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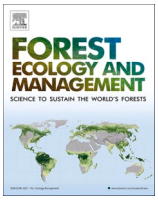

Adjacent and downstream effects of forest harvest on the distribution and abundance of larval headwater stream amphibians in the Oregon Coast Range

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A B S T R A C T

Forest harvest is a primary landscape-scale management action affecting riparian forests. Although concerns about impacts of forest harvest on stream amphibians is generally limited to areas adjacent to harvest, there is a paucity of information regarding potential downstream effects of forest harvest on these species. We designed a before-after, control-impact (BACI) experiment to quantify potential impacts of clearcut logging that included 12-m buffers or smaller variable-width buffers on the distribution and abundance of headwater stream amphibians in adjacent and downstream areas. We sampled larval coastal tailed frogs (*Ascaphus truei*), coastal giant salamanders (*Dicamptodon tenebrosus*), and Columbia torrent salamanders (*Rhyacotriton kezeri*) across 3,915 sampling occasions that spanned 13 study reaches in 2008–2011 (pre-harvest) and 2013–2016 (post-harvest) as part of the Trask River Watershed Study in the Oregon Coast Range, U.S.A. We analyzed these data using occupancy models to estimate occupancy and (when possible) relative abundance, while accounting for various sources of imperfect detection. All species exhibited reduced occupancy adjacent to clearcuts with variable-width buffers (odds ratios [ORs] ranged = 0.24–0.48), and these negative impacts were not always diminished when increasing the buffer size to 12 m (ORs ranged = 0.20–3.56). *Dicamptodon tenebrosus* was the only species to have occupancy impacted in downstream areas, and this negative impact was related to clearcut logging with uniform 12-m buffers (OR = 0.60). This species was also the only species to have abundance negatively impacted by forest harvest in downstream areas (OR = 0.41 with uniform 12-m buffers, OR = 0.38 with variable-width buffers), albeit impacts to abundance were not evaluated for *R. kezeri*. *Ascaphus truei* abundance increased in areas downstream of clearcut logging with uniform 12-m buffers (OR = 2.92). Although we found the direction and magnitude of responses varied by species, our study confirms that clearcut logging can have negative impacts on amphibians that inhabit the adjacent stream areas. Perhaps more importantly, we also found that forest harvest can have negative effects on stream amphibians downstream of the harvested area and that increasing the buffer size to 12 m did not necessarily diminish these impacts in adjacent and downstream areas. Altogether, our study provides a nuanced picture of adjacent and downstream effects of forest harvest on three endemic headwater stream amphibians, and our findings demonstrate that forest management practices should consider downstream effects on aquatic taxa when assessing the impact of harvesting trees near headwater streams.

1. Introduction

Globally, deforestation represents one of the most detrimental land-use changes to amphibians (reviewed in Cordier et al., 2021). A recent quantitative assessment indicated global forest loss disproportionately eroded biodiversity in relatively intact forest landscapes, with the highest negative impacts exhibited in amphibians (Betts et al., 2017). Although managed for multiple uses, forest harvest is one of the primary management actions that affects riparian habitats in forests of the Pacific Northwest, U.S.A. Similar to patterns uncovered elsewhere, historical production-based logging practices in this region contributed to declining physical and biotic stream conditions (Brown, 1970; Gregory and Bisson, 1997). This prompted a shifting paradigm toward ecosystem-based management (Wissmar, 1993; Federal Register, 2005; Olson et al., 2007). However, best management practices are primarily based on research from larger, fish-bearing streams (Richardson et al., 2012). Considerably less attention has been given to effects of forest management on headwater streams and their biota (Kampf et al., 2021). Yet, headwater streams comprise the majority of stream networks (Benda and Dunne, 1997), provide critical ecosystem functions affecting downstream water quality (reviewed in Lowe and Likens, 2005), and support diverse fauna, including at-risk amphibian species (reviewed in Olson et al., 2007).

Amphibian responses to forest harvest can be highly variable

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depending on the biome and community diversity. Although some studies indicate negative associations between harvest and amphibian species richness (Chaudhary et al., 2016), abundance (Corn and Bury, 1989; Ashton et al., 2006; MacNeil et al., 2014) and vital rates (Semlitsch et al., 2009), others have found positive effects of harvest on population and individual-level responses (Murphy et al., 1981; Diller and Wallace, 1999; Russell et al., 2004; Kroll et al., 2008). Individual species and stream habitats, which vary in surface geology and environmental conditions, undoubtedly exhibit a range of sensitivities to forest harvest practices (Adams and Bury, 2002; Wilkins and Peterson, 2000). However, inconsistent findings may also be an artifact of limitations in study design, such as narrow geographical and temporal scales, the lack of experimental replicates with comparisons to pre-harvest conditions, and inability to account for sources of bias inherent in animal survey data. Moreover, interpretation of responses is complicated by the biphasic lifecycles common to amphibians, where aquatic (egg and larvae) and terrestrial (usually adults) life stages are exposed to a distinct suite of changes related to forest harvest practices. Post-harvest, aquatic stages can be exposed to in-stream factors such as increased sedimentation (Peterman and Semlitsch, 2009; Welsh and Ollivier, 1998) and light penetration/peak temperatures (reviewed in Warren et al., 2016), whereas terrestrial life stages are additionally exposed to microhabitat variables that influence overland movements, such as soil moisture and structure (Rittenhouse et al., 2009; Peterman et al., 2013).

Taken along with the general underrepresentation of amphibians in the conservation literature (Bonnet et al., 2002; Womack et al., 2022), there is a need to control for as many sources of error as possible in study designs to better understand the effects of forest harvest practices on amphibians. For example, in lotic systems where enforcing closure to immigration/emigration at sample units is not practical, accounting for directional movement patterns is necessary to avoid biased estimates of population responses. Spatial aggregations of larval amphibians will often fluctuate over the season as individuals disperse from natal areas, move between resource patches, or undergo phenological shifts in habitat needs. However, disturbance due to harvest may also prompt movements while simultaneously influencing survival, and the magnitude of the effects can be dependent on intensity, spatial extent, and spatial proximity of the harvest. Thus, the spatial scale at which harvest impacts headwater stream amphibians may be much larger when factoring in broader population dynamics and species vagility (Lowe and Bolger, 2002).

We conducted a multi-year, large-scale manipulative before-after, control-impact (BACI) experiment to measure the responses of larval coastal tailed frogs (*Ascaphus truei*), coastal giant salamanders (*Dicamptodon tenebrosus*), and Columbia torrent salamanders (*Rhyacotriton kezeri*) to variable intensity forest harvest in stream sections that were adjacent to and downstream of forest management actions. These species comprise ancient families that are endemic to the Pacific Northwest and are unique from other amphibians around the world in their phylogeny, life history, and specialized habitat requirements (see species descriptions in Table 1). They occur broadly across forested lands and are important species within the context of forest ecology and management. This investigation builds on a previous analysis by Chelgren and Adams (2017), who estimated survival and movement of larval *A. truei* and *D. tenebrosus* in the same study reaches, by including another species (*R. kezeri*) and focusing on a different objective: to evaluate whether physical changes in stream conditions from clearcut forest harvest altered the distribution and (when possible) abundance of larvae for these species. Connecting patterns of abundance with previous estimates of survival allow for a more complete picture of the demographic processes behind observed responses, as survival and abundance are not necessarily linked (Otto et al., 2014; Todd and Rothermel, 2006). We hypothesized that harvest effects on stream amphibian occupancy and abundance would be largely limited to areas adjacent to forest harvest and be negative, and that harvests would have muted-to-no effects on amphibians downstream of treatment areas. Furthermore, we hypothesized that clearcut logging when leaving smaller variable-width buffers would have more pronounced negative effects on stream amphibians when compared to clearcut logging while leaving larger uniform 12-m buffers, which we expected would have diminished negative effects on stream amphibians.

