

RESEARCH ARTICLE

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

Reed Ojala-Barbour^{1,2}  | Aimee P. McIntyre¹  | Eric M. Lund¹  | Marc P. Hayes¹ ¹Washington Department of Fish and Wildlife, Olympia, Washington, USA²The Evergreen State College, Olympia, Washington, USA**Correspondence**

Reed Ojala-Barbour

Email: reed.ojala-barbour@dfw.wa.gov**Present address**

Eric M. Lund, Minnesota Department of Natural Resources, 1801 S. Oak Street, Lake City, Minnesota 55041, USA

Marc P. Hayes, Aquatic & Herpetological Research Cooperative, 1574 Brentwood Drive, Eagle Point, Oregon 97524, USA

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Handling Editor: Andrea Costa**Abstract**

1. Stream-associated amphibians are sensitive bioindicators in headwater streams across the Pacific Northwest moist coniferous forests of North America. Much of this landscape is intensively managed for timber. Forest Practice (FP) rules determine harvest prescriptions on most private lands in Washington State and cover over 3.7 million hectares. Under these rules, non-fish-bearing headwater streams receive buffers on at least 50% of the stream length, including FP Sensitive Sites that receive 15–17 m radius no-cut patch buffers.
2. We evaluated how torrent (*Rhyacotriton* spp.) and giant (*Dicamptodon* spp.) salamander relative abundance is influenced by headwater stream network features that correspond to FP Sensitive Sites. In particular, we examined how salamander relative abundance in the two most common FP Sensitive Sites, tributary junctions (TJs) and perennial initiation points (PIPs), compared to densities in non-Sensitive Site stream reaches, hereafter branches. We also evaluated salamander relative abundance and two hydrologic characteristics, dry channel and seeps. We analysed data collected in 2006 and 2007 from 17 amphibian-occupied, non-fish-bearing basins in Western Washington with managed forest ages 30–80.
3. We found no relationship between torrent salamander relative abundance and PIPs and TJs or between giant salamander relative abundance and TJs compared to branches. Consistent with expectations, giant salamander relative abundance was less in PIPs than in TJs and branches, and less in first-order than second- and third-order streams. Conversely, torrent salamander relative abundance lacked a clear relationship to stream order. Giant and torrent salamander relative abundance showed a negative relationship with the proportion of dry channels, but torrent salamanders were observed in short reaches of surface water located in predominantly dry channels.
4. Importantly, reaches with seeps had 123% (CI: +103% to +146%) and 81% (CI: +49% to +121%) greater relative abundance of torrent and giant salamanders, respectively, than reaches without seeps.
5. Practical implication: Current FP rules protect select side-slope seeps as another category of Sensitive Sites but may too narrowly define the criteria of seeps to

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protect the full range of those being utilized by stream-breeding salamanders. Studies focused on seeps and adjacent stream channel characteristics may better inform features important to stream-breeding salamanders.

KEYWORDS

dendritic network, forest management, headwater stream, intermittent stream, seep, stream-breeding salamander

1 | INTRODUCTION

Management of multiple-use forested landscapes is often complicated by a range of differing and seemingly incompatible objectives, such as economic logging interests and conservation goals (Horstkotte et al., 2015; Ma et al., 2016). Setting aside no-cut riparian buffers can help mitigate the effects of timber harvest but remove that land from economically productive uses (Olson et al., 2022; Richardson et al., 2012). Evaluating landscape features with disproportionately large ecological functions, such as stream-riparian areas, may help prioritize the placement of buffer protections used to meet environmental standards and protect biota (Olson et al., 2022; Richardson et al., 2012). Amphibians are often touted as bioindicators of aquatic systems because of their sensitivity and frequently rapid response to environmental change (Semlitsch et al., 2009; Stuart et al., 2004; Welsh Jr. & Ollivier, 1998) and thus present an opportunity for evaluating landscape features of ecological importance to inform conservation goals.

In moist-coniferous forests of North America's Pacific Northwest, torrent salamanders (*Rhyacotriton* spp.) and giant salamanders (*Dicamptodon* spp.; hereafter collectively referred to as stream-breeding salamanders; Figure 1) with obligate aquatic reproductive natural histories often comprise a majority of the vertebrates within

fishless stream systems (Bury et al., 1991). Stream-breeding salamanders reproduce in flowing water and are closely tied to streams for much of their life cycle, and their longevity, low reproductive potential and reliance on microhabitat conditions underscore their role as environmental indicators (Reinke et al., 2022; Welsh Jr. & Ollivier, 1998). Stream-breeding salamanders appear sensitive to loss of canopy associated with harvest (Pollett et al., 2010; Stoddard & Hayes, 2005). Many headwater basins where stream-breeding salamanders occur are intensively managed for timber. Stream-breeding salamanders were considered when evaluating buffer effectiveness (McIntyre et al., 2018) and has led to their consideration in timber harvest regulations, known as Forest Practice (FP) rules, and associated adaptive management in Washington, USA (WADNR, 2005). However, the species' patchy distributions coupled with the small scale of traditional sampling efforts makes discerning spatial patterns at management scales challenging. Broad-scale associations of stream-breeding salamander abundance across environmental gradients have been suggested (Adams & Bury, 2002; Wilkins & Peterson, 2000), but intensively evaluating short (<100m long) discrete stream reaches is a common approach that complicates inferring what may control the patterns at forest management scales (reviewed in Kroll, 2009).

In this study, we evaluate stream-breeding salamander relative abundance across stream network features known as 'FP Sensitive



FIGURE 1 Stream-breeding salamander study species, left: post-metamorphic torrent salamander (*Rhyacotriton* spp., photo credit: Reed Ojala-Barbour); right: larval giant salamander (*Dicamptodon* spp., photo credit: Daniel Trovillion).

