coast Range and Cascade Range, but is not known to occur on the Olympic Peninsula. The two species of giant salamander co-occur in the Cascades and Coast Range of southwestern Washington and northwestern Oregon. Distinguishing between the two species as larvae in the field is difficult (McIntyre *et al.* 2018).

Giant salamanders are more widely distributed throughout stream networks occupying small to mid-sized streams. They are also known to occupy fish-bearing streams (Hunter 1998; Foster and Olson 2014). Hunter (1998) found that giant salamanders were found throughout a watershed-scale sampling effort composed of many large and small streams but occurrence generally increased downstream peaking in basins of 20-100 ha, before slightly decreasing in the largest basins. The same study found the distribution of small giant salamander larvae was skewed toward the smallest streams, while large basins (up to 500 ha) had a larger portion of large larvae. In another study,

body length was significantly higher in pools than in riffles (Roni 2002). Giant salamander captures have been associated with wider streams (Olson and Weaver 2007) and negatively correlated with stream gradient (Roni 2002).

However, many apparent conflicts exist within these general patterns pointing to their ability to occupy a wide range of stream conditions. Study designs utilizing different sampling techniques and scales may also contribute to conflicts. For example, others have found that giant salamanders are positively associated with gradient (Hawkins *et al.* 1983). Interestingly, one study found that densities of Coastal Giant Salamanders were positively correlated with stream gradient in logged stands but not in uncut forests suggesting that the impacts of increased sedimentation are greatest in low-gradient streams (Corn and Bury 1989).

At a micro-habitat scale, giant salamanders are frequently associated with pools, but also occurred in riffles (Bury *et al.* 1991; Cudmore and Bury 2014). They can be found under stones, slabs of bark or other stream cover. Pools with more coarse substrates had higher densities of Coastal Giant Salamander (Parker 1991). Egg masses consist of individual eggs attached to at least a cobble-sized substrate and are generally linked to coarse substrate.

Occupancy patterns and micro-habitat associations suggest that giant salamanders are habitat generalists compared to the more restricted occupancy patterns and life history of torrent salamanders. This pattern was also supported in a diet analysis that showed giant salamanders consume a wider range of macroinvertebrate prey, in part due to their larger size (Cudmore and Bury 2014).

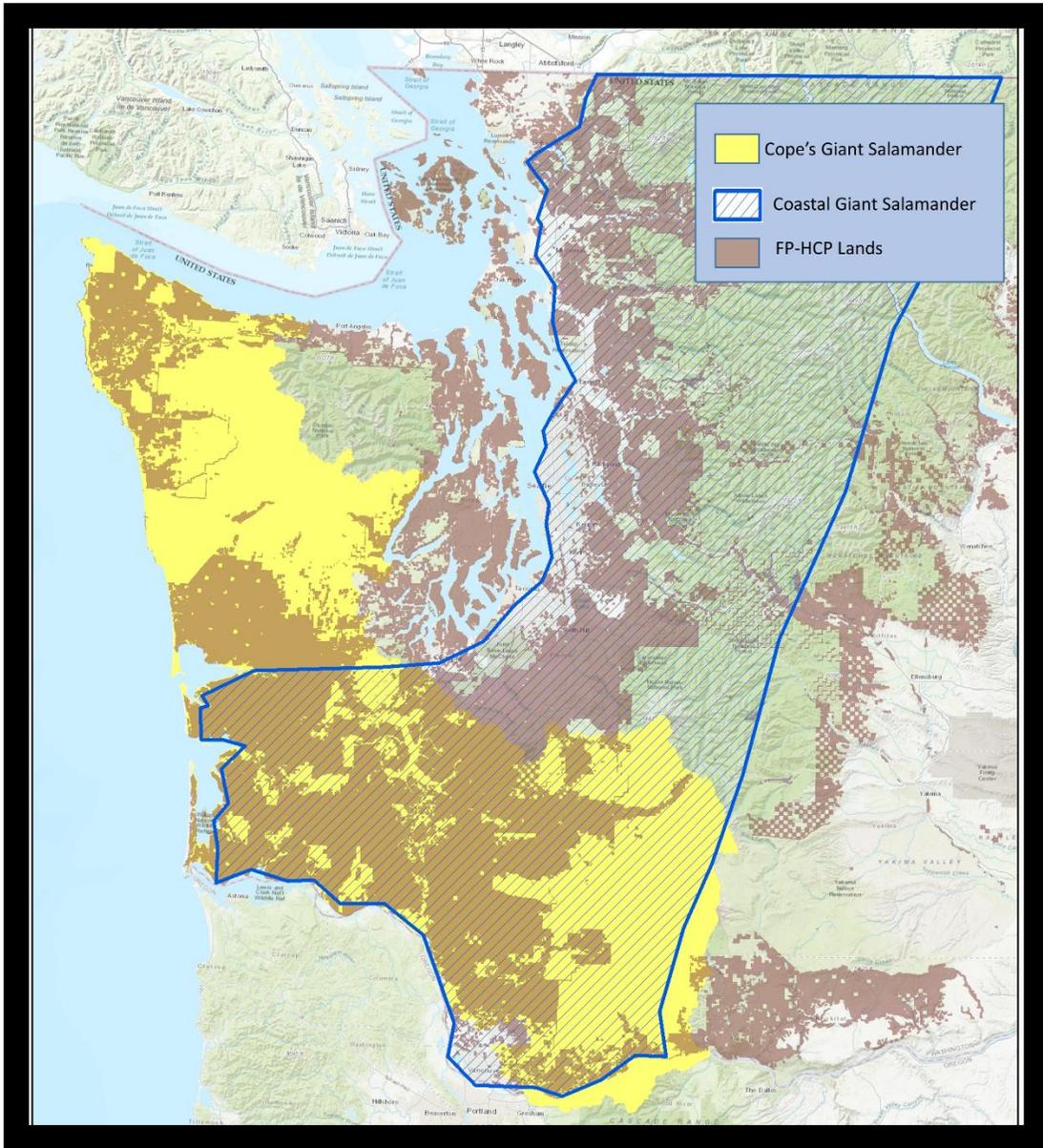


Figure 6. Distribution of Cope's Giant Salamander (*Dicamptodon copei*) and Coastal Giant Salamander (*Dicamptodon tenebrosus*) in WA (Sources: Species distributions, WDFW; CMER Lands, DNR; Basemap, ESRI).

2.4 SAMPLING OF STREAM-BREEDING AMPHIBIANS

Stream-breeding amphibian-sampling methods range from intensive sampling in small plots to less destructive methods of visual encounter that cover a larger area of

stream. The most intensive methods, often called rubble-rouse, involve excavation and removal of substrates from a reach of stream to more effectively obtain counts in that reach (Bury and Corn 1991; Quinn *et al.* 2007). These counts have been used to estimate abundance, but can be problematic for inferencing larger-scale patterns due to the highly variable distribution of SAAs within streams (Diller and Wallace 1996; Russell *et al.* 2004). Additionally, rubble-rouse methods can be highly destructive to stream habitats making repeat visits and long-term monitoring problematic (O'Donnell *et al.* 2007). At the other end of the spectrum, the light-touch method involves flipping cover objects while moving up the stream channel in search of amphibians (McIntyre *et al.* 2018). Light-touch techniques can only detect surface-active individuals (**Figure 7**). This method has been shown to be effective for estimating abundance of amphibians, but requires statistical models to account for the limited probability of encountering all of the animals present in a reach (McIntyre *et al.* 2012). A variety of variables have been identified as affecting detection probability for giant and torrent salamanders (Kroll *et al.* 2008; McIntyre *et al.* 2012), including stream order, stream temperature, Julian date and stand age (Kroll *et al.* 2008; McIntyre *et al.* 2012). Comparisons using light-touch survey methods that do not account for detection probability across co-variates could be biased (Kroll 2009). Unadjusted counts obtained from light-touch methods should not be interpreted as densities, but rather as an index of abundance (Olson and Weaver 2007).