Table 1
Habitat and life history characteristics of coastal tailed frog (*Ascaphus truei*), coastal giant salamander (*Dicamptodon tenebrosus*), and Columbia torrent salamander (*Rhyacotriton kezeri*).

Species	General Habitat	Egg	Larva	Post-metamorph
Ascaphus truei	Clear, cold, rocky streams in moist forests.[a]	Eggs laid after spring runoff under large rocks in streambed. Hatch in 3–6 weeks, in summer.[b,c]	Periphyton and diatoms are primary food sources. Larvae transform in 1–4 years and development is heavily influenced by temperature.[d]	Reproductive at 2–5 years.[e,f] Females may breed every other year.[e] Adults are closely tied to streams but may forage in uplands during cool, wet weather.[g]
Dicamptodon tenebrosus	Similar to *A. truei*, but may better tolerate fine sediments, low flow, and warmer water temperatures.[h]	Eggs laid in protected, water-filled crevices or under rocks. Hatch in 6–7 months, in late fall.[i]	Feed on aquatic invertebrates and fish fry. Larvae transform in 1.5–3 years.[g]	Facultative paedomorphosis. Reproductive at 5–6 years.[i] Females likely only breed once every few years. Terrestrial adults typically remain within 50 m of a stream.[j]
Rhyacotriton kezeri	Clear, cold, high gradient rocky streams, seeps, and splash zones.[k]	Eggs laid in deep rock crevices, in seeps, or in spring heads.[i] Hatch in 2.5–3 months.[l]	Feed on aquatic invertebrates.[g] Larvae transform in 3–4 years.[m]	Reproductive at 4–5 years.[g] Adults rarely venture more than a few meters from aquatic habitat[n]

[a] Adams and Pearl (2005)
[b] Karraker et al. (2006)
[c] Palmeri-Miles et al. (2010)
[d] Brown (2005)
[e] Thomson et al. (2016)
[f] Burkholder and Diller (2007)
[g] Nussbaum et al. (1983)
[h] Jones and Welsh (2005)
[i] Nussbaum (1969)
[j] McComb et al. (1993)
[k] Hallock and McAllister (2005)
[l] Petranka (1998)
[m] Nussbaum and Tait (1977)
[n] Good and Wake (1992).

2. Methods

2.1. Study area

Our experiment focused on 14 headwater streams (albeit we omitted one during analyses – see below) in the Trask River Watershed during the summer low-flow period four years before and four years after forest harvest occurred. We studied larval amphibians in the headwaters of Pothole Creek, Gus Creek, Upper Mainstem, and Rock Creek drainages in the South Fork of the Trask River in the Coast Range of northwestern Oregon, U.S.A. The 26 km^2 study area varies from 305 to 1100 m elevation. The region's maritime climate is characterized by mild wet winters and dry summers (Taylor and Hannan, 1999), with 158–272 cm of annual precipitation over the course of the study. The study area had forest fires during the decade of the historic Tillamook fires, 1933–1945. Salvage logging followed the wildfires, and the extensive disturbance is thought to have reduced the occurrence of large wood and increased sediment in streams (May and Gresswell, 2003). In the first year of our study, prior to our experimental harvest treatment, forest stands were 45–60 years old. These forests were primarily Douglas-fir (*Pseudotsuga menziesii*), and the riparian over-story also included abundant red alder (*Alnus rubra*) in some drainages. The riparian shrub layer supported dense thickets of stink currant (*Ribes bracteosum*), devil's club (*Oplopanax horridum*), and salmonberry (*Rubus spectabilis*). Further description of the study area can be found in Reiter et al. (2020) and Johnson et al. (2022).

2.2. Study design

We established a 300-m study reach on 14 headwater streams, which ranged from seasonally intermittent to perennial. Study reaches were positioned so that the boundary of planned harvest treatments bisected each reach into two 150-m sections. Within each study reach, we subdivided the 300-m stream into continuous 5-m long stream segments (hereafter referred to as plots) that we used for sampling larval amphibians and measuring habitat conditions (see below). This relatively small sample unit allowed us to accurately measure habitat conditions, which is needed to appropriately link population responses to changing habitat conditions (Duarte and Peterson, 2021). Furthermore, it allowed us to quantify habitat use at a smaller spatial scale to capture associations with favorable habitat conditions pre- and post-harvest. We sampled larval amphibians and measured habitat conditions from May to September 2008–2011 and 2013–2016. For safety reasons, no sampling occurred during 2012, when logging was in operation. There were eight treatment reaches where trees were harvested and six control reaches that were not harvested during the study period. Control reaches included Pothole Creek 3, Gus Creek 1, Upper Mainstem 1, and Rock Creek 1, 2, and 3.

Forest harvest varied among the eight treated reaches. In three reaches publicly owned and managed by Oregon Department of Forestry (Pothole Creek 1, 2, and 4), trees were harvested by clearcut and modified clearcut logging, except for a 12-m no-touch buffer of trees adjacent to each side of the stream within the harvested upstream 150-m section. We refer to the harvest in these study reaches as clearcut with a uniform 12-m buffer (CC_Uniform). In the only study reach publicly owned and managed by the Bureau of Land Management (Gus Creek 2), the density of trees was reduced by thinning, although a 15-m no-touch buffer of trees was retained adjacent both sides of the stream in the upstream 150-m section. We refer to the harvest in this study reach as thinned with 15-m uniform buffer (TH_Uniform) but note that this reach was ultimately omitted during analyses (see below). The remaining treated study reaches were private forests owned by Weyerhaeuser (Upper Mainstem 2 and 3 and Gus Creek 3 and 4). Although buffers were not required along small streams on private forest lands in areas that do not support salmonids, implementors can and often do leave trees to help stabilize stream banks and/or avoid working in areas where the ground is too moist to operate heavy machinery. This practice led to some stream segments having a small riparian buffer and others having no buffer at all. We refer to the harvest in these study reaches as clearcut with a variable-width buffer (CC_Variable), and note that this treatment resulted in much smaller buffer widths than CC_Uniform. More harvest details are available online (https://traskstudy.forestry.oregonstate.edu) and aerial photos of post-harvest conditions are published in the supplemental materials of Johnson et al. (2022).

The upper 150-m sections of the study reaches served as the experimental harvest or reference section and the lower 150-m sections were used to quantify downstream impacts of the experimental harvest. However, the boundary of the harvested area shifted significantly at two of the reaches from what had been planned at the design stage of the experiment. At one of the exceptions (Pothole Creek 1), the lower edge of the harvested area was approximately 120 m downstream of what was planned, with the result that only 30 m remained for assessing downstream impacts. At the other exception (Gus Creek 3), the entire 300-m reach was harvested, leaving no section suitable for measuring downstream impacts but a full 300 m in which to measure the impact of harvest adjacent to the stream.