Sites', including tributary junctions (TJ) and perennial initiation points (PIP), that receive buffers in most of Washington State's privately owned forests. We use species-habitat relationships to develop predictions about how stream-network position and hydrologic characteristics may affect salamander abundance (Table 1). First, we use dendritic ecological networks (Grant et al., 2007) to emphasize spatial relationships for taxa that are highly constrained to the physical stream network, explained further below. Second, we use stream order (Strahler, 1952), a scaling property that quantifies the upstream reach branching complexity, to organize reaches hierarchically. This scaling relates directly to stream power, a key factor regulating stream channel morphology and habitat (Benda et al., 2004). Lastly, we consider additional hydrological characteristics that can be rapidly assessed and may affect amphibian densities at the reach scale: the proportion of dry channels and channel-connected seeps (Olson & Weaver, 2007; Sheridan & Olson, 2003). Note that select hydrologic features meeting the definition of 'side-slope seep' are protected by a 15 m (50 ft) buffer under current FP rules, however, we included all channel-connected seeps in our evaluation, regardless of whether they met that more restricted definition.

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 (TJs), 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 & Chesson, 2018; Wallin et al., 1998). In addition, TJs may provide unique habitat features and increased diversity (Benda et al., 2004). For example, in larger stream systems, confluences have been associated with increased pool depth, large wood accumulations and coarser substrate (Benda et al., 2004). In contrast, first-order streams near the PIPs are generally the smallest, most isolated, with lowest stream power and can be dominated by colluvium, that is, unsorted fractured bedrock and erosional deposits (Montgomery

& Buffington, 1997) that provide an interstitial matrix through which cool, low-flows are frequent. Lastly, seeps are areas of saturation connected to the stream channel network via surface flow and have been identified as important amphibian habitats in multiple studies (Hayes et al., 2002; Wilkins & Peterson, 2000). Similar to PIPs, seeps provide stable inputs of cool groundwater.

Torrent salamanders are often associated with the uppermost reaches of headwater basins, that is, at or near PIPs, in habitats with low fluvial power such as seeps and low-order streams (Nussbaum & 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 (Sheridan & Olson, 2003). Their potential vulnerability to forest harvest has been tied to their desiccation intolerance (Ray, 1958), association with cool water (Steele et al., 2003), and presumed low dispersal potential (Nijhuis & Kaplan, 1998; Nussbaum & Tait, 1977). In a pilot study, Hayes et al. (2002) found high densities of torrent salamander larvae at PIPs. In addition, streams located on competent lithologies may have more stable hydrologic regimes at PIPs (Jaeger et al., 2007). We predict that PIPs and seeps provide cool wet refugia for torrent salamanders during summer drought (Russell et al., 2002; Thompson et al., 2018). Torrent salamanders are recognized as sensitive by state and federal wildlife agencies (USFWS, 2015; WDFW [Washington Department of Fish and Wildlife], 2019). Columbia Torrent Salamander (*R. kezeri*) and Cascade Torrent Salamander (*R. cascadae*) are currently being reviewed for potential listing under the Endangered Species Act (USFWS, 2015). In contrast, giant salamanders, a top predator in headwater streams, are thought to be habitat generalists and less diet-specialized (Cudmore & Bury, 2014; Murphy & Hall, 1981). Giant salamanders are frequently associated with pools (Bury et al., 1991; Wilkins & Peterson, 2000). While considerable overlap exists, giant salamanders are more typical of larger headwater streams than torrent salamanders (Hunter, 1998; Olson & Weaver, 2007). We predict that giant salamander abundance will have a positive association

TABLE 1 Predictions for the direction of effect for predictor variables on salamander relative abundance.

Variable	Torrent salamander		Giant salamander	
	Direction	Literature	Direction	Literature
Dendritic reach type				
Perennial initiation point (PIP)	Positive	Good and Wake (1992), Hayes et al. (2002) and Russell et al. (2002)	Negative	Hunter (1998) and Olson and Weaver (2007)
Branch	Neutral		Neutral	
Tributary junction (TJ)	Neutral		Positive	Wilkins and Peterson (2000), Benda et al. (2004) and Grant et al. (2007)
Stream order				
Stream order	Negative	Hunter (1998), Wilkins and Peterson (2000) and Jackson et al. (2007)	Positive	Hunter (1998) and Olson and Weaver (2007)
Hydrological characteristics				
Seep present	Positive	Hayes et al. (2002); Sheridan and Olson (2003) and Thompson et al. (2018)	Neutral	
Dry channel	Negative	Olson and Weaver (2007)	Negative	Sheridan and Olson (2003) and Kaylor et al. (2019)

with stream order and TJs that may have greater potential to contain deeper pools in our headwater study sites.

Forest Practice rules that dictate timber harvest and riparian buffer requirements apply to over 3.7 million hectares [9.3 million acres] of managed forest in Washington State (WADNR, 2005). These rules designate TJs, PIPs and some seeps as FP Sensitive Sites that receive either a 15- or 17-m [50- or 56-ft] no-cut patch buffer in the upper extent of headwater basins that are often otherwise clearcut to the stream channel. The buffering strategy, established in 2001, was the result of a policy compromise based on practical concepts but limited empirical data (Wilhere & Quinn, 2018). For example, TJs were buffered because they contain multiple stream reaches and increase the total length of buffered stream at a single site with fewer trees retained. Here, we examined dendritic features and other hydrological characteristics that could be easily and quickly assessed in the field to evaluate their relationship with an amphibian abundance index in second-growth managed forests prior to timber harvest. With growing interest in the deployment of site-specific buffers, we 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.