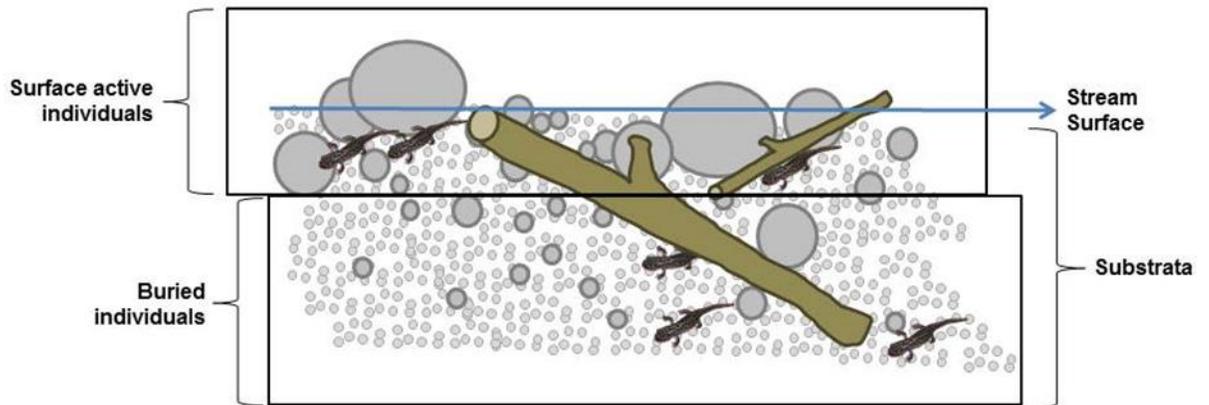


Figure 7. A cross-section of a hypothetical stream channel occupied by SAAs. Only surface-active individuals can be detected using the light-touch technique (from McIntyre *et al.* 2018).

2.5 CONCLUSION

Stream-associated amphibians dominate many headwater streams and but are patchily distributed across the landscape and within basins. The spatial structure of stream networks provides an organizational structure for recognizing ecological processes and spatial patterns. Torrent salamanders are widely recognized as a sensitive species and are often found in the uppermost reaches of streams habitats with low fluvial power. Torrent salamanders have elevated conservation status according to multiple agencies, are under review for ESA-listing by the US Fish and Wildlife Service and are covered under the FP-HCP. Giant salamanders are more of a habitat generalist associated with pools and higher order streams. They are generally thought to be more resistant to disturbance and do not have an elevated conservation status. The FP-HCP and associated rules apply to 9.3 million acres in Washington and encompass many headwater stream systems. Riparian buffers are used to protect wildlife habitat and water quality. Type N streams receive buffers on at least 50% of stream length. Buffers are prioritized on lower

reaches of basins and at sensitive site, namely TJs and PIPs. Although scientific literature provides a basis for buffering these features, no studies address amphibian use of the stream network features that receive Sensitive Site buffers. The ecological and morphological role of tributary junctions has not been thoroughly evaluated in small streams. This thesis is the first evaluation of amphibian use of the features that receive buffers prior to harvest. It uses extensive light-touch surveys to assess distributional patterns at a spatial scale tailored to current management rules on privately owned managed forest.

3 MANUSCRIPT

Stream-breeding salamander use of headwater stream networks in managed forests of western Washington

3.1 INTRODUCTION

Buffers are widely deployed to minimize impacts of anthropogenic disturbance on sensitive organisms and the degradation of environmental conditions (Marczak *et al.* 2010). Specific buffer prescriptions are often policy compromises in a complex decision space at the intersection of competing interests, ecosystem complexity and uncertainty (Richardson *et al.* 2012; Phalan *et al.* 2019). This dynamic, along with the administrative desire for simplicity, has led to fixed-width retention strategies becoming the standard approach (Richardson *et al.* 2012). Site-specific buffering strategies and emulation of natural disturbance approaches have been proposed as alternatives, but considerable challenges hinder the application of these strategies at broad scales (Sibley *et al.* 2012). Evaluation of features with large functional roles may help prioritize buffer placement and optimize benefits where land is removed from economically productive uses to meet environmental standards and protect biota.

In forest management, buffering strategies often emphasize the protection of instream sensitive taxa such as fish and amphibians, as well as water quality. In the Pacific Northwest, forests are economically important multiple-use landscapes that encompass entire distributions of sensitive taxa (USFWS 2015). Within those landscapes, riparian corridors play a disproportionately important role in maintaining biodiversity and ecosystem function (Naiman *et al.* 2000). Tree retention along streams seeks to reduce

impacts of timber harvest and promote natural processes through the recruitment of wood and organic matter to provide instream function (McDade *et al.* 1990); mitigate reduction in canopy and associated temperature increases (Bowler *et al.* 2012; Ehinger *et al.* 2018); and reduce mechanical disturbance to streams that lead to inputs of sediment and logging debris (Jackson and Sturm 2002). Harvest prescriptions dictate buffer placement and vary with regulatory body, stream size and whether or not a stream contains fish (Lee *et al.* 2004). All streams with fish receive continuous buffers in California, Oregon, and Washington (Sheridan and Olson 2003). In contrast, prescriptions on non-fish-bearing streams vary widely by region and land ownership.

Headwater streams present a unique management dilemma. They comprise a large majority of the stream length in the broader landscape. For example, in western Washington, approximately 70% of total stream length is non-fish-bearing headwaters (Rogers and Cooke 2007). Despite their abundance on the landscape, they are less studied than downstream reaches that contain fish (Richardson and Danehy 2007). Headwater streams are coupled to hillslopes and play an important role in providing flow and other exports to downstream reaches that have fish species listed under the Endangered Species Act (USFWS 1999; Benda *et al.* 2005; Wipfli *et al.* 2007). Trade-offs related to cost, regulatory certainty, and overall objectives for landowners has produced divergent buffering strategies, even though in the case of Washington State, similar science informed the management for state, federal, and private lands (Wilhere and Quinn 2018).

On private industrial timberlands in Washington State, Forest Practices (FP) rules determine harvest prescriptions, and permit clearcut harvest adjacent to up to 50% of the non-fish-bearing perennial stream length (WFPB 2001). Buffers are required immediately

above the uppermost fish-bearing waters to minimize impacts to downstream fish. Forest Practices-rules also designate Sensitive Sites in headwater stream basins that receive 50- to 56-ft radius patch buffers intended to protect water quality and wildlife (WADNR 2005). Tributary junctions (TJs) and the uppermost points of perennial flow (or Perennial Initiation Point; PIPs) are the two most common categories of Sensitive Site and are easily defined by the dendritic structure of the stream network. Side-slope seeps and alluvial fans also receive patch buffers, but vary considerably in their local distribution and must meet specific criteria (WFPB 2010). Unbuffered stream reaches, PIPs and many TJs are located in the upper extent of headwater basins where forest management practices may place headwater-obligate species at risk (Corn and Bury 1989).

In the Pacific Northwest, torrent salamanders (*Rhyacotriton* spp.), giant salamanders (*Dicamptodon* spp.) and tailed frogs (*Ascaphus* spp.), hereafter referred to collectively as stream-associated amphibians, often become the dominant instream vertebrates as fish densities decline with upstream position. Stream-associated amphibians all reproduce in flowing water and are closely tied to streams for much of their life cycle, which contrasts with most stillwater-breeding amphibians that spend considerable time in upland habitats and may move long distances overland. Stream-associated amphibians, like amphibians in general, are touted as bioindicators of aquatic systems because of their sensitivity and rapid response to environmental change (Welsh and Ollivier 1998; Stuart *et al.* 2004). Many lower-elevation headwater basins where stream-associated amphibians occur are intensively managed for timber, which underscores the importance of considering amphibians when evaluating buffer effectiveness and placement.

Stream-associated amphibian distributions are patchy both across the landscape and within occupied watersheds. These taxa generally favor basins with competent lithologies that produce larger-clast substrates (Wilkins and Peterson 2000) and cooler water temperatures (Ehinger *et al.* 2018). Torrent salamanders are often associated with the uppermost reaches of headwater basins in habitats with low fluvial power such as seeps and low-order streams (Nussbaum and Tait 1977), which may reflect their habit of depositing unattached eggs (Thompson *et al.* 2018). Torrent salamanders are also mostly restricted to water saturated areas and are thought to rarely use uplands even as post-metamorphs (Sheridan and Olson 2003). Their potential vulnerability to forest harvest has been linked to their desiccation intolerance (Ray 1958), association with cool water (Steele *et al.* 2003), and presumed low dispersal potential (Good and Wake 1992). Torrent salamanders are recognized as sensitive by state and federal wildlife agencies (USFWS 2015; WDFW 2019). A recent evaluation of genetic diversity suggests habitat fragmentation has led to reduced genetic variation (Emel *et al.* 2019). In contrast, giant salamanders, thought to be habitat generalists, seem less habitat- and diet-specialized (Cudmore and Bury 2014). Giant salamanders are frequently associated with pools (Bury *et al.* 1991; Wilkins and Peterson 2000). While considerable overlap exists, giant salamanders are more typical of larger headwater streams than torrent salamanders (Hunter 1998; Olson and Weaver 2007).

The patchy distributions of stream-breeding salamanders coupled with the small scale of traditional sampling efforts makes discerning spatial patterns at management scales challenging. Broad-scale associations of stream-associated amphibian abundance across environmental gradients have been suggested (Wilkins and Peterson 2000; Adams

and Bury 2002), but intensive evaluations of small (<100 meters) discrete stream reaches has become a common approach (reviewed in Kroll 2009). However, a replicated network-wide evaluation of stream features that receive patch buffers at management scales has not been conducted.