Each year the 14 study reaches were repeatedly visited in a rotating design where the rotation interval was irregular (every one to four weeks). Each week that we returned to a reach we randomly selected a sample of 5-m plots to be surveyed. We surveyed one to 35 plots within a reach in a single week. The variable number resulted from variation in the time it took to complete surveys and to mark and handle amphibians. We strove to survey equal numbers of plots in four spatial quadrants of the reaches to achieve spatial balance. We used block nets (3.2-mm mesh size) at the upstream and downstream end of plots to maximize population closure (i.e., minimize the exchange of individuals in and out of the plots) during surveys. We captured larval amphibians by electrofishing using a Smith-Root LR-24 electrofisher with constant settings (standard pulse type, 300 V, 40 hz, and 6 ms pulse width; Honeycutt et al., 2016). During electrofishing, we used kick nets to capture mobile individuals, and headlamps to aid hand-capture of animals exposed by electrofishing. Of the plots randomly chosen to be electrofished in a specific week, a subsample were randomly selected to be resampled after a two-day rest. At this subset of plots, we individually marked larval amphibians during the first visit to estimate survival and movement (e.g., Chelgren and Adams, 2017) and potentially abundance. During resampling, we sampled the plot using identical methods described above. Block nets were removed as soon as sampling at a plot in that specific week was complete, either after the single pass of sampling or a double pass (passes separated by 48 hrs) of sampling. We refer to these single and double pass surveys of a plot on a given week as plot-level primary sampling occasions. Notably, our sampling effort focused on capturing individuals in their aquatic stage and we could not distinguish larval *D. tenebrosus* from sexually mature paedomorphic *D. tenebrosus*, which are also fully aquatic. Thus, although we refer to individuals in this study as larval amphibians, there are an unknown number of paedomorphic *D. tenebrosus* in our catch data we analyzed herein.

We measured environmental factors we hypothesized would be related to the distribution, abundance, and detectability of our focal amphibian species (Table 2). Stream gradient can be related to water flow velocity. Thus, we measured stream gradient in each plot to the nearest 0.1° using a Nikon Forestry 550 laser hypsometer. The overall size of the plot could influence our ability to detect species through search effort and concomitantly increase the chances individuals are present in a plot. Thus, we estimated the surface area of plots by multiplying the plot length by the average stream wetted width that was measured at three regularly spaced transects per plot. Given the association between our focal species and substrate type (Table 1), we estimated the proportion of cobble in each plot by measuring 30 substrate surface particles regularly spaced along three cross-sectional transects. Particles were classified as cobble if the B-axis (representing the smallest hole the particle could fit through) was in the range 64–256

Table 2
Summary statistics for explanatory variables included in the global occupancy models to estimate the probability that a sample unit is occupied (ψ); the probability that a sample unit is occupied by a large number of larvae (abundant), given that the sample unit is occupied ($\psi^{abundant}$ for *A. truei* and *D. tenebrosus* only); the probability that the species is detected, given that the sample unit is occupied (p); and the probability that evidence of the abundant state is collected, given that the sample unit is in state 2 and the species was detected (δ for *A. truei* and *D. tenebrosus* only).

Variable	Model parameter	Summary
Amount of light	p, δ	Range: 7.00 to 93.30 % Mean (SD): 79.14 % (20.26 %)
Day of year	p, δ,ψ	Range: 121 to 267 d Mean (SD): 211.52 d (28.65 d)
Gradient	ψ	Range: −3.60 to 42.70° Mean (SD): 8.76° (5.48°)
Location	ψ, $\psi^{abundant}$	Upstream: 1868 Downstream: 1407
Occupancy state (*A. truei* and *D. tenebrosus* only)	p	Yes: modeled No: modeled
Proportion cobble	ψ	Range: 0 to 1 Mean (SD): 0.70 (0.18)
Surface area	p, δ,ψ	Range: 0.25 to 30.36 m^2 Mean (SD): 6.47 m^2 (3.47 m^2)
Survey number	p, δ	1st: 3275 2nd: 640
Treatment	ψ, $\psi^{abundant}$	Control: 2456 Adjacent to CC_Uniform: 207 Adjacent to CC_Variable: 316 Downstream of CC_Uniform: 124 Downstream of CC_Variable: 172

mm. All substrate sampling occurred during the pre-harvest period. Canopy cover can be related to in-stream detrital inputs, light exposure, water temperature, runoff, and much more, which may influence our ability to capture amphibian species during surveys. Thus, we quantified canopy cover for each reach in a single year during pre- and post-harvest using the average of five canopy percent cover measurements measured using digital hemispherical photographs. Photography occurred during August from 80 cm above the stream thalweg at 25-m spacing using a Nikon FC-E8 fisheye converter lens. The WinSCANOPY image analysis software (Regent Instruments Inc., Quebec, Canada) was used to process these images. We used the amount of light (i.e., the inverse of canopy cover) as a covariate in analyses. The distribution, abundance, and detectability of our focal amphibian species can be related to the day of year since this variable is often correlated with ambient temperature, life history stage, and animal activity. Thus, we recorded the date of the first survey for each plot-level primary occasion. Finally, observer disturbance when surveying a plot may influence our ability to catch these species in secondary visits within a plot-level primary occasion. Therefore, we also kept track of the survey number of each survey visit.

2.3. Statistical analyses

We used multistate occupancy models to estimate the distribution and relative abundance of *A. truei* and *D. tenebrosus* while accounting for incomplete capture (Royle and Link, 2005; Nichols et al., 2007). A multistate occupancy model is similar to a standard occupancy model (e.g., MacKenzie et al., 2002) except that it allows our plots to be in more than two occupancy states. Specifically, we allowed plots to be in one of three occupancy states: 1) unoccupied ($m = 0$), 2) occupied ($m = 1$), and 3) abundant given the plot is occupied ($m = 2$). We used a conditional probability parameterization to differentiate between the two occupied states and allowed for potential misclassifications (i.e., detecting species presence but failing to detect the abundant state given the plot is in state $m = 2$). Thus, these models estimated the following parameters: the probability that a plot is occupied (ψ); the probability that a plot is occupied by a large number of larvae (abundant), given that the plot is occupied ($\psi^{abundant}$); the probability that the species is detected, given that the plot is in state 1 (p); the probability that the species is detected, given that the plot is in state 2 ($p^{abundant}$); and the probability that evidence of state 2 is collected, given that the plot is in state 2 and the species was detected (δ) (Online Resource 1). Given our conditional probability parameterization, the total probability that a plot is in state 2 is $\psi \times \psi^{abundant}$, and the total probability of correctly classifying a plot in state 2 is $p^{abundant} \times \delta$. We opted to fit multiseason multistate occupancy models, rather than dynamic multistate occupancy models (MacKenzie et al., 2009), due to the difficulty in estimating state transitions with a rotating panel design with random plot selections at varying temporal intervals. We followed the recommendation of Steen et al. (2023) to distinguish between occupied states. We classified a survey record as abundant ($m = 2$) if the number of captures was greater than or equal to the 0.8 quantile in the distribution of the non-zero captures during plot-level primary occasions, where we used the maximum number of captures when a plot was resampled during a plot-level primary occasion. This threshold was four and six captured individuals for *A. truei* and *D. tenebrosus*, respectively. We evaluated the same explanatory variables when analyzing the data for *A. truei* and *D. tenebrosus*. We had no *a priori* expectations that the relationship between detection probability and explanatory variables would differ for state 1 and state 2. Therefore, we shared intercepts and coefficients when modeling p and $p^{abundant}$, but we allowed them to differ using an intercept adjustment for $p^{abundant}$ (i.e., an additive model). We included this intercept adjustment because the probability of detecting a species, given it is present, is related to the probability of capturing at least one individual and the number of individuals available for capture (Bayley and Peterson, 2001; Royle and Nichols, 2003). Thus, species detection probability should increase with increasing abundance. We modeled variation in p on the logit scale as a function of the occupancy state, the survey number, the day of year, the amount of light, and the surface area of the plot. Similarly, we modeled variation in δ on a logit scale as a function of the survey number, the day of year, the amount of light, and the surface area of the plot. We modeled variation in ψ on a logit scale as a function of day of year, proportion of the plot with cobble substrate, the surface area of the plot, the gradient within the plot, general location of the plot relative to actual (treatment reach) or potential (control reach) treatment (*Location;* i.e., upstream vs. downstream section), and treatment category (i.e., control, adjacent to CC_Variable, adjacent to CC_Uniform, downstream of CC_Variable, and downstream of CC_Uniform). Finally, we modeled variation in $\psi^{Abundant}$ on a logit scale as a function of the general location of the plot relative to actual or potential treatment and treatment category. Logit-normal random year and reach effects centered on zero were included for both ψ and $\psi^{abundant}$ to account for spatial and temporal heterogeneity in the data that were not captured by our covariates. This parameterization treated pre-harvest plots in the upstream section as the reference category and allowed the effect of location to be independent of any treatment effects.