2 | MATERIALS AND METHODS

2.1 | Study sites

Stream reaches evaluated in this study were located in 17 amphibian-occupied non-fish-bearing stream basins in western Washington that were part of the Type N Experimental Buffer Treatment Study (McIntyre et al., 2018; see McIntyre et al., 2009 for a detailed account of site selection process that screened for the following criteria). All sites (i.e. headwater basins) were located on competent lithologies (i.e. produce durable coarse grain sizes) in managed second-growth Douglas fir and western hemlock-dominated forests in Washington State. Site elevation ranged from 22 to 601 m [72 to 1972 ft] above mean sea level and site size ranged from 12.1 to 53.8 ha [30 to 133 acres]. Stand ages ranged from 30 to 80 years since the last harvest and stands were located in the Olympic Peninsula, southern Cascades Range and Willapa Hills of Washington State on federal, state and private ownerships (Figure 2).

2.2 | Amphibian sampling

We designated dendritic reach types by their spatial proximity to stream network nodes (i.e. TJs and PIPs), and by extension, whether they fell within circular (17-m radius) FP Sensitive Site no-cut patch buffer criteria (Figure 3). Consistent with buffer requirements for FP Sensitive Sites, stream reaches within 17 m [56 ft] of a network node were designated as TJ or PIP dendritic reach types; all other reaches were designated as branches. Branch

lengths varied considerably ($\bar{x} = 129$, $SD = 105$ m). Amphibian observations were grouped by site and dendritic reach type for analysis. The stream order (sensu Strahler, 1952) of each stream reach was verified in the field.

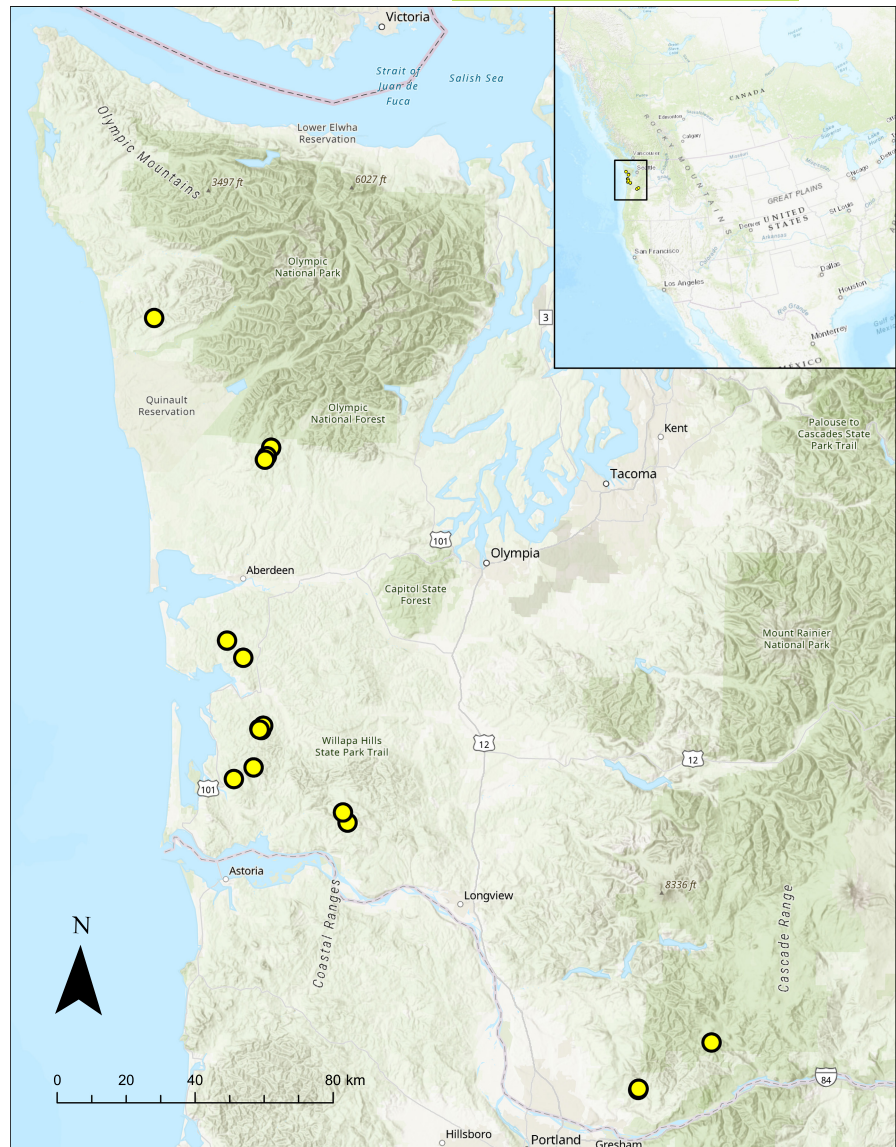
During 2006, we recorded the location of channel-connected seeps. We defined seeps as small wetland features where the water table met the ground surface and lacked a scour channel (Brooks et al., 1997; O'Donnell et al., 2007), but we only included those connected to the channel by overland flow in our survey. 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.

We collected salamander count data from streams that were sampled each year using a modified light-touch technique (Lowe & Bolger, 2002; Quinn et al., 2007). We conducted an active search as we moved upstream, turning all moveable surface substrates ≥ 64 mm [2.5 inches] within the ordinary high-water mark, including in dry reaches, and within the saturated area of channel-connected seeps. Surveys were conducted during daylight hours between June and October in 2006 and 2007. Upon capture, animals were promptly identified, measured and returned to their capture location. Handling of animals adhered strictly to animal care and use guidelines (Beaupre et al., 2004). Scientific collection permits were not required because this work was conducted by the Washington State Department of Fish and Wildlife, the permitting agency. 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 m [66 ft] of any road crossing to minimize the effects of roads. The intent was to sample the entire stream network but due to logistical constraints, 77% and >99% of the total stream lengths were sampled in 2006 and 2007, respectively.