I propose to characterize the spatial structure of stream habitats by network topology, stream order, and hydrologic characteristics. Species-habitat relationships enable development of a hypothesis-based approach for evaluating stream-breeding amphibian distributional patterns at a scale that can potentially inform forest management harvest prescriptions (**Table 2**). First, I use dendritic ecological networks to emphasize spatial relationships and highlight the ecosystem as being highly constrained to the physical stream network (Grant *et al.* 2007). Second, I use stream order (Strahler 1952), a scaling property that quantifies the upstream branching complexity, to organize reaches hierarchically. This scaling relates directly to stream power, a key factor regulating stream channel morphology (Benda *et al.* 2004b). Lastly, I consider additional hydrological characteristics that can be rapidly assessed and may affect amphibian densities at the reach scale: proportion of stream channel lacking surface water and channel-connected seeps (Sheridan and Olson 2003; Olson and Weaver 2007).

Table 2. Hypotheses for direction of effect for predictor variables on salamander abundance.

Variable	Torrent Salamander		Giant Salamander	
	Direction	Literature	Direction	Literature
Dendritic Structure Variables				
Perennial initiation point (PIP)	Positive	(Good and Wake 1992; Hayes <i>et al.</i> 2002; Russell <i>et al.</i> 2002)	Negative	(Hunter 1998; Olson and Weaver 2007)
Branch	0		0	
Tributary junction (TJ)	0		Positive	(Wilkins and Peterson 2000; Benda <i>et al.</i> 2004b; Grant <i>et al.</i> 2007)
Stream Order				
Stream order	Negative	(Hunter 1998; Wilkins and Peterson 2000; Jackson <i>et al.</i> 2007)	Positive	(Hunter 1998; Olson and Weaver 2007)
Hydrological Characteristics				
Seep present	Positive	(Hayes <i>et al.</i> 2002; Sheridan and Olson 2003; Thompson <i>et al.</i> 2018)	0	
Dry channel	Negative	(Olson and Weaver 2007)	Negative	(Sheridan and Olson 2003; Kaylor <i>et al.</i> 2019)

Dendritic ecological networks organize the spatial structure of stream networks into branches and nodes, which are important in regulating ecological processes (Grant *et al.* 2007). Tributary junctions, as network nodes, provide access to multiple tributaries, potentially increasing habitat heterogeneity and serving as conduits for dispersing individuals that may be constrained to the stream network (Holt and Chesson 2018). In addition, TJs may provide unique habitat features and increased diversity (Benda *et al.*

2004b). For example, in larger stream systems, confluences have been associated with increased pool depth, large wood accumulations, and larger substrate (Benda *et al.*

2004b). I hypothesize that giant salamanders, as habitat generalists that tend to be pool-focused, may be more abundant in TJs.

First-order streams near the PIP can be dominated by colluvium, i.e. unsorted fractured bedrock and erosional deposits (Montgomery and Buffington 1997) that provide an interstitial matrix through which cool, low-flows are frequent. This unique habitat may benefit torrent salamanders, a headwater obligate known to occupy and use seeps and springs for reproduction (Russell *et al.* 2002; Thompson *et al.* 2018). In a pilot study, Hayes and colleagues (2002) found high densities of torrent salamander larvae at PIPs. In addition, competent rock lithologies have more stable hydrologic regimes at PIPs (Jaeger *et al.* 2007) that I hypothesize may provide cool wet refugia for torrent salamanders during summer drought.

Literature suggests that as stream order (and catchment area) increases, giant salamander abundance increases while torrent salamander abundance declines (Hunter 1998). Higher-order streams have more fluvial power to sort and transport material, developing step-pool morphologies (Montgomery and Buffington 1997). This downstream habitat configuration, with an increase in pool frequency and stream depth, has been linked to greater giant salamander abundance (Hunter 1998; Olson and Weaver 2007; Cudmore and Bury 2014). Wilkins and Peterson (2000) suggested that torrent salamanders were most abundant in first-order reaches and decline in higher-order stream reaches.

Surface water intermittency and channel drying during low-flow periods have been well documented in streams across the Pacific Northwest (Hunter *et al.* 2005; Jaeger *et al.* 2007). While giant salamanders have been observed using hyporheic zones of otherwise dry channels (Feral *et al.* 2005), some assessments of stream-associated amphibians suggest fewer surface observations in dry reaches (Sheridan and Olson 2003; Olson and Weaver 2007). Olson and Weaver (2007) found giant salamanders to be associated with deeper water, while torrent salamanders occupied smaller, discontinuous streams.

Seeps are areas of saturation connected to the stream channel network via surface flow and have been identified as important habitat in multiple studies (Wilkins and Peterson 2000; Hayes *et al.* 2002). Similar to PIPs, seeps provide inputs of cool ground water and have been identified as a predictor of torrent salamander abundance (Welsh and Lind 1996). Seeps are also used by torrent salamanders for oviposition (Thompson *et al.* 2018). I hypothesize that seeps and associated reaches will have greater torrent salamander abundance.

The use of TJ and PIP Sensitive Sites by amphibians has not been evaluated for species covered in the FP-Habitat Conservation Plan. Here, I evaluate these dendritic features and other hydrological characteristics that could be rapidly assessed at management scales to assess their relationship with an amphibian abundance index in second-growth managed forests prior to timber harvest. Forest Practices rules apply to approximately 9.3 million acres of managed forest in Washington State (WADNR 2005). The rules designate Sensitive Sites that receive either a 15- or 17- meter [50-ft or 56-ft] no-cut patch buffer in the otherwise clearcut upper extent of headwater basins. With

growing interest in site-specific buffers, I seek to evaluate easily recognizable features that may be important to sensitive taxa to help guide optimal placement of buffers in multiple-use landscapes with diverse management objectives.

3.2 METHODS

Study Sites- I used the 17 amphibian-occupied non-fish-bearing stream basins in western Washington that were part of the Type N Experimental Buffer Treatment Study (see McIntyre *et al.* 2009 for detailed account of site selection process). All sites were located on competent (i.e., basaltic) lithologies in 2nd-growth managed Douglas-fir and western hemlock dominant forests in Washington State. Site elevation ranged from 22 to 601 meters [72 to 1972 feet] above mean sea level and basin size ranged from 12.1 to 53.8 hectares [30 to 133 acres]. Stand ages ranged from 30 to 80 years since last harvest and were located in the Olympics, Willapa Hills, and South Cascades physiographic regions on federal, state, and private ownership (**Figure 8**).