The number of *R. kezeri* captured during sampling bouts was lower than what is needed to reliably estimate abundance states (Steen et al. 2023). Therefore, we used a standard multiseason occupancy model to estimate the distribution of *R. kezeri* while accounting for incomplete capture (MacKenzie et al., 2002). This model structure allowed plots to be in one of two occupancy states: unoccupied ($m = 0$) and occupied ($m = 1$). Thus, these models estimated ψ and p (Online Resource 1). We used the same covariates and random effects structure on parameters as we used in analyses for *A. truei* and *D. tenebrosus*.

Model selection for all analyses was carried out using indicator variables (Kuo and Mallick, 1998). In particular, we multiplied each model coefficient by a latent, binary variable (including the random effects). We then examined the posterior probabilities of the indicator

variables to evaluate variable importance, where an explanatory variable was considered important if the mean posterior estimate for its indicator variable was greater than the prior probability. We adopted a sequential-by-submodel strategy for our model selection procedure due to the large number of explanatory variables we wanted to consider across the different model parameters. We started by evaluating models for p while holding all other parameters constant (i.e., intercept models). We then carried the p model with the greatest support (i.e., the highest posterior probability) forward to the next step. For *A. truei* and *D. tenebrosus*, we repeated the procedure for δ, then ψ, and then $\psi^{abundant}$. For *R. kezeri*, we only had to repeat the procedure for ψ. We evaluated the support for adjacent and downstream treatment effects on ψ and $\psi^{abundant}$ separately during model selection procedures.

These analyses were completed using a Bayesian framework with JAGS (Plummer 2003), which was called from program *R* (R Development Core Team, 2016) using the *jagsUI* package (Kellner, 2014; Online Resource 1). All continuous variables were standardized to have a mean of zero and standard deviation of one, and they were assessed for collinearity (all pairs had $|r|\langle 0.7$). We used diffuse priors for all model intercepts and coefficients ($normal(\mu = 0, \tau = 0.368)$) as well as the variance for the random effects ($uniform(0, 20)$). The prior for indicator variables was set to 0.5 (i.e., random). Model runs involved three independent chains, each consisting of 50,000 iterations following a burn-in and adaption phase of 50,000 each. We omitted the thinned study reach from our analyses because it was the only one treated by thinning and preliminary analyses indicated it was also the source of convergence issues when including random reach effects in our models. This means we were, unfortunately, unable to evaluate the effects of thinning (TH_Uniform) on amphibians in our study. Altogether, this resulted in convergence for all parameter estimates based on the Brooks and Gelman diagnostic ($\widehat{R} < 1.01$; Brooks and Gelman, 1998) and visual inspection of trace and density plots of the posterior distributions. We described model parameters by their mean, standard deviation, and 95% credible interval (95% CI). We also calculated odds ratios (ORs) for model coefficients (Hosmer and Lemeshow, 2000). We considered a covariate to have a strong effect if the 95% CI did not overlap zero.

3. Results

In 2008–2011 (pre-harvest) and 2013–2016 (post-harvest), we had 3,275 plot-level primary sampling occasions in summer months (May–September). The number of plot-level primary sampling occasions per year was variable, with the lowest number (124) sampled in 2011 and the highest number (785) sampled in 2008. Collectively, there were 1,804 plot-level primary sampling occasions in our pre-harvest data and 1,471 plot-level primary sampling occasions in our post-harvest data. Notably, all post-harvest years were dryer than pre-harvest years and 2015 was classified as a drought. The number of plot-level primary sampling occasions in each of the 13 study reaches used in our analyses ranged from 218 to 278 across the study period. The maximum number of *A. truei* captured in a plot-level primary sampling occasion ranged from 0 to 88 individuals (mean = 2.99, SD = 6.68). The maximum number of *D. tenebrosus* captured in a plot-level primary sampling occasion ranged from 0 to 35 individuals (mean = 3.81, SD = 4.10). The maximum number of *R. kezeri* captured in a plot-level primary sampling occasion ranged from 0 to 18 individuals (mean = 0.51, SD = 1.40). Mean counts per plot-level primary sampling occasion varied across treatments and species (Fig. 1). *Dicamptodon tenebrosus* was relatively common across all study reaches, whereas *R. kezeri* and *A. truei* were rare in some reaches; only 8 total *R. kezeri* were ever found in the Rock Creek 3 upstream section, and only 1 *A. truei* was ever found in the Pothole Creek 3 upstream section and the Pothole Creek 4 reach. As expected, the most supported covariates and their influence on model parameters varied by species (Table 3, 4).

3.1. Habitat associations

Among upstream pre-harvest plots, occupancy probability was, on average, much higher for *D. tenebrosus* (probability = 0.95, 95% CI = 0.87–0.99) than it was for both *A. truei* (probability = 0.28, 95% CI = 0.05–0.69) and *R. kezeri* (probability = 0.38, 95% CI = 0.20–0.60) (Figs. 2–4). Occupancy probability was higher in downstream plots relative to upstream plots for *A. truei* (OR = 11.32, 95% CI = 6.72–20.10) and *D. tenebrosus* (OR = 2.75, 95% CI = 1.54–5.37), but lower for *R. kezeri* (OR = 0.41, 95% CI = 0.31–0.54). Occupancy of all three species was positively related to proportion of cobble and surface area. For *A. truei*, occupancy probability decreased later in the year (OR = 0.65, 95% CI = 0.55–0.76). As the gradient of the plot increased, *A. truei* occupancy decreased (OR = 0.57, 95% CI = 0.48–0.68) while *R. kezeri* occupancy increased (OR = 1.21, 95% CI = 1.06–1.39). The estimated random effects indicate there was greater spatial and temporal variation in occupancy probability for *A. truei* when comparing the estimates among species.

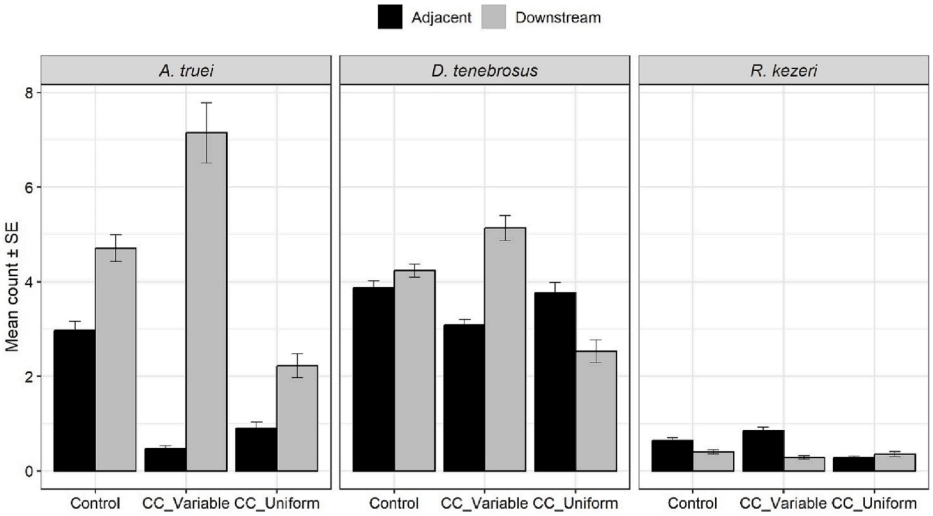

Fig. 1. Unadjusted mean counts across plot-level primary sampling occasions in upstream and downstream plots across treatment categories (i.e., control, adjacent to clearcut with a variable-width buffer [CC_Variable], adjacent to clearcut with a 12-m buffer [CC_Uniform], downstream of a clearcut with a variable-width buffer [CC_Variable], and downstream of a clearcut with a 12-m buffer [CC_Uniform]).