The light-touch technique has the benefits of minimizing disturbance (O'Donnell et al., 2007) and covering a greater spatial area with less cost than traditional methods (Quinn et al., 2007), but due to imperfect detection, observations/unit of stream only index abundance. Hence, we describe our indexed abundance as relative abundance. Previous research has shown that detection probability varies with stream order and temperature (McIntyre et al., 2012). To ensure reliable detection of amphibians, we set a minimum reach length of 15 m [50 ft] to ensure the sampling effort was adequate to detect amphibians in each unit of analysis (Quinn et al., 2007). Furthermore, surveys of all stream reaches in a site were conducted over no more than seven consecutive days to minimize variability in stream temperature and other environmental covariates that may influence detection, thus minimizing the likelihood that detection effects influenced our results.

We grouped species of giant salamander (*Dicamptodon*) and torrent salamander (*Rhyacotriton*) into two phylogenetic entities for analysis. Cope's Giant Salamander (*D. copei*) and Coastal Giant Salamander (*D. tenebrosus*) were treated as one taxon because distinguishing them in the field is difficult (Foster et al., 2015). Cope's Giant Salamander was found at all study sites whereas Coastal Giant Salamander was found in most Willapa Hills and all southern

FIGURE 2 Distribution of 17 study sites in western Washington (Basemap, ESRI).



Cascades Range sites (Spear et al., 2011). Torrent salamander species do not co-occur, but they occupy similar habitats with the Olympic Torrent Salamander (*R. olympicus*), Cascade Torrent Salamander (*R. cascadae*) and Columbia Torrent Salamander (*R. kezeri*), respectively, found in the Olympic Peninsula, southern Cascades Range and Willapa Hills of Washington State (Good & Wake, 1992).

2.3 | Statistical analysis

We developed generalized linear mixed models (log link, Poisson distribution) with the light-touch amphibian counts as the dependent variable. We tailored the parameterization of fixed effects for each model to individually test variables listed in Table 2. Our aim was to compare amphibian relative abundance across (1) dendritic reach types (PIP, TJ, branch) to evaluate FP Sensitive Sites and related dendritic structure hypotheses and (2) hydrological variables including the stream order, presence/absence of channel-connected

seeps and proportion of dry channels. We evaluated torrent and giant salamander relative abundance separately. For the comparison of dendritic reach type, we evaluated PIPs, TJs and branches in first-order streams and separately evaluated all TJs and branches in a network-wide comparison. For the evaluation of proportion of dry channel, we used data from the dendritic reach type dataset from 2006 when channel dryness was censused.

We separately included site ($n=17$) and detection segment ($n=132$) as random effects, where detection segment was the stream reach between PIPs and TJs in first-order reaches and between all TJs of different stream orders. This allowed us to create blocks with similar stream temperatures and order to control for imperfect detection (Banks-Leite et al., 2014; McIntyre et al., 2012) and spatial autocorrelation (Wagner et al., 2006). Detection segments were nested within sites. We included year as a fixed effect in all models that included both years of data, but we do not consider it of focal interest. A log offset was used to account for different length of stream surveyed among reaches.

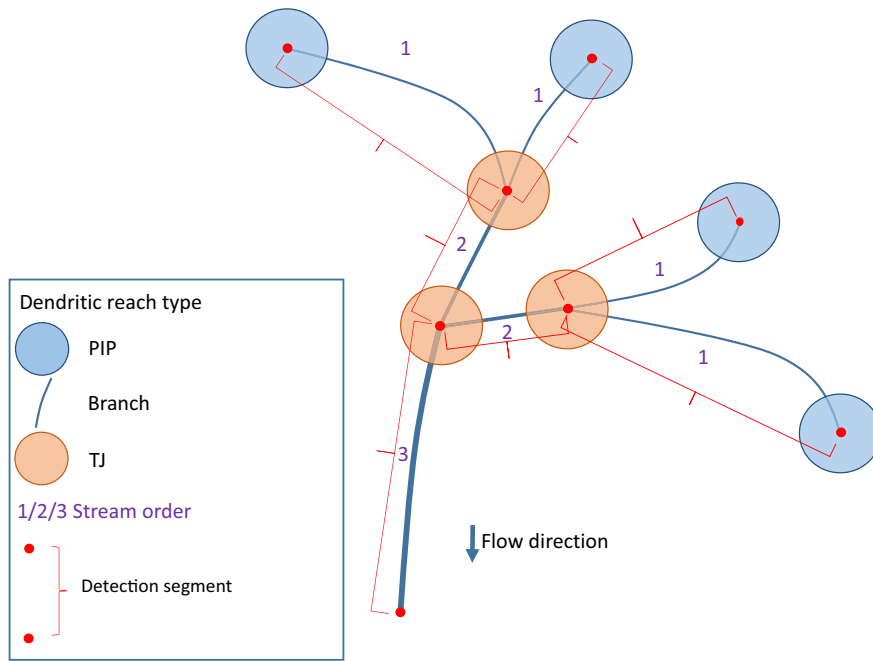


FIGURE 3 Schematic of dendritic reach type used in study design. Stream reaches within 17 m [56 ft] of network nodes were designated as tributary junctions (TJs) and perennial initiation points (PIPs), respectively, while the remaining reaches were designated as branches. Detection segments were used as a random effect to block reaches with similar environmental characteristics.

TABLE 2 Sample size of stream reaches across 2 years used in each comparison.

Model	Variable	Sample size
Dendritic reach type models		
First-order only	Perennial initiation point (PIP)	102
	Branch	150
	Tributary junction (TJ)	144
Network-wide	Branch	202
	TJ	210
Hydrologic models		
Stream order	First	344
	Second	188
	Third	46
Seep in reach	Absent	450
	Present	76
Dry channel	Wet (0% dry)	194
	Dry (>0%)	71

All statistical analyses were conducted in R[®] v4.1.0 using Bayesian models fitted in STAN with the brms package v2.18 (Bürkner, 2017). We assessed model convergence using posterior predictive diagnostic plots and the potential scale reduction factor. We used diffuse, weakly regularizing priors (McElreath, 2016). We ran four Hamiltonian Monte Carlo chains of 5000 iterations each (warm-up=2500, thin=1). The generalized linear mixed model produces parameter estimates on the natural log scale. We exponentiated estimates to back-transform them to the original scale and normalized them to observations/100m of stream length to facilitate the interpretation of salamander densities. Figures of the

transformed posterior distributions were based on the mode and 95% highest density credible interval using the ggdist package from Kay (2023). The proportional difference of the mean estimates is based on the mode of the contrast distribution and the 95% highest density credible interval (HDI). To visualize salamander spatial distribution, we plotted salamander observations for each 10-m segment (Figure 4).