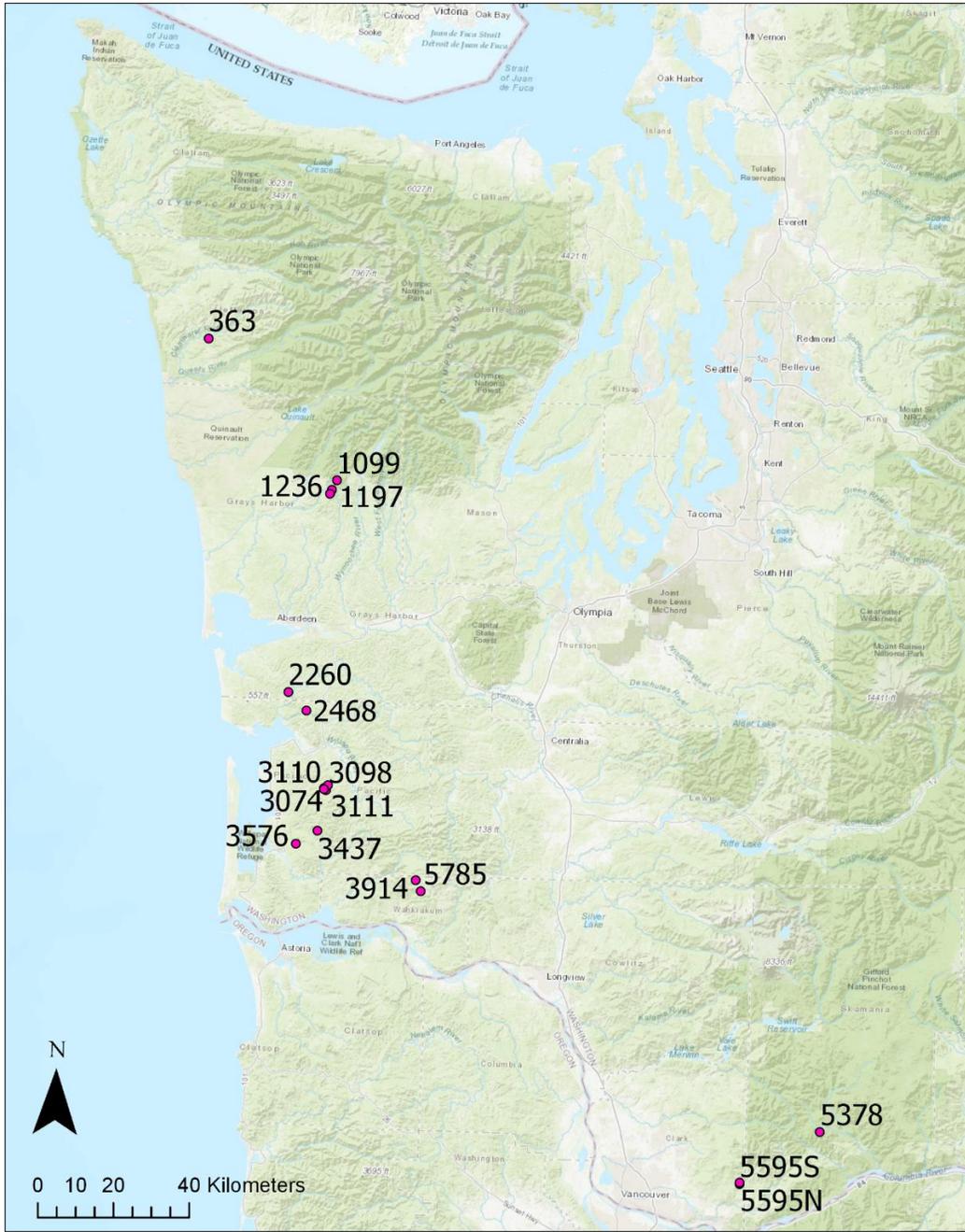


Figure 8. Distribution of study sites in western Washington labeled with Basin ID (full site descriptions in McIntyre *et al.* 2009; Basemap, ESRI).

Amphibian Sampling- I used data from streams that were sampled using light-touch techniques (Lowe and Bolger 2002), conducted during daylight hours between June and October in 2006 and 2007. Searches for stream-breeding salamanders were visual, and

involved moving upstream and turning all moveable surface substrates ≥ 64 mm [2.5 inches] and within the ordinary high-water mark and channel-connected seeps. Upon capture, animals were identified, measured and returned to their capture location. Handling of animals followed animal care and use guidelines (Beaupre *et al.* 2004). Overturned cover objects were returned to their original position and care was taken to preserve in-channel structures such as steps and large wood. We did not sample within 20 meters [66 feet] of any road crossing to minimize the effects of roads. Seventy-seven and >99 percent of the total stream lengths were sampled, respectively, in 2006 and 2007. Due to logistical constraints, entire basins were not sampled in 2006, but an effort was made to systematically sample over the entire stream network at evenly spaced intervals.

The light-touch technique has the benefits of minimizing disturbance (O'Donnell *et al.* 2007) and covering a greater footprint with less cost than traditional methods (Quinn *et al.* 2007), but observations/unit of stream only index abundance due to imperfect detection. Previous research has shown that detection probability varies with stream order and temperature (McIntyre *et al.* 2012). To ensure reliable detection of amphibian presence, I set a minimum reach length of 15 meters [50 feet] to ensure the sampling effort was adequate to detect amphibian presence in each unit of analysis (Quinn *et al.* 2007).

I designated dendritic reach types by their spatial proximity to stream network nodes (**Figure 9**). Stream reaches within 17 meters [56 feet] of a network node were designated as *tributary junction* (TJ) and reaches within 17 meters [56 feet] of the uppermost point of surface water were designated as *perennial initiation point* (PIP); all other reaches were designated as *branch*. Amphibian observations were grouped by

basin, detection segment and stream reach type for analysis. The stream order (*sensu* Strahler 1952) of each stream reach type was verified in the field. During 2006 the location of channel-connected seeps were recorded. We defined seeps as any area of saturation that was connected to the channel by overland flow, but lacked a scour channel. We also recorded the location of intermittently dry channel segments to the nearest meter during the low flow period in 2006, concurrent with amphibian sampling.

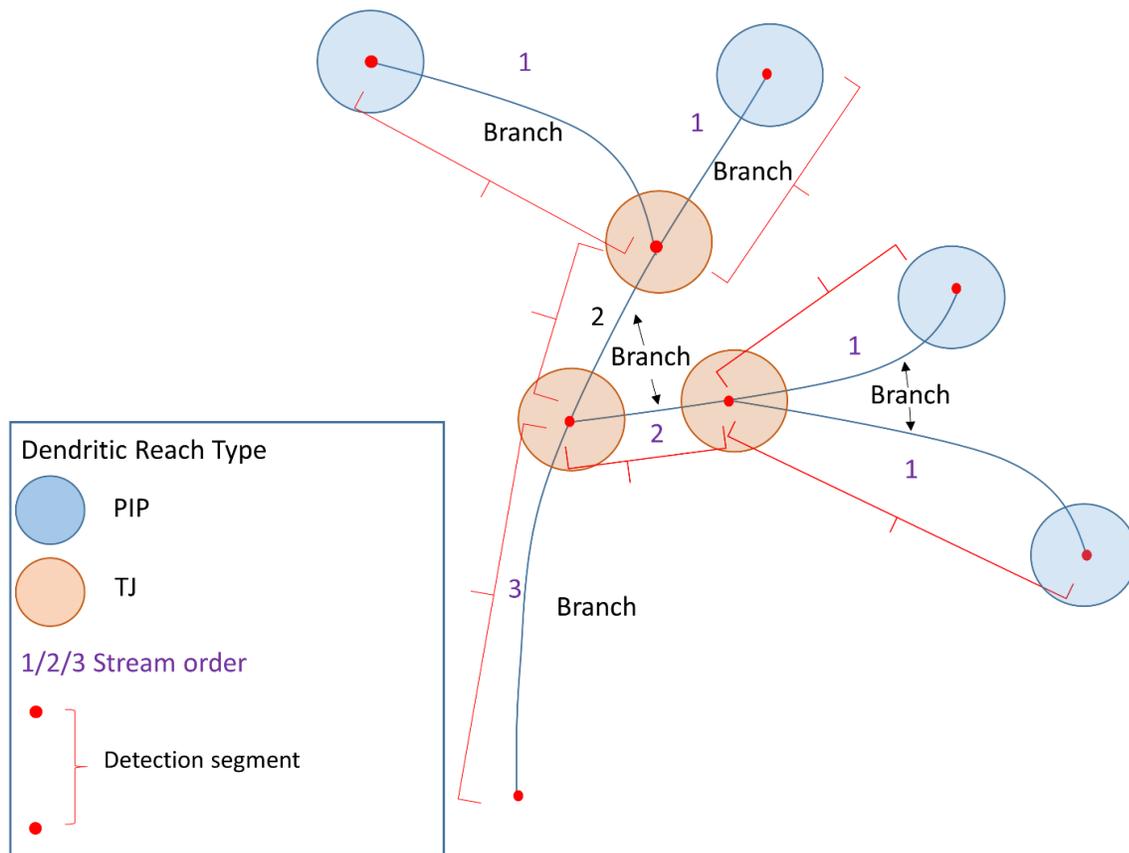


Figure 9. Schematic of study design. Stream reaches within 17 meters [56 feet] of network nodes and the uppermost point of flow were designated as tributary junctions (TJs) and perennial initiation points (PIPs), respectively, while other reaches were designated as branches. Detection segments were used as a random effect to block similar stream characteristics.

I grouped species of giant salamander (*Dicamptodon*) and torrent salamander (*Rhyacotriton*) into two respective phylogenetic groups for analysis. Cope's Giant

Salamander, (*D. copei*) and Pacific Giant Salamander (*D. tenebrosus*) were treated as one taxon because it is difficult to distinguish the species in the field. Pacific Giant Salamander was found at all study sites while Cope's Giant Salamander was found in the Olympics and the northernmost Willapa Hills sites (Spear *et al.* 2011). Torrent salamander species do not co-occur but they occupy similar habitats with the Olympic Torrent Salamander (*R. olympicus*), Cascades Torrent Salamander (*R. cascadae*) and Columbia Salamander (*R. kezeri*), respectively, found in the Olympics, South Cascades, and Willapa Hills of Washington State (Good and Wake 1992).

Analysis- I developed a generalized linear mixed model (log link, Poisson distribution) with the light-touch amphibian abundance index (measured as linear density) as the dependent variable. I tailored the parameterization of fixed effects for each model to individually test variables listed in **Table 3**. My aim was to (1) compare amphibian abundance across reach types to evaluate Sensitive Sites and related dendritic structure hypotheses, and (2) test hydrological variables: stream order, presence/absence of channel connected seeps, and proportion of channel lacking surface water. I evaluated torrent and giant salamanders separately. For the comparison of dendritic reach type, I evaluated PIPs, TJs, and branches in first-order streams and separately evaluated all TJs and branches in a network-wide comparison.

Table 3. Sample size of stream reaches across two years used in each comparison.