Table 3
Posterior means of the indicator variables for explanatory variables in the global occupancy models to estimate the probability that a plot is occupied (ψ); the probability that a plot is occupied by a large number of larvae (abundant), given that the plot is occupied ($\psi^{abundant}$ for *A. truei* and *D. tenebrosus* only); the probability that the species is detected, given that the plot is occupied (p); and the probability that evidence of the abundant state is collected, given that the plot is in occupancy state 2 and the species was detected (δ for *A. truei* and *D. tenebrosus* only). Values in bold had higher posterior than the prior probability and were used in subsequent analyses.

	A. truei				*D. tenebrosus*				*R. kezeri*	
Variable	p	δ	ψ	$\psi^{abundant}$	p	δ	ψ	$\psi^{abundant}$	p	ψ
Amount of light	**>0.999**	0.306			0.172	0.094			**0.659**	
Day of year	0.053	**0.734**	**>0.999**		**0.810**	**0.575**	0.105		0.074	0.050
Gradient			**>0.999**				0.079			**0.707**
Location			**>0.999**	**0.760**			**0.934**	0.171		**>0.999**
Occupancy state	**0.538**				**0.988**					
Proportion cobble			**>0.999**				**>0.999**			**>0.999**
Surface area	**>0.999**	**>0.999**	**>0.999**		**>0.999**	**>0.999**	**0.751**		**0.888**	**>0.999**
Survey number	0.134	0.107			**0.552**	**0.999**			0.099	
Treatment: adjacent			**>0.999**	0.313			**0.996**	**0.975**		**>0.999**
Treatment: downstream			0.187	**0.703**			**0.872**	0.098		0.155
Random effect: year			**>0.999**	**>0.999**			**>0.999**	**>0.999**		**0.962**
Random effect: reach			**>0.999**	**>0.999**			**>0.999**	**>0.999**		**>0.999**

3.2. Adjacent and downstream effects of harvest

Clearcut logging that included 12-m buffers or smaller variable-width buffers had a negative effect on occupancy in plots adjacent to forest harvest for *D. tenebrosus* (OR for CC_Uniform = 0.20, 95% CI = 0.08–0.44; OR for CC_Variable = 0.22, 95% CI = 0.06–0.65) and *R. kezeri* (OR for CC_Uniform = 0.51, 95% CI = 0.28–0.92; OR for CC_Variable = 0.24, 95% CI = 0.13–0.44). For *A. truei*, occupancy decreased in plots adjacent to clearcuts with variable-width buffers (OR = 0.48, 95% CI = 0.24–0.98), however when the adjacent clearcut had a larger uniform 12-m buffer, occupancy probability increased (OR = 3.55, 95% CI = 1.70–7.51). Upstream harvest had no effect on downstream occupancy for *A. truei* and *R. kezeri*, but for *D. tenebrosus* occupancy decreased downstream from clearcuts with 12-m buffers (OR = 0.22, 95% CI = 0.08–0.57) and increased downstream of clearcuts with smaller variable-width buffers (but this effect was not strong – 95% CI overlapped zero).

The probability that a plot is occupied by a large number of larvae given it is occupied (state 2), was relatively low for *A. truei* (probability = 0.34, 95% CI = 0.10–0.67) and *D. tenebrosus* (probability = 0.31, 95% CI = 0.12–0.55) in upstream plots pre-harvest (Figs. 2, 3). For *A. truei*, this probability was higher in plots downstream (OR = 1.54, 95% CI = 1.07–2.21) and increased in plots downstream of clearcuts with 12-m buffers (OR = 2.90, 95% CI = 1.15–7.62). Although the results indicate this probability for *A. truei* also increased in plots downstream of clearcuts with smaller variable-width buffers, the effect was not strong (95% CI overlapped zero). For *D. tenebrosus*, this probability decreased in plots adjacent to clearcuts with variable-width buffers (OR = 0.38, 95% CI = 0.22–0.68) and larger uniform 12-m buffers (OR = 0.40, 95% CI = 0.17–0.94). There was no detected effect of forest harvest on *D. tenebrosus* abundance in downstream plots. The estimated random effects indicate there was greater spatial and temporal variation in the probability that a plot is occupied by a large number of larvae given it is occupied for *A. truei* than *D. tenebrosus*.

3.3. Imperfect detection

Detection probability was, on average, high across species (probabilities = *A. truei*: 0.69, 95% CI = 0.62–0.75; *D. tenebrosus*: 0.86, 95% CI = 0.84–0.89; *R. kezeri*: 0.70, 95% CI = 0.65–0.75). As expected, the odds of detection were 54.14 (95% CI = 20.32–177.07) times higher for *A. truei* and 18.69 (95% CI = 6.83–66.03) times higher for *D. tenebrosus* when these species were relatively abundant compared to when a plot was occupied but not relatively abundant. The remaining results concerning detection probability varied by species. The probability of detecting *D. tenebrosus* decreased during the second survey visit within a plot-level primary sampling occasion when compared to the first survey visit (OR = 0.59, 95% CI = 0.43–0.78) but increased with increasing day of year (OR = 1.14, 95% CI = 1.00–1.30) and surface area of the plot (OR = 1.84, 95% CI = 1.40–2.35). In contrast, the probability of detecting *R. kezeri* was lower with increasing surface area of the plot (OR = 0.73, 95% CI = 0.61–0.90). Although other variables were included in the selected detection probability models, their effect was not strong because the 95% CIs overlapped zero.

The probability that evidence of the abundant state is collected given that the plot is in state 2 and the species is detected was, on average, also relatively high for *A. truei* (probability = 0.75, 95% CI = 0.70–0.80) and *D. tenebrosus* (probability = 0.59, 95% CI = 0.51–0.68). For *A. truei*, this probability decreased with day of year (OR = 0.72, 95% CI = 0.59–0.89) but increased as the surface area of the plot increased (OR = 1.69, 95% CI = 1.34–2.19). For *D. tenebrosus*, this probability decreased during the second survey visit of a plot-level primary sampling occasion when compared to the first survey visit (OR = 0.41, 95% CI = 0.29–0.59) and also increased as the surface area of the plot increased (OR = 1.64, 95% CI = 1.40–1.94). Although day of year was included in the selected model for *D. tenebrosus*, the effect was not strong because the 95% CI overlapped zero.

4. Discussion

The stream amphibians of the North American Pacific Northwest are globally unique in their combination of ancient lineages, adaptations to cold, cascading headwater streams, and overlap with highly productive coniferous forests that are often heavily managed for timber production. The conservation of these important and sensitive taxa is undoubtedly linked to science-based forest management policies. Our study adds to the understanding of current in-place forest management guidelines, ranging from thinning to clearcuts with uniform and variable-width buffers, on headwater stream amphibians at multiple scales. Overall, we found that clearcut logging with a 12-m buffer or smaller variable-width buffer influenced the distribution and abundance of these species in their larval life stages, that impacts were not always diminished when leaving a larger 12-m buffer, and that some effects were detected downstream of harvest areas.

4.1. Distributions along headwater streams

Occupancy and abundance varied across species based on plot location and forest harvest treatment type. On average, *D. tenebrosus* occupancy probability was much greater compared to the other two

Table 4
Posterior means, standard deviations (in parentheses), and upper and lower limits of the 95% credible interval (CI) for the best-approximating models for the probability that a sample unit is occupied (ψ); the probability that a sample unit is occupied by a large number of larvae (abundant), given that the sample unit is occupied ($\psi^{abundant}$ for *A. truei* and *D. tenebrosus* only); the probability that the species is detected, given that the sample unit is occupied (p); and the probability that evidence of the abundant state is collected, given that the sample unit is in state 2 and the species was detected (δ for *A. truei* and *D. tenebrosus* only).