2.4 | Stream habitat characterization

Stream habitat metrics are summarized to help interpret results and provide context about our study sites. We characterized habitat at a systematically selected subset of stream segments along the main-stem of each site to describe amphibian habitat by dendritic reach type and stream order. Point measures included wetted width and bankfull width, stream depth and gradient. We did not model these metrics.

3 | RESULTS

We sampled 32,837 stream meters from 17 study sites for stream-breeding salamanders using the light-touch technique that resulted in 3,704 observations of torrent salamanders and 1,313 observations of giant salamanders over the 2 study years. Stream-breeding salamander abundance was patchy within sites (Figure 4). Channel widths were small with mean wetted width ranging from 0.7 to 1.4 m and were relatively consistent across dendritic reach types and stream order. With increasing stream order, mean depth increased and gradient decreased (Table 3). Stream habitats observed within study sites were characteristic of small headwater channels.

FIGURE 4 Count category values of torrent and giant salamander observations in 10-m survey reaches to visually demonstrate species distribution throughout the headwater network in 2006 (Basemap, WADNR).

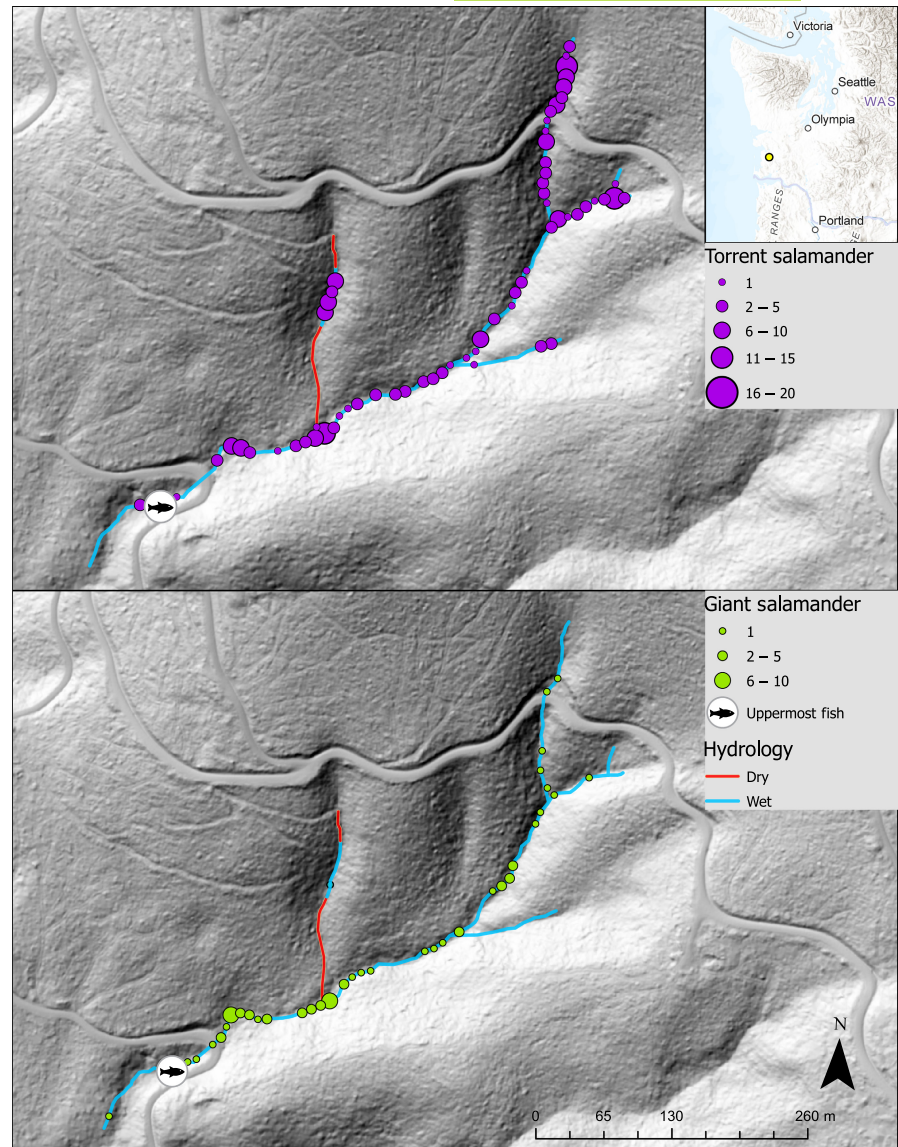


TABLE 3 Habitat characteristics by dendritic reach type and stream order (mean \pm SD; range in parenthesis).

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

3.1 | Dendritic reach type

We found no evidence that TJs had an effect on relative abundances of either species (Figure 5; Table 4). Perennial initiation points showed evidence of a negative effect for only giant salamanders. Giant salamander relative abundances in PIPs were 50% and 60%

less than in branches (CI: –73% to –18%) and TJs (CI: –78% to –21%), respectively. For both contrasts, credible intervals did not overlap 0% indicating a high probability of a direction to the effect. In first-order streams, torrent salamanders were observed slightly less often in PIPs and TJs than in branches, but relative abundance estimates had large overlapping credible intervals.