Variable	Sample Size
Dendritic Reach Type	
First order only	
Perennial Initiation Point (PIP)	120
Branch	150
Tributary Junction (TJ)	144
Network-wide	
Branch	202
Tributary Junction (TJ)	265
Stream Order	
First	344
Second	188
Third	46
Seep Reach	
Absent	450
Present	76
Proportion Dry	
Wet	194
Dry >0%	71

I included basin (n=17) and detection segment (n=132) as random effects. The detection segment is designated between tributary junctions to create blocks with similar stream temperature and order, in an effort to control for imperfect detection (Banks-Leite *et al.* 2014) and spatial autocorrelation (Wagner *et al.* 2006) in analysis. Detection segments were nested within basins. I included year as a fixed effect in all models that included both years of data, but I do not consider it to be of focal interest. A log offset was used to account for different length and survey effort among reaches.

All statistical analyses were conducted in R[®] 3.5.1 using Bayesian models fitted in STAN with the brms package (Bürkner 2017). I assessed model convergence using posterior predictive diagnostic plots and the potential scale reduction factor. I used

diffuse, weakly regularizing priors (McElreath 2016). I ran four Hamiltonian Monte Carlo chains of 5000 iterations each (warm-up = 2500, thin = 1). Figures of the posterior distributions were based on the mode and 95% highest density interval using the plotPost function from Kruschke (2014). I exponentiated parameter estimates to the original scale and normalized them to observations/100 m of stream length to facilitate interpretation. To calculate contrasts of proportional difference on the original scale, I exponentiated the posterior distributions for each estimate and divided them. The proportional difference of the mean estimates is based on the mean of the contrast distribution and 95% credible interval.

Habitat Characterization- Stream habitat was characterized at a systematically selected subset of amphibian sample segments along the mainstem of each basin to describe amphibian habitat by reach type. Point measures included wetted width and bankfull width. I did not model these metrics.

3.3 RESULTS

I used 32,837 stream meters sampled for stream-breeding salamanders using the light-touch technique that resulted in 3,704 observations of torrent salamander and 1,313 observations of giant salamander over the two sample years. I evaluated a total of 57 PIPs, 115 TJs, and 102 branch reaches. Stream-breeding salamander abundance was variable within basins (**Figure 10**).

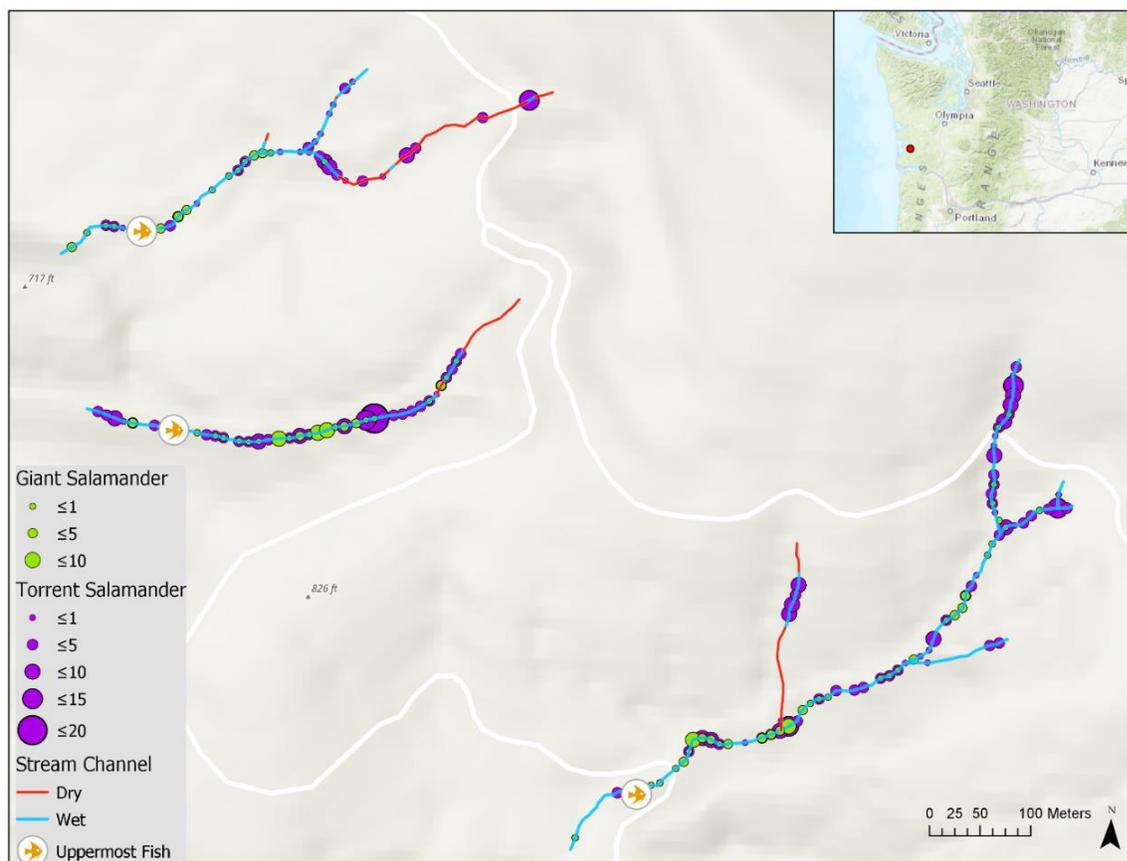


Figure 10. Three adjacent study basins showing counts of torrent and giant salamanders in 10-meter survey reaches in 2006 (Basemap, ESRI).

Dendritic Reach Type- TJs did not have a significant effect on abundance of either species. PIPs had a significant negative effect only on giant salamanders. In first-order

streams, torrent salamanders were observed slightly less often in PIPs and TJs than in branches but abundance estimates had large overlapping credible intervals. Reach type contrasts (**Table 4**) indicate that PIPs had 14% less torrent salamander abundance than branches (95% CI: -31% to +2%). The credible interval overlapped no difference, but the negative direction of the effect is supported by a 95% probability. Tributary junctions had 11% less torrent salamander abundance than branches (95% CI: -26% to +8%), supported by an 86% probability of the direction of the effect. PIPs had 10% less torrent salamander abundance than TJs (95% CI: -28% to +19%). In my network wide comparison of reach type, TJs and branches had nearly identical abundance estimates for both taxa. Giant salamanders had abundances in PIPs that were 52% and 59% less than in branches (CI: -70% to -20%) and TJs (CI: -81% to -26%), respectively. For both contrasts, credible intervals did not overlap 1 suggesting a high probability of the direction of the effect. TJs had 8% greater abundance than branches (CI: -27 to +67) with a wide credible interval. The posterior distribution indicates a 76% likelihood that TJs have greater abundance than branches. In the network-wide comparison torrent salamanders had 8% less detections in TJs than branches (CI: -18% to +2%), with a 93% likelihood of the direction of the effect. Giant salamanders had 1% greater abundance in TJs than in branches (CI: -20% to +18%), with only a 56% likelihood of the direction of the effect.