Parameter	*A. truei*	*D. tenebrosus*	*R. kezeri*
p			
Intercept	0.78 (0.15) CI: 0.49, 1.08	1.86 (0.12) CI: 1.64, 2.12	0.85 (0.12) CI: 0.61, 1.10
Occupancy state: abundant	3.99 (0.55) CI: 3.01, 5.18	2.93 (0.58) CI: 1.92, 4.19	na
Amount of light	−0.21 (0.18) CI: −0.60, 0.12	–	0.00 (0.09) CI: −0.20, 0.17
Survey number: 2nd	–	−0.54 (0.15) CI: −0.84, −0.24	–
Day of year	–	0.13 (0.07) CI: 0.01, 0.27	–
Surface area	0.08 (0.11) CI: −0.14, 0.31	0.61 (0.13) CI: 0.34, 0.85	−0.32 (0.10) CI: −0.50, −0.11
δ			
Intercept	1.12 (0.14) CI: 0.86, 1.40	0.37 (0.18) CI: 0.04, 0.73	na
Survey number: 2nd	–	−0.88 (0.19) CI: −1.25, −0.52	na
Day of year	−0.33 (0.11) CI: −0.53, −0.12	0.17 (0.09) CI: −0.01, 0.35	na
Surface area	0.53 (0.13) CI: 0.29, 0.79	0.50 (0.08) CI: 0.34, 0.66	na
ψ			
Intercept	−1.14 (0.98) CI: −2.93, 0.81	3.20 (0.66) CI: 1.89, 4.51	−0.51 (0.46) CI: −1.39, 0.42
Day of year	−0.43 (0.08) CI: −0.60, −0.27	–	–
Proportion cobble	0.45 (0.09) CI: 0.28, 0.62	0.78 (0.12) CI: 0.55, 1.02	0.52 (0.08) CI: 0.37, 0.67
Surface area	0.54 (0.11) CI: 0.34, 0.75	0.50 (0.22) CI: 0.08, 0.96	0.67 (0.13) CI: 0.43, 0.92
Gradient	−0.56 (0.09) CI: −0.74, −0.39	–	0.19 (0.07) CI: 0.06, 0.33
Location: downstream	2.43 (0.28) CI: 1.91, 3.00	1.01 (0.32) CI: 0.43, 1.68	−0.88 (0.14) CI: −1.16, −0.61
Treatment: adjacent to CC_Uniform	1.27 (0.38) CI: 0.53, 2.02	−1.63 (0.43) CI: −2.5, −0.82	−0.68 (0.31) CI: −1.28, −0.08
Treatment: adjacent to CC_Variable	−0.73 (0.36) CI: −1.44, −0.02	−1.52 (0.60) CI: −2.77, −0.43	−1.42 (0.31) CI: −2.05, −0.81
Treatment: downstream of CC_Uniform	–	−1.51 (0.50) CI: −2.53, −0.57	–
Treatment: downstream of CC_Variable	–	0.67 (1.27) CI: −1.47, 3.43	–
Random effect: reach	4.10 (1.15) CI: 2.53, 6.89	1.98 (0.83) CI: 0.96, 4.10	1.47 (0.37) CI: 0.94, 2.35
Random effect: year	1.16 (0.44) CI: 0.61, 2.28	0.78 (0.38) CI: 0.34, 1.69	0.56 (0.24) CI: 0.25, 1.17
$\psi^{abundant}$			
Intercept	−0.75 (0.74) CI: −2.2, 0.70	−0.87 (0.55) CI: −1.96, 0.22	na
Location: downstream	0.43 (0.18) CI: 0.07, 0.79	–	na
Treatment: adjacent to CC_Uniform	–	−0.90 (0.44) CI: −1.78, −0.06	na
Treatment: adjacent to CC_Variable	–	−0.96 (0.29) CI: −1.54, −0.39	na
Treatment: downstream of CC_Uniform	1.07 (0.48) CI: 0.14, 2.03	–	na
Treatment: downstream of CC_Variable	0.24 (0.57) CI: −0.88, 1.36	–	na
Random effect: reach	2.34 (0.78) CI: 1.30, 4.26	1.77 (0.50) CI: 1.07, 2.97	na
Random effect: year	0.92 (0.36) CI: 0.47, 1.82	0.58 (0.23) CI: 0.27, 1.16	na

species we studied, although baseline *A. truei* and *D. tenebrosus* conditional abundance probabilities were similar. Together, this indicates *D. tenebrosus* was generally more widespread and abundant than *A. truei* within our study reaches. Our raw catch data and estimated random effects showed more heterogeneity for *A. truei* distribution and abundance than for the other two species, which indicates the species is more patchily distributed within our study reaches. *Ascaphus truei* differs from the other species in this study in that larvae are specialized periphyton grazers as opposed to predators, and other work has suggested *A. truei* larvae congregate where food resources are abundant (Dupuis and Steventon, 1999; Hawkins et al., 1988). This same hypothesized mechanism for patterns in *A. truei* distribution might explain why *A. truei* occupancy and conditional abundance probability was higher in downstream plots relative to upstream plots. Hawkins et al. (1988) reported higher densities of *A. truei* larvae in warmer, downstream reaches, and periphyton growth can be positively affected by light exposure (Mallory and Richardson, 2005) which can be linked to canopy closure and stream width (Rutherford et al., 2018). However, in our study reaches periphyton standing stocks/concentrations and stream metabolism were not affected by increased light exposure related to harvest or nutrients, and the community is primarily diatoms, which showed limited response to light (Johnson et al., 2023). Downstream movement bias in *A. truei* has been observed elsewhere and is thought to be driven by a colonization cycle, where upstream dispersal of post-metamorphic stages compensates for downstream drift by larvae (Corn and Bury, 1989; Müller, 1974; Wahbe and Bunnell, 2003). Chelgren and Adams (2017) found the proportion of surviving *A. truei* in our study reaches increased with accelerated downstream movements following harvest, but suggested passive drift of individuals was unlikely to greatly influence downstream biomass because annual survival probabilities were low (0.01–0.12).

Downstream movements have also been observed in *D. tenebrosus*. This species had greater occupancy, but not abundance, in downstream