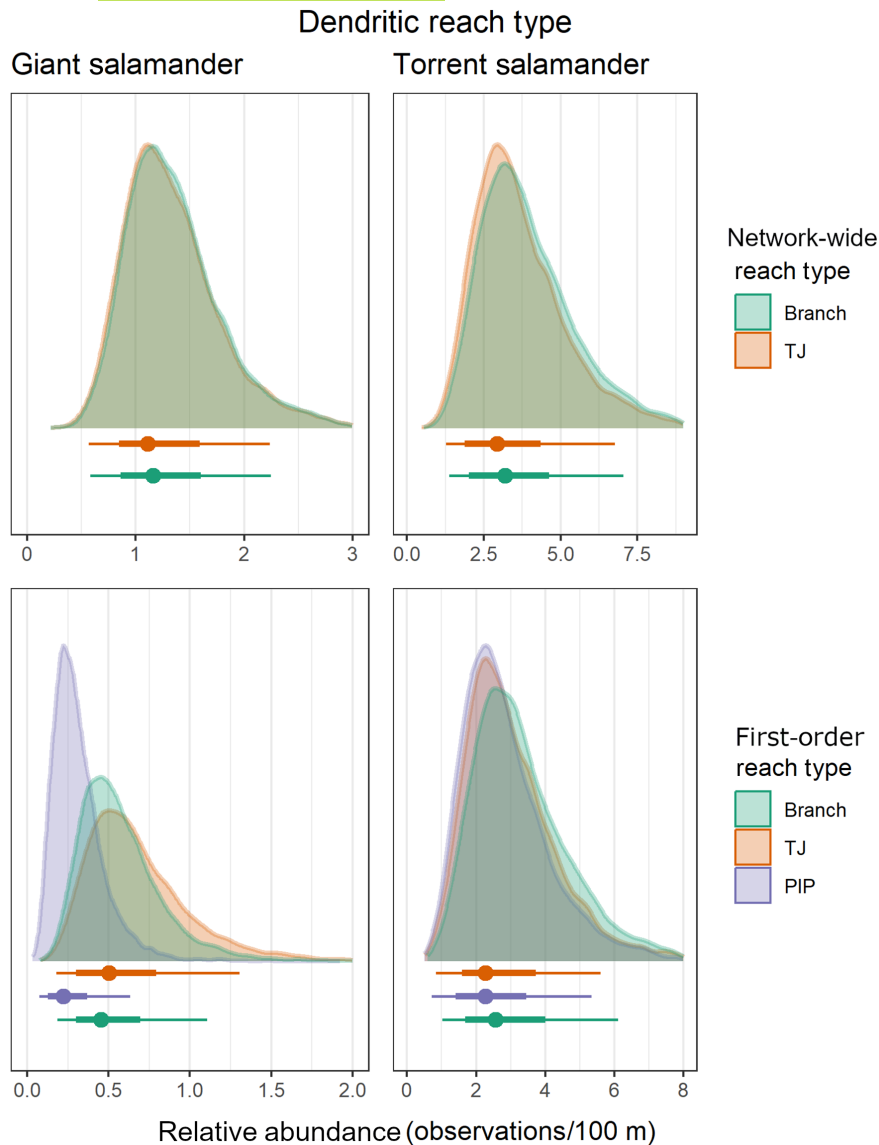


FIGURE 5 Mean estimate of torrent and giant salamander relative abundance (observations/100 m) by dendritic reach type. Coloured polygon shows the posterior distribution, the solid dot shows the estimated mode of the posterior, the thick horizontal line below each polygon shows the 80% highest posterior density interval (HDI) for the density polygon, whereas the thin horizontal line shows the 95% HDI.

TABLE 4 Proportional difference contrasts of relative abundance by dendritic reach type.

Contrast	Torrent salamander	Giant salamander
First-order only		
PIP versus branch	-16% (-31% to +2%)	-50% (-73% to -18%)
PIP versus TJ	-8% (-28% to +19%)	-60% (-78% to -21%)
TJ versus branch	-9% (-26% to +9%)	+17% (-27% to +70%)
Network-wide		
TJ versus branch	-8% (-17% to +4%)	-2% (-19% to +18%)

Note: Contrasts that had an effect direction supported by a 95% credible interval are shown in bold.

3.2 | Stream order

Decreasing stream order had a strong negative effect on giant salamander relative abundance with a -82% (CI: -89% to -74%) and -89% (CI: -96% to -75%) less than in first-order stream reaches compared to second- and third-order reaches, respectively

(Figure 6 and Table 5). Mean estimates for torrent salamander relative abundances were similar across stream orders and the wide credible intervals suggest high variability. For both taxa, the relatively wide credible intervals around third-order estimates may partly reflect the smaller sample size, with only 4 of 17 sites containing third-order reaches.

3.3 | Dry channel

The proportion of dry channels at the time of survey during summer low-flow had a consistent negative effect on relative abundance estimates for both taxa. We saw greater variability in torrent salamander densities in reaches with some dry channels than for giant salamanders, which had a stronger negative association with dry channels. For a change from wet to dry, torrent salamander relative abundance would be multiplied by 0.54 (CI: 0.31-0.94) and giant salamanders would be multiplied by 0.04 (CI: 0.01-0.16). Dry channels, which we measured only in 2006, were

FIGURE 6 Mean estimate of torrent and giant salamander relative abundance (observations/100 m) by stream order. Coloured polygon shows the posterior distribution, the solid dot shows the estimated mode of the posterior, the thick horizontal line below each polygon shows the 80% highest posterior density interval (HDI) for the density polygon, whereas the thin horizontal line shows the 95% HDI.