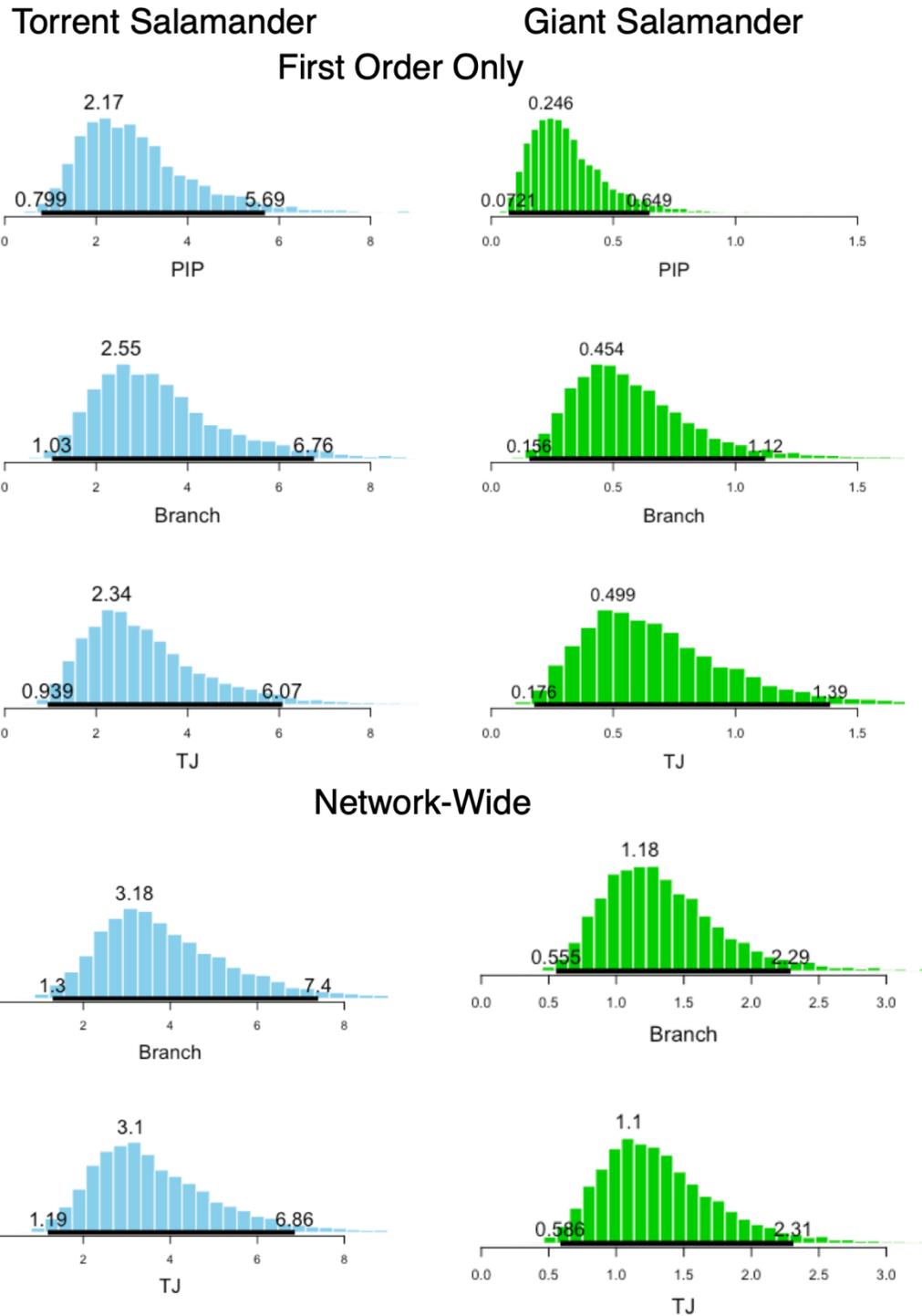


Figure 11. Mean estimate of torrent and giant salamander abundance (observations/100 meter) by dendritic reach type. Values signify the mode and 95% highest density interval of the posterior distribution for each parameter estimate.

Table 4. Proportional difference contrasts of abundance by dendritic reach type. Significant contrasts and 95% credible interval in bold.

Contrast	Torrent Salamander	Giant Salamander
	First Order Only	
PIP vs. Branch	-15% (-30% to +2%)	-48% (-70% to -13%)
PIP vs. TJ	-5% (-26% to +21%)	-53% (-77% to -16%)
TJ vs. Branch	-9% (-26% to +9%)	+16% (-24% to +76%)
	Stream Network-Wide	
TJ vs. Branch	-7% (-17% to +4%)	-1% (-19% to +18%)

Stream Order- Increasing stream order had a strong positive effect on giant salamander abundance with a -82% and -86% decrease in second-order (CI: -89% to +73%) and third-order stream reaches (CI: -94% to -72%), respectively compared to 1st order reaches (**Figure 12**). Torrent salamander had 22% greater abundance (CI: -22% to +82%) in first-order stream reaches than second-order reaches and 2% less abundance (CI: -61% to +127%) in third-order streams than second-order streams. The wide credible intervals for torrent salamanders in first- and second-order streams suggest high variability within stream order compared to the less variable estimates for giant salamanders. For both taxa, the relatively wide credible intervals around third-order estimates partially reflect the smaller sample size, with only 4 of 17 sites containing third-order reaches.

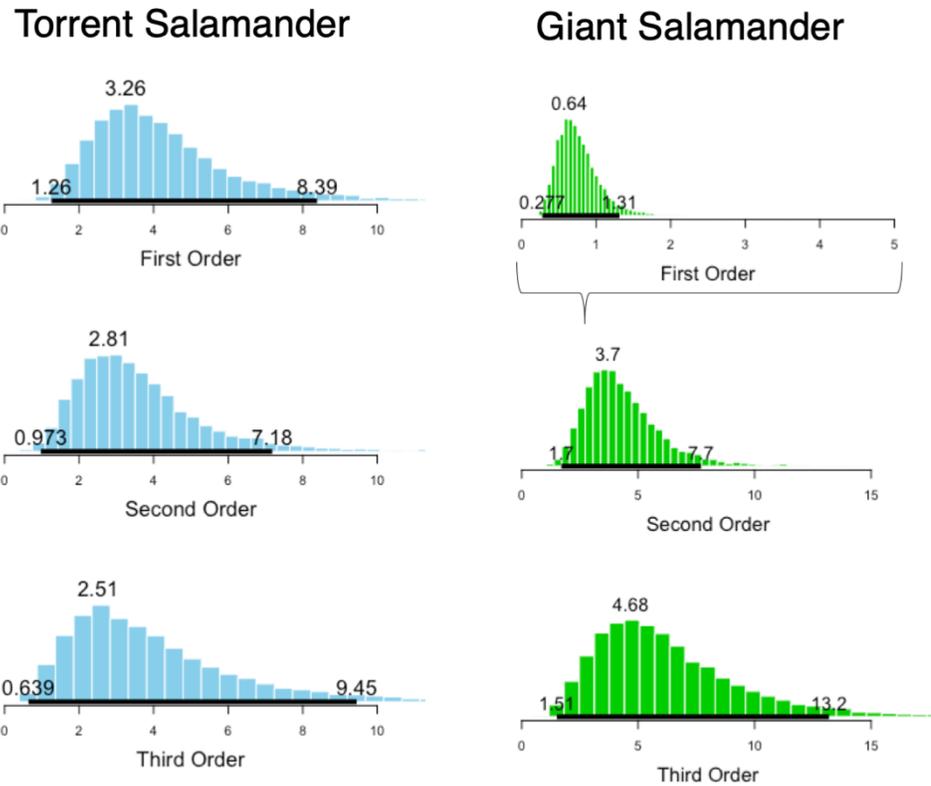


Figure 12. Mean estimate of torrent and giant salamander abundance (observations/100 meter) by stream order. Values based on the mode and 95% highest density interval of the posterior distribution for each parameter estimate. The x-axis for giant salamander in first-order streams has an adjusted scale.

Table 5. Proportional difference contrasts of abundance by stream order. Significant contrasts and 95% credible interval in bold.

Contrast	Torrent Salamander	Giant Salamander
First vs. Second	+22% (-22% to +82%)	-82% (-89% to -73%)
First vs. Third	+21% (-51% to +165%)	-86% (-94% to -72%)
Second vs. Third	+2% (-61% to +127%)	-21% (-68% to 67%)

Proportion Dry- The proportion of channel lacking surface water had a consistent negative effect on abundance estimates for both taxa. For a change from wet to dry, torrent salamander abundance would be multiplied by 0.54 (CI: 0.31 to 0.94) and giant salamanders would be multiplied by 0.04 (CI: 0.01 to 0.16).