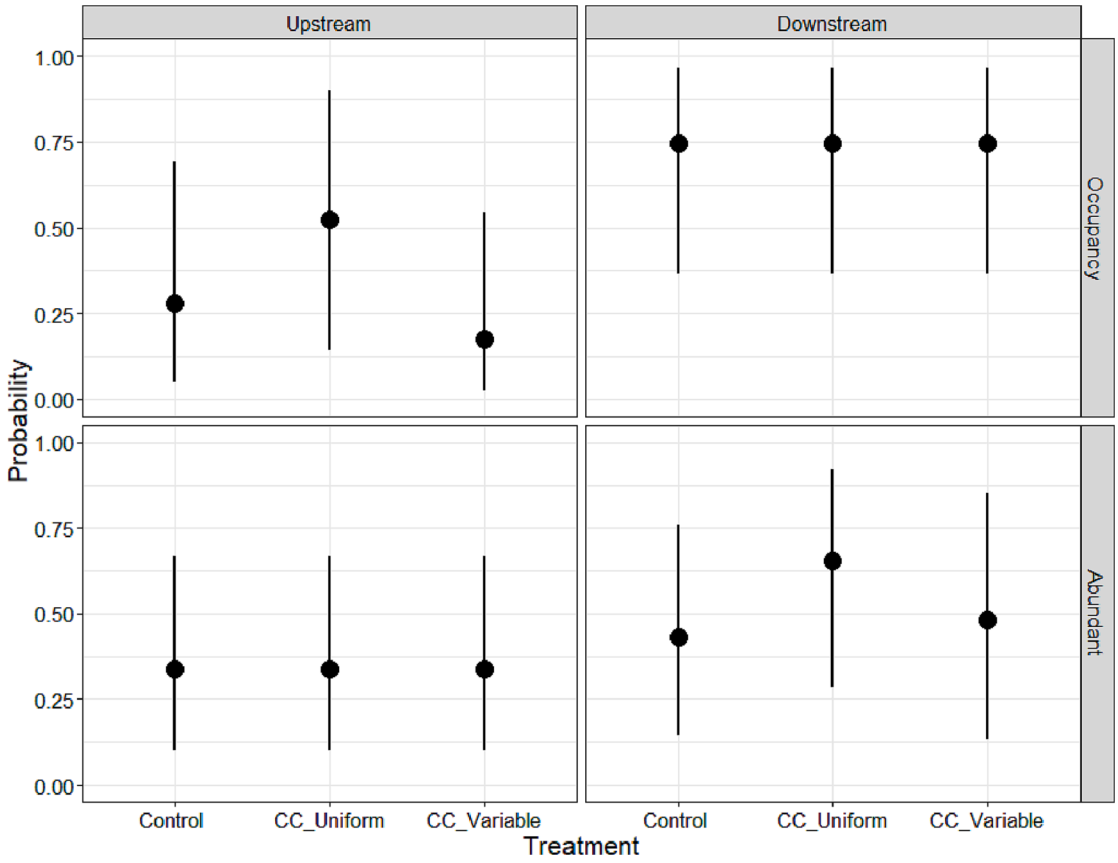

Fig. 2. Posterior means and 95% credible interval (CI) for the on average probability that a plot is occupied (Occupancy, ψ) by *A. truei* and the on average probability that a plot is occupied by a large number of larval *A. truei* given that the sample unit is occupied (Abundant, $\psi^{abundant}$) in upstream and downstream locations across treatment categories (i.e., control, adjacent to clearcut with a variable-width buffer [CC_Variable], adjacent to clearcut with a 12-m buffer [CC_Uniform], downstream of a clearcut with a variable-width buffer [CC_Variable], and downstream of a clearcut with a 12-m buffer [CC_Uniform]).

segments in our study reaches. Chelgren and Adams (2017) found *D. tenebrosus* downstream movements in our study reaches were more likely to be made by young-of-year individuals than older individuals. Lower survival in the smaller size class, observed in other populations (Sagar et al., 2007), could limit downstream abundances. Still, Chelgren and Adams (2017) estimated survival to be similar between the two age classes, albeit with relatively large uncertainty around estimates. Similarly, the tendency for *R. kezeri* to occupy upstream plots could be a function of resource partitioning resulting between this species and *D. tenebrosus*. Indeed, Cudmore and Bury (2014) found high dietary overlap between *R. kezeri* and small, early-stage *D. tenebrosus*, and *R. kezeri* appears unpalatable to *D. tenebrosus* despite the latter achieving much greater body size. Greater upstream occupancy for *R. kezeri* could also be related to the fact that larvae of this species are more likely to originate from natal habitats higher in the headwaters (Russell et al., 2004).

4.2. Adjacent and downstream effects of forest harvest

All species exhibited a decline in occupancy in plots adjacent to clearcuts with smaller variable-width buffers. Retaining a larger uniform 12-m buffer reduced the magnitude of the negative effect on occupancy in adjacent plots for *R. kezeri*. Out of our three species, *R. kezeri* may have the lowest tolerance for harvest-induced changes to physical stream attributes (Bury, 2008; Corn and Bury, 1989). This species requires cool, clear streams or seeps, and stream buffers can help maintain temperatures and prevent sediment or logging debris from entering streams (Jackson et al., 2007; Reiter et al., 2020). Arismendi et al. (2017) found minimal increases in suspended sediment concentrations and turbidity and Johnson et al. (2023) observed no increase in benthic fine sediment in our study reaches following forest harvest. Reiter et al. (2020) found increased stream temperatures where smaller variable-width buffers were retained (the largest increase of 3.6° C), but little-to-no change in stream temperatures where 12-m buffers were retained in our study reaches. Although this leads us to believe changes in stream temperatures associated with forest harvest may be a strong factor in this study, Reiter et al. (2020) never recorded a stream temperature that exceeded critical thermal thresholds for these species. The lack of debris input from harvests and the relatively narrow uniform riparian buffers (12 m) used in our study may in part explain why uniform stream buffers were less effective at maintaining relatively high occupancy compared to another study (46-m buffers) east of the coast range (Wilson et al., 2009). In a review of forest buffer effects on amphibians, Martin et al. (2021) reported widely different effect sizes among studies and the notion of a single best universal buffer width in managed riparian habitats has been disputed (Luke et al., 2019; Graziano et al., 2022).

Occupancy of *A. truei* increased in plots adjacent to clearcuts with 12-m buffers, and there were positive cumulative effects on abundance downstream of this treatment type as well. This pattern might be indicating that clearcuts with uniform 12-m buffers caused *A. truei* to disperse, increasing the proportion of occupied plots upstream and crowding to occur downstream. However, Chelgren and Adams (2017) did not detect an effect of forest harvest intensity on larval *A. truei* downstream movement or survival in our study reaches, and there was no indication larval *A. truei* abundance decreased in upstream plots. Another possible hypothesis is that the positive effects are related to water availability. The volume of water in streams at low flows can