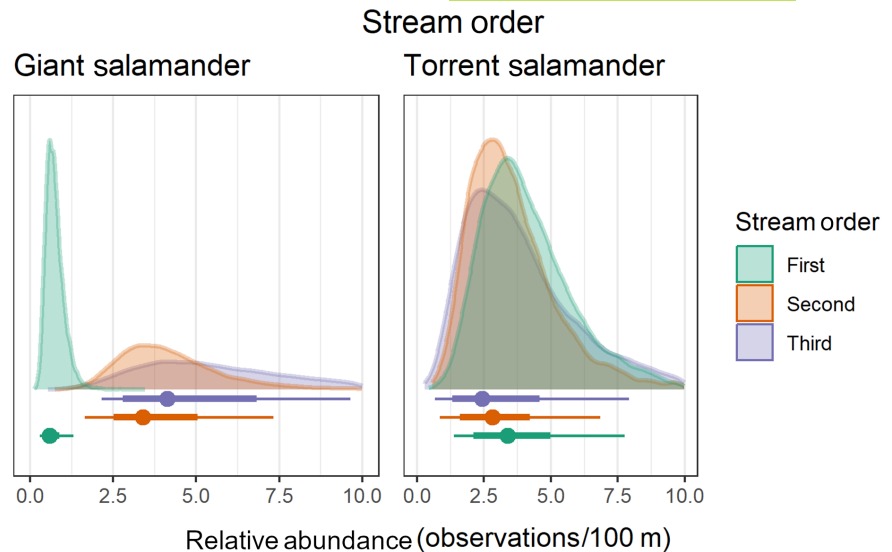


TABLE 5 Proportional difference contrasts of relative abundance by stream order.

Contrast	Torrent salamander	Giant salamander
First versus second	+11% (-25% to +76%)	-82% (-89% to -74%)
Second versus third	-23% (-72% to +99%)	-40% (-75% to 43%)
First versus third	-1% (-63% to +135%)	-89% (-96% to -75%)

Note: Contrasts that had an effect direction supported by a 95% credible interval are shown in bold.

more common in first-order than in higher-order reaches (Table 6). In first-order reaches, PIPs had proportionally less dry stream length than branches.

3.4 | Seeps

We evaluated 55 seep-present reaches across our study sites. Reaches with seeps had 123% greater torrent salamander relative abundance (CI: +103% to 146%). In the same reaches, giant salamanders had 81% greater relative abundance (CI: +49% to +119%) (Figure 7). In 2006 and 2007, respectively, 19% and 18% of the total torrent salamander observations in seep-present reaches occurred in channel-connected seep features with most observations occurring in the stream channel of the reach adjacent to the seep. Only one giant salamander was observed in a seep outside of the stream channel.

We estimated that 2007 had a positive effect on relative abundances for both species, with increases of 41% (CI: 26%–59%) and 33% (CI: 24%–43%) for giant and torrent salamanders, respectively. In most of western Washington, the summer of 2006 was considered a moderate drought, whereas 2007 was neutral (Hegewisch et al., 2024).

4 | DISCUSSION

Our analyses revealed that PIPs and TJs, a focal part of the patch-buffering strategy for non-fish-bearing headwater streams under

Washington State's FP rules, do not stand out as having greater amphibian relative abundances. Consistent with our predictions, we found lower giant salamander densities in PIPs. Several authors have suggested that giant salamander density decreases as one moves towards the uppermost extent of headwaters (Bury et al., 1991; Hunter, 1998; Olson & Weaver, 2007). Benda et al. (2004) found that stream confluences had deeper pools and coarse substrate, so we hypothesized TJs might support more giant salamanders. The small size of our study streams and the lack of contrast between channel sizes at TJs (see Table 3) may mute the effect of increased complexity at confluences that Benda et al. (2004) suggest. Moreover, pool-forming features, such as wood and boulders, beneficial to giant salamanders may be stochastically distributed throughout small streams rather than concentrated at TJs as low-flow conditions limit their transport (Jackson & Sturm, 2002). Hence, variability in TJ complexity may have been too limited to translate into differences in salamander relative abundance. Our prediction that torrent salamanders would be more frequent in PIPs based on their preference for low flows seemed unsupported. In general, this finding agrees with Wilkins and Peterson's (2000) observation of Columbia Torrent Salamander in first-order streams near PIPs as they generally observed an increase in torrent salamander abundance downstream to the first TJ. One possibility is that the low-flow habitat with which torrent salamanders are associated extends over a rather large spatial footprint in headwater streams, perhaps even larger than most of our sites. If that is the case, one would not expect a pronounced gradient in the abundance of torrent salamanders over the spatial scale we conducted our analysis, especially given the very small spatial scale of PIPs. Another alternative is that unmodeled habitat variables such as gradient, substrate, and temperature may be more important in controlling torrent salamander abundance (Diller & Wallace, 1996; Russell et al. 2004) than the reach-scale variables we evaluated.

Importantly, we found hydrological characteristics generally had stronger effects on salamander abundances for both taxa than

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

TABLE 6 Summary of dry stream length by order and reach type in 2006.

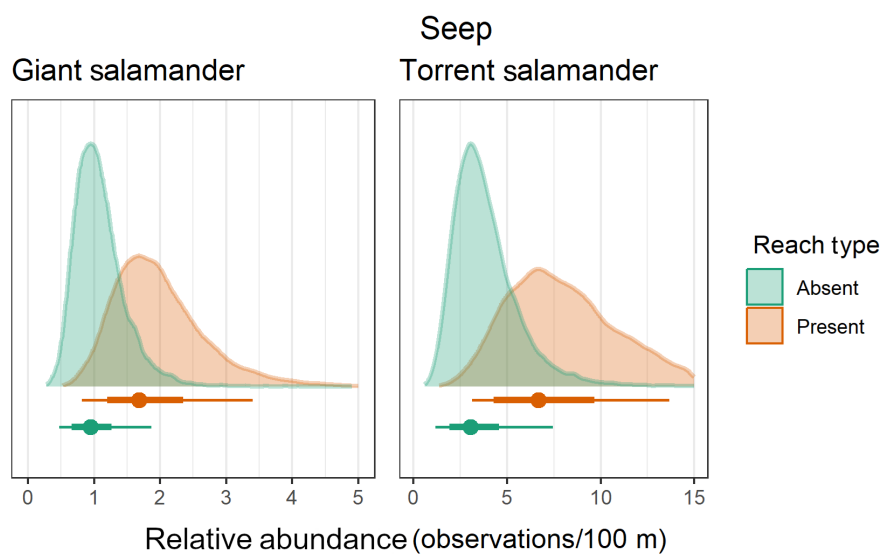


FIGURE 7 Mean estimate of torrent and giant salamander relative abundance (observations/100 m) in seep-present reaches compared to reaches without seeps. Coloured polygon shows the posterior distribution, the solid dot shows the estimated mode of the posterior, the thick horizontal line below each polygon shows the 80% highest posterior density interval (HDI) for the density polygon, whereas the thin horizontal line shows the 95% HDI.