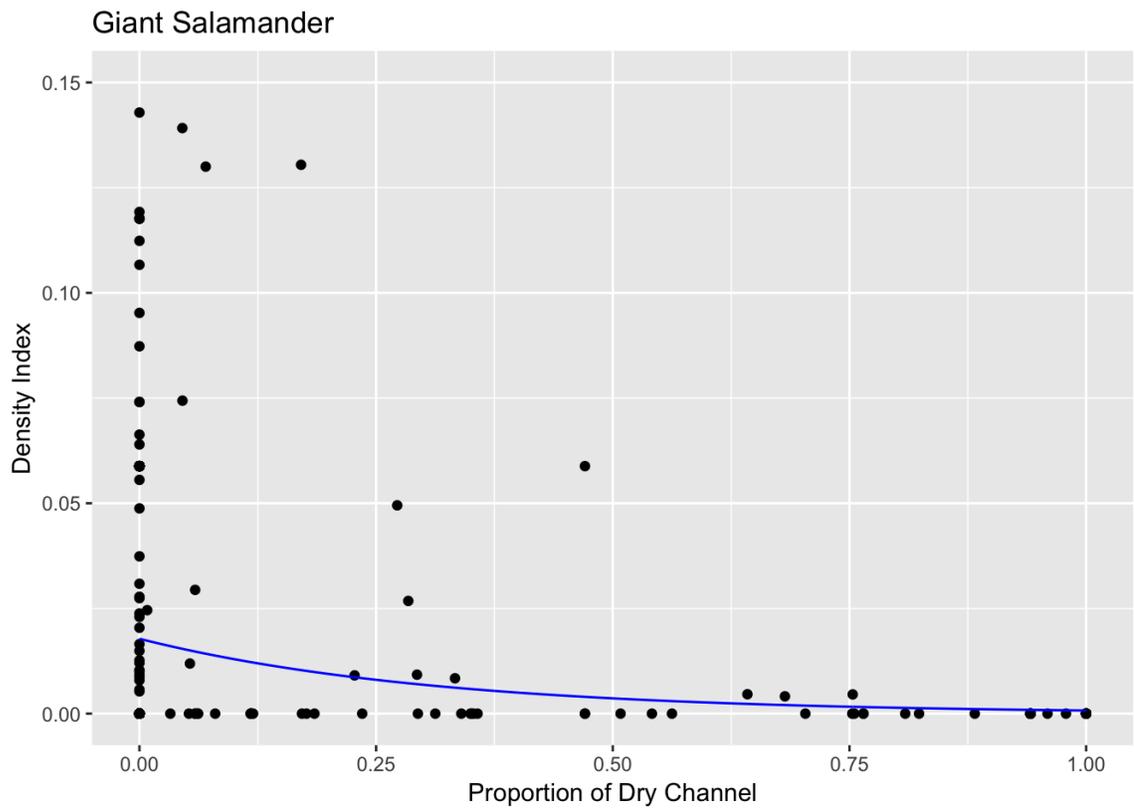
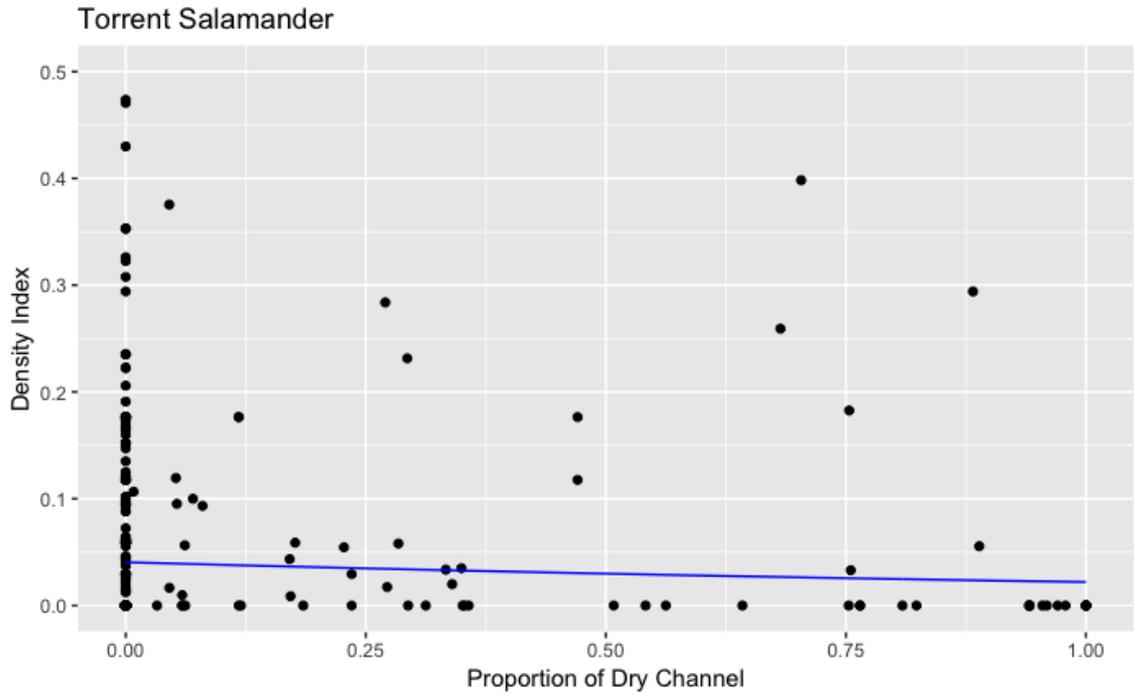


Figure 13. Effect of proportion of dry channel on salamander abundance (observations/meter).

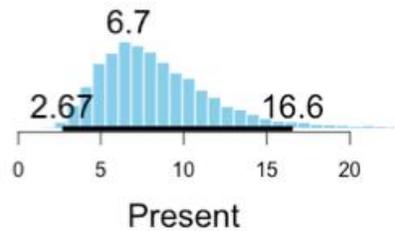
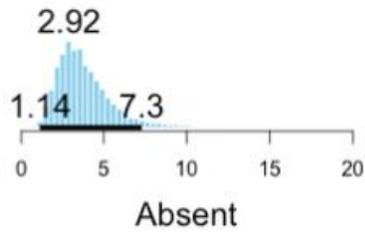
Dry channel, which we measured only in 2006, was more common in first order than in higher order reaches (**Table 6**). In first order tributaries, PIPs had proportionally less dry stream length than branches.

Table 6. Summary of dry stream length by order and reach type.

Stream Order	Dendritic Reach Type	Dry Length (m)	Total Length (m)	% Dry
1	PIP	105	764	13.7
1	Branch	2287	9103	25.1
1	TJ	155	895	17.3
2	Branch	412	4526	9.1
2	TJ	113	992	11.4
3	Branch	0	1219	0
3	TJ	0	300	0

Seeps- I evaluated a 55 seep reaches across our 17 study sites. Reaches with seeps had 124% greater torrent salamander observations/m (CI: +101% to 144%). In the same reaches, giant salamander had 83% greater observations/m (CI: +50% to +121%) (**Figure 14**). In 2006 and 2007, respectively, 19% and 18% of the total torrent salamander observations occurred in channel-adjacent seep features with the majority of observations occurring in the stream channel of the 30-m reach. Only one giant salamander was observed in a seep.

Torrent Salamander



Giant Salamander

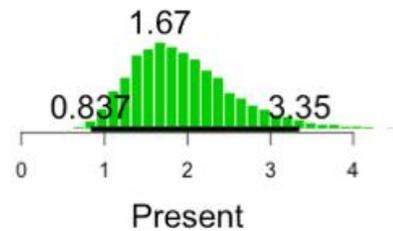
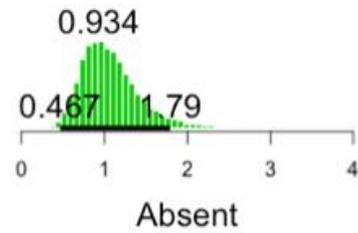


Figure 14. Mean estimate of torrent and giant salamander abundance (observations/100 meters) in stream reaches within 15 meters of a seep (present) compared to reaches without seeps. Estimates based on the mode and 95% highest density interval of the posterior distribution for each parameter estimate.

Table 7. Proportional difference contrast of mean observations in reaches with seeps present and absent. Significant contrasts and 95% credible interval in bold.

Contrast	Torrent Salamander	Giant Salamander
Present vs. Absent	+123% (+103% to +146%)	+84% (+49% to +121%)

Mean bankfull and wetted widths were small and remained relatively consistent across reach types and stream order. With increasing stream order, mean depth increased and gradient decreased (**Table 8**).

Table 8. Habitat characteristics by dendritic reach type and stream order (mean \pm SD; range in parenthesis).

Stream Order	Reach Type	<i>n</i>	Bankfull Width (m)	Wetted Width (m)	Depth (cm)	Gradient (°)
1	PIP	25	1.7 \pm 1.5	1.0 \pm 1.2	2.4 \pm 1.8	16.2 \pm 6.2
			(0.3 - 6.0)	(0.0 - 6.0)	(0 - 8)	(9 - 28)
1	Branch	584	1.6 \pm 1.0	0.7 \pm 0.7	3.1 \pm 3.45	12.1 \pm 6.6
			(0.3 - 7.0)	(0 - 5)	(0 - 32)	(0 - 38)
1	TJ	46	1.6 \pm 0.9	0.9 \pm	3.7 \pm 2.94	11.9 \pm 4.5
			(0.4 - 5.1)	(0 - 4.1)	(0 - 15)	(1 - 26)
2	Branch	520	2.0 \pm 1.1	1.3 \pm 0.8	5.7 \pm 4.6	8.8 \pm 5.2
			(0.3 - 6.4)	(0 - 4.4)	(0 - 41)	(1 - 40)
2	TJ	155	1.8 \pm 1.0	1.1 \pm 0.7	5.2 \pm 3.8	11.9 \pm 4.5
			(0.3 - 5.5)	(0 - 4.4)	(0 - 23)	(1 - 24)
3	Branch	193	2.5 \pm 1.4	1.4 \pm 1.2	7.4 \pm 7.8	9.9 \pm 6.4
			(0.4 - 8.2)	(0 - 7.8)	(0 - 44)	(1 - 34)
3	TJ	46	2.0 \pm 1.0	1.2 \pm 0.7	6.8 \pm 5.4	9.0 \pm 5.5
			(0.5 - 4.4)	(0.2 - 3)	(1 - 28)	(1 - 23)

3.4 DISCUSSION

Torrent and giant salamander abundance showed a stronger response to seep presence and proportion of dry channel than to dendritic reach type. In first order streams, PIPs appeared to have slightly lower torrent salamander abundances compared to branches. My hypothesis that torrent salamander observations would be more frequent in PIPs based on their preference for low flow colluvium was not supported. This finding aligns with a study that consistently observed Columbia Torrent Salamander near PIPs but also generally saw increased abundance downstream until the first tributary junction (Wilkins and Peterson 2000). Similarly, I did find some support for a stronger association with first-order than higher-order streams, although the contrasts were not statistically significant. This lack of significant findings suggest that torrent salamanders are more variably distributed throughout small headwater stream networks than I hypothesized. Other unmeasured habitat variables such as gradient, substrate, and hydrologic conditions

may be a more important driver of abundance than the FP-based dendritic reach type variables I evaluated (Diller and Wallace 1996; Russell *et al.* 2004).

In contrast, giant salamander abundance demonstrated a consistent, significant pattern of low densities in PIP reaches with increasing abundance in downstream reaches. This pattern is consistent with my hypothesis and other longitudinal evaluations that found them to be associated with larger headwater streams (Hunter 1998; Olson and Weaver 2007). In first order streams, giant salamanders had slightly greater abundance in TJs than in branches where they may benefit from the proximity to larger second order streams. Benda and colleagues (2004b) found that stream confluences had deeper pools and coarse substrate that I hypothesized could support greater abundances of giant salamander. However, I did not observe a giant salamander preference for TJs in the network-wide comparison of reach type. The small size of our study streams and the lack of contrast between stream sizes at tributary junctions may mute the confluence effect (Benda *et al.* 2004b). Pool-forming features such as wood and boulders that are beneficial to giant salamanders may be distributed stochastically, throughout small streams rather than concentrated at tributary junctions. Low flow conditions may limit the transport of these features and lack power to form pools (Jackson and Sturm 2002). The habitat characteristics demonstrate increasing depth and decreasing gradient as stream order increases which may drive greater giant salamander observations for higher order headwater streams (Hunter 1998).

Generally, hydrologic characteristics had stronger effects on salamander abundances for both species. Channel-connected seeps had a strong positive effect on abundances for both species. Other studies have also observed torrent salamanders in

seeps (Nussbaum and Tait 1977; Wilkins and Peterson 2000), a feature that appears to be common in forested headwater landscapes (Hayes *et al.* 2002; Janisch *et al.* 2011). While torrent salamanders are known to occupy and oviposit in seeps (Thompson *et al.* 2018), the benefit of seeps to giant salamanders is less apparent. It is possible that the stream channel adjacent to seeps had other beneficial hydrologic activity that supports a higher abundance of stream-breeding salamanders. For example, reaches with groundwater upwelling were found to have cooler, more stable temperatures than reaches with downwelling or neutral flow paths (Guenther *et al.* 2014). Current FP-rules require buffers on side-slope seeps, but the definition of these features limits it to those with >20% gradient that lack muck (WFPB 2001). Hayes and colleagues (2002) found that shallow accumulations of mucky substrates such as fine sediment and leaf litter comprised $\geq 15\%$ of the surface area of all seep features they evaluated. Seeps lack the power to flush muck, even in features underlain by fractured bedrock and interstitial matrices that provide important habitat for torrent salamanders (Hayes *et al.* 2002). A study design that more explicitly targets amphibian's use of seeps and reaches adjacent to seeps could help elucidate which characteristics of seeps support increased abundances of stream-breeding salamanders.

Dry channel had a strong negative effect on both species, but the effect was strongest for giant salamander. Torrent salamanders continue to occupy wet patches of stream channel with intermittent surface water. Across our 17 study basins, first-order streams were the most prone to dryness and, by definition, are the most isolated from the rest of the dendritic network. Surface water intermittency is a characteristic that is common across the landscape (Hunter *et al.* 2005). Logically, channel drying in upper

portions of the stream network may limit abundances of desiccation intolerant aquatic organisms, but it may also impact our ability to detect animals that occupy the hyporheic zone if animals bury themselves in the channel substrate (Feral *et al.* 2005) and are not available for sampling with a particular method. Our data suggest that the 17-m PIP reaches have a greater proportion of wet length relative to other first order reaches. Jaeger and colleagues (2007) found that the locations of PIPs in basins underlain with competent lithologies had relatively stable hydrologic conditions, with less change in locations throughout the year, even in the presence of downstream intermittent reaches. Conversely, PIPs in basins underlain with sedimentary lithologies tend to migrate downstream as the channel dries. The hydrological stability of PIPs in competent lithologies may help reduce desiccation risks for torrent salamanders occupying the upper reaches of basins. Under climate change scenarios with more extreme precipitation patterns (Mote *et al.* 2003), PIPs may continue to provide greater stability as they could be less prone to channel scour during winter peak flows and, as long as ground water recharge occurs, they may provide more consistent cool surface-water habitats, even during periods of prolonged drought. Kaylor and colleagues (2018) found that giant salamander biomass responded negatively to drought, but more research is needed to understand the effects of streams intermittency and the influence of groundwater inputs on temperature and stream-associated amphibian populations, especially in first-order reaches prone to warming caused by clearcut harvest (Janisch *et al.* 2012).

Heterogeneity in stream channel habitats may have a more important role in determining amphibian distribution within headwater basins than the dendritic structure alone (Holt and Chesson 2018). Headwater stream morphology and hydrology is highly

variable (Wipfli *et al.* 2007). Stochastic events like debris flows and windthrow may play an important functional role in structuring channel morphology, beyond the effect of TJs alone. For example, literature suggests that gradient and ground water inputs may help predict amphibian occupancy (Wilkins and Peterson 2000). As high-resolution remote sensing data such as LiDAR becomes available at landscape scales there may be more opportunities to evaluate stream heterogeneity to inform management.

My results are based on an index of abundance that has imperfect rates of detection. I included a detection segment random effect in these analyses to at least partly control for variation in detection rates by grouping reaches with similar stream conditions, however a more robust strategy would be to adjust observations by detection probability to obtain less-biased abundance estimates. My evaluation provides a snapshot of amphibian distributions within headwater stream basins at a biologically important time of year when flows are at their lowest and the risk of thermal stress, desiccation, and mortality is at its highest (Sagar 2004; Chelgren and Adams 2017). However, with my sample, I cannot evaluate the inter-seasonal importance of these stream features.

Movement patterns and dispersal distances of these highly constrained aquatic organisms remains poorly understood. Giant salamander post-metamorphs may be less restricted to the riparian corridor for dispersal in forested sites (Johnston and Frid 2002). Torrent salamanders are desiccation intolerant (Ray 1958) and are likely more closely associated with water even in their adult form. Torrent salamanders do not appear to be detected far from streams (Sheridan and Olson 2003) and may be especially dependent upon tributary junctions as dispersal nodes.

Under current FP-rules, first-order streams are the most vulnerable to the effects of clearcut harvest. Current patch buffer prescriptions target PIPs and TJs, but my analysis indicates these features do not appear to support greater amphibian abundances, at least under conditions unaltered by recent management activities. Seeps were found to be an important indicator of abundance for both taxa. Side-slope seeps also receive buffers, and, however their current definition may be too narrow and ambiguous to protect biologically important features (Hayes *et al.* 2002). Giant salamanders are more frequently detected in higher-order streams and may receive more protection from the majority of the buffer length that is placed contiguous with downstream fish buffers. In contrast, torrent salamanders are more likely to have patchy distributions across the upper reaches of stream networks that receive proportionately more clearcut reaches. Further, torrent salamander's continued occupancy of intermittent stream segments suggest that they may be more vulnerable to the risks of increased temperature and decreased humidity after harvest (Brattstrom 1963; Bury 2008). To be operationally feasible, determining site-specific buffer locations that can be drawn from a map is far more realistic than costly habitat surveys. However, further evaluation of environmental characteristics that can be rapidly assessed like seeps and channel dryness may help to inform efficient buffer placement.

This research focuses on amphibian use of TJs, PIPs and other variables that influence the use of stream reaches at management scales in forests of harvestable age. However, I do not evaluate the post-harvest effects of patch buffers. Amphibian use of patch buffers is poorly understood. Studies suggest that clearcut reaches receive a large pulse of wood associated with harvest that may provide cover for amphibians, but also

may impede sediment transport, posing a risk to species that rely on interstitial spaces between coarse substrate (Bury and Corn 1988; Jackson and Sturm 2002; McIntyre *et al.* 2018). PIP buffers may help to protect water quality by mitigating against sediment and slash inputs, and providing a clear reference point to the location of small streams during harvest operations. However, PIP buffers are often isolated and high on wind exposed slopes causing elevated tree mortality compared to intact forests and larger continuous buffers (Schuett-Hames and Stewart 2018). Seeps and water-surface area play an important role in how small streams respond to harvest (Janisch *et al.* 2012). Evaluation of the post-harvest response of amphibians and physical characteristics of stream networks, seeps and channel drying may help inform land managers as they strive to meet diverse objectives in multiple-use forest landscapes.

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