dendritic reach type. Prominent among these were seeps. Seeps had a strong positive effect on the abundance of the two salamander taxa. In particular, reaches with seeps had estimated salamander relative abundances about twice that of reaches lacking seeps (see Figure 7). Other studies have observationally reported torrent salamanders in seeps (Nussbaum & Tait, 1977; Wilkins & Peterson, 2000), which appear common in forested headwater landscapes in the Pacific Northwest (Hayes et al., 2002; Janisch et al., 2011). Torrent salamanders deposit eggs in seeps (Thompson et al., 2018 and references therein), but how giant salamanders may benefit from seeps or their proximity is unclear. Stream channels near seeps may accrue hydrological or food-resource benefits that may support higher abundances of both stream-breeding salamander taxa. For example, reaches with groundwater upwelling were found to have cooler, more stable temperatures than reaches with down-welling or neutral flow paths (Guenther et al., 2014). Current FP rules require buffers on side-slope seeps, but these features, by definition, are limited to seeps with >20% gradient lacking muck (WFPB, 2001). Seeps at our study sites were evaluated in 2010 and 76% were found to not meet FP criteria for side-slope seeps based on having a gradient <20% or being dominated by fine sediment (unpublished data, WDFW). Similarly, Hayes et al. (2002) found that shallow accumulations of mucky substrates such as fine sediment and leaf litter comprised $\geq 15\%$ of the surface area of all seeps they evaluated. By definition, seeps

are on the low-flow end of the fluvial spectrum, so many may 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 second hydrological feature we found important was dry channels. Dry channels had a negative effect on both species, but the effect seemed stronger for giant salamanders. We observed that torrent salamanders may continue to occupy wet patches of stream channels in reaches with intermittent surface water. Across our study sites, first-order stream reaches tended to be driest (see Table 6) and, by definition, are the most isolated from the rest of the dendritic network. Surface-water intermittency is common in our headwater landscape (Hunter et al., 2005). Logically, channel drying in the upper stream network could limit abundances of desiccation-intolerant aquatic organisms, but it may also impact our ability to detect animals that occupy the hyporheic zone if animals retreat to refuges concealed in the subsurface channel substrate (Feral et al., 2005) and are thus undetectable with a particular sampling method. Our evaluation provides a seasonal low-flow snapshot of amphibian distributions within headwater stream basins when flows are at their lowest and the risk of thermal stress, desiccation, and mortality is thought to be highest (Chelgren & Adams, 2017; Sagar, 2004). Since these data were collected in 2006 and 2007, the headwater landscape of the Pacific Northwest has experienced greater thermal stress from climate

change and habitat loss via greater seasonal headwater stream drying (Olson & Burton, 2019), which increases uncertainty about the status and efforts to conserve sensitive stream-obligate taxa and associated habitats.

Detectability is a valid concern in our analysis. Our results are based on an index of abundance rather than on abundance estimates corrected for imperfect detection. We included a detection segment random effect to account for variation in detection rates by grouping reaches with similar stream conditions. The refined alternative, unavailable with this dataset, would be to adjust observations by detection probability to limit bias in the abundance estimates (McIntyre et al., 2012). We also recognize that our study does not address potentially broader habitat use during the wet season nor the nocturnal activity that may be different from the diurnal activity observed during our daytime sampling.

These results may support a reevaluation of the criteria for side-slope seeps, especially related to gradient and fine sediments under the current FP rules. We did not evaluate the post-harvest effects of no-cut patch buffers here, but rather focused on stream-breeding salamander use of TJs, PIPs and other variables at management-relevant scales in forests of harvestable age. Amphibian use of patch buffers remains poorly understood (Kroll, 2009). Previous studies suggested that clearcut reaches receive a large pulse of wood associated with harvest (i.e. slash) 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 & Corn, 1988; Jackson & Sturm, 2002; McIntyre et al., 2018). Perennial initiation point and TJ buffers may help to protect water quality by stabilizing banks, mitigating against sediment and slash inputs and providing shade and litter. However, PIP buffers are often isolated patches located on upper slopes with greater wind exposure causing increased tree mortality compared to intact forests and larger continuous buffers (Schuett-Hames & Stewart, 2018). Evaluation of the immediate 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 vulnerable to climate change.

AUTHOR CONTRIBUTIONS

Reed Ojala-Barbour, Aimee P. McIntyre, Eric M. Lund and Marc P. Hayes conceived the ideas and designed the methodology; Aimee P. McIntyre, Eric M. Lund, Marc P. Hayes and field technicians collected the data; Reed Ojala-Barbour analysed the data; Reed Ojala-Barbour led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

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DATA AVAILABILITY STATEMENT

Data available from Dryad Repository <https://doi.org/10.5061/dryad.x3ffb7tt> (Ojala-Barbour et al., 2024).

ORCID

Reed Ojala-Barbour  <https://orcid.org/0009-0007-3015-3410>

Aimee P. McIntyre  <https://orcid.org/0000-0001-8269-6715>

Eric M. Lund  <https://orcid.org/0000-0002-1000-3753>

Marc P. Hayes  <https://orcid.org/0000-0002-5629-8219>

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