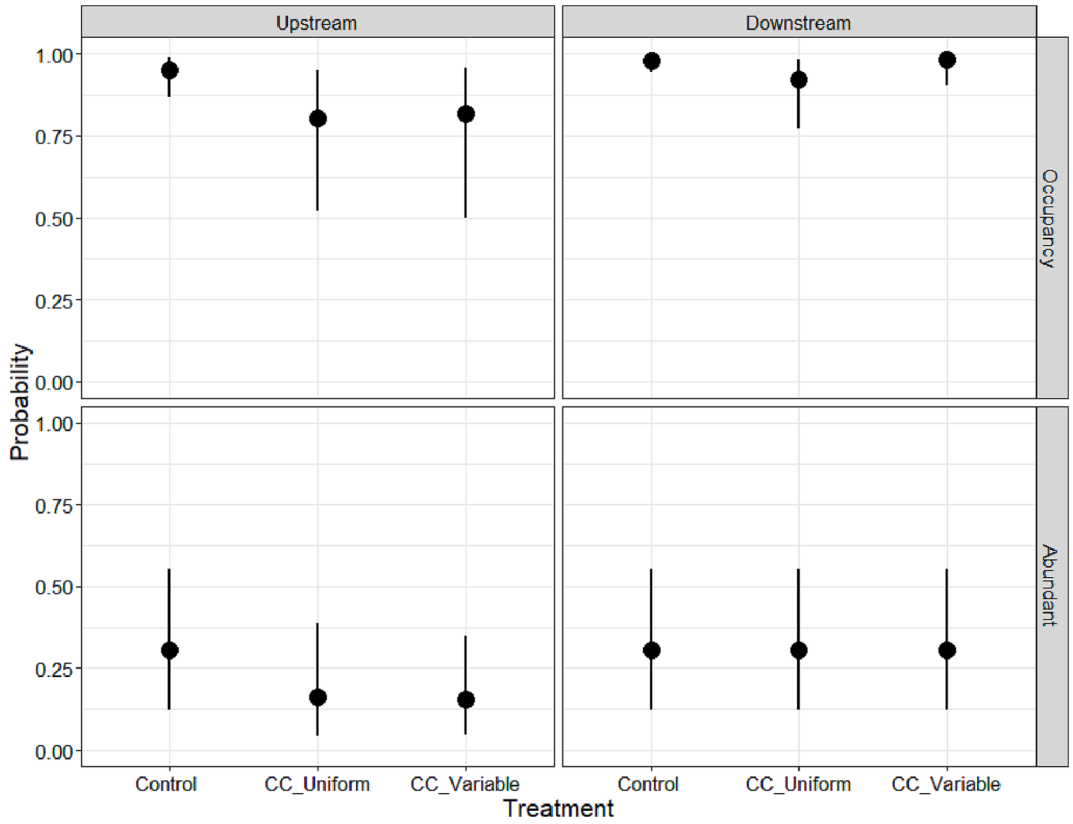

Fig. 3. Posterior means and 95% credible interval (CI) for the on average probability that a plot is occupied (Occupancy, ψ) by *D. tenebrosus* and the on average probability that a plot is occupied by a large number of larval *D. tenebrosus* given that the plot is occupied (Abundant, $\psi^{abundant}$) in upstream and downstream locations across treatment categories (i.e., control, adjacent to clearcut with a variable-width buffer [CC_Variable], adjacent to clearcut with a 12-m buffer [CC_Uniform], downstream of a clearcut with a variable-width buffer [CC_Variable], and downstream of a clearcut with a 12-m buffer [CC_Uniform]).

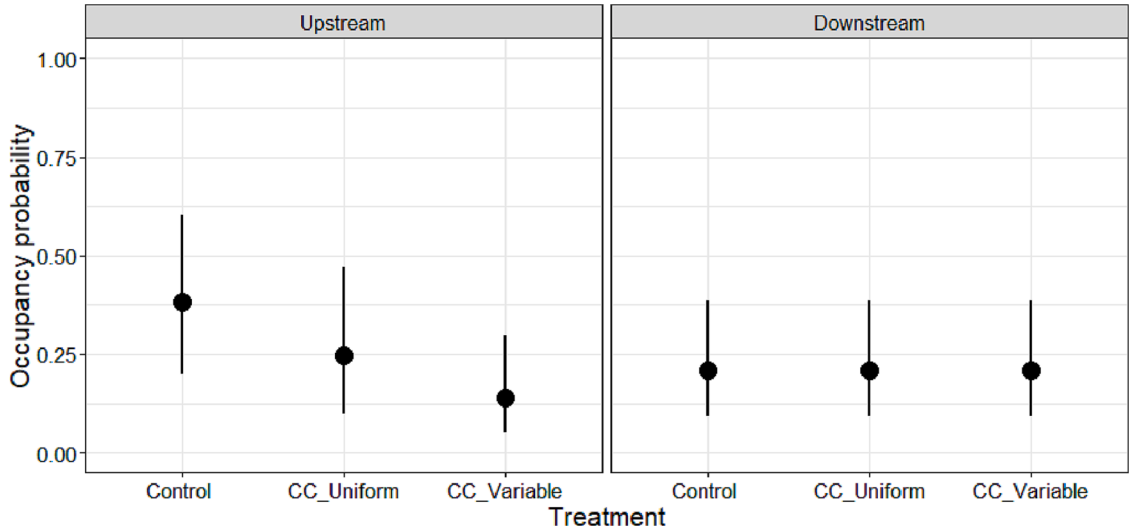

Fig. 4. Posterior means and 95% credible interval (CI) for the on average probability that a plot is occupied (Occupancy, ψ) by *R. kezeri* in upstream and downstream locations across treatment categories (i.e., control, adjacent to clearcut with a variable-width buffer [CC_Variable], adjacent to clearcut with a 12-m buffer [CC_Uniform], downstream of a clearcut with a variable-width buffer [CC_Variable], and downstream of a clearcut with a 12-m buffer [CC_Uniform]).

increase following logging due to reduced evapotranspiration caused by the removal of trees (reviewed in Moore and Wondzell, 2005). This has the potential to benefit headwater stream amphibians that may frequently be stranded in drying reaches, particularly during our summer study window and during periods of drought like we experienced during some of the post-harvest years. However, we did not see the same response in the other two species, which leads us to believe this hypothesis is unlikely to be true. Adult *A. truei* can migrate upstream from oviposition sites to intermittent reaches (Hayes et al., 2006) and the forested buffers along streams can facilitate terrestrial movements (Wahbe et al., 2004). Perhaps quantifying potential negative impacts to larvae on this species in our study was complicated by the life history

strategy of the terrestrial adult life stage, the lifespan of this species, and the length of our study.

Patterns in occupancy and abundance for *D. tenebrosus* following harvest suggest the number of *D. tenebrosus* decreased, rather than a redistribution of individuals within a reach. This was also supported by the decrease in *D. tenebrosus* survival following forest harvest detected in our study reaches (Chelgren and Adams, 2017). Notably, *D. tenebrosus* was also the only species to exhibit a strong negative response to clearcuts with 12-m buffers in downstream plots. A similar negative relationship between *D. tenebrosus* and clearcuts with buffers was observed in the southern Washington Cascade Range by Pollett et al. (2010). This species is more of a habitat generalist, occurring over a broader range of stream orders and substrate types, and has a higher critical thermal maxima ca. 29 °C (when acclimated at 11 °C; Bury, 2008) than the other two species in this study. Although it was somewhat unexpected, the downstream impact of clearcuts with smaller variable-width buffers was more muted than clearcuts with a larger uniform 12-m buffers. Habitat changes associated with clearcutting while leaving smaller variable-width buffers may have positive effects for *D. tenebrosus* (as indicated by the weak positive effect we estimated). For example, this type of harvest treatment could increase stream temperatures and potential metabolic changes leading to faster growth. Another possible explanation was that movements of terrestrial adults were restricted in clearcuts with narrower (or absent) buffers, leading to shorter-distance breeding migrations and greater local concentrations of the species (Johnston and Frid, 2002). Last, most *Dicamptodon* spp. are known to exhibit facultative metamorphosis, meaning it is possible that forest harvest increased the rate of transformation to terrestrial life stages and, by extension, emigration out of our sampling extent.

4.3. Probability of detection when abundant and rare

Our initial intent was to take advantage of the marked individuals in our study to estimate total abundance using the closed population capture–recapture model of Huggins (1989, 1991) within a Bayesian framework. By sharing information across strata (in our case plot-level primary sampling occasions), this approach has been used to increase the precision of estimated parameters (Bowden et al., 2003; Converse et al., 2006) and expand the scope of analysis into strata where data may be sparse (Converse and Royle, 2012; Sollmann et al., 2015; Duarte et al., 2017; Millward et al., 2022). However, the heterogeneity in the individual capture data, along with our use of only one or two sampling passes, led to a lack in convergence across species when using this model structure without the use of heavily informative priors. Another option we considered was to use *N*-mixture models but, due to the sensitivity of such models to assumption violations and unmodeled heterogeneity in count data (Barker et al., 2018; Duarte et al., 2018; Link et al., 2018), we opted to fit occupancy models for the analyses we presented herein. Our use of multistate occupancy models for *A. truei* and *D. tenebrosus* was particularly useful because it allowed us to differentiate plots that were occupied from those that were unoccupied or occupied by large numbers of individuals. In doing so, it also allowed us to account for two types of imperfect detection: not encountering any individuals when the species is present and only encountering few individuals when the species is present in relatively large numbers. This approach has proven useful for other systems and species (MacKenzie et al., 2009; Martin et al., 2010; Peterson and Barajas, 2018; Royle, 2004; Royle and Link, 2005; Whitlock et al., 2020; Wohner et al., 2023), and extensive simulations demonstrate this model structure can provide unbiased estimates of relative abundance when using count/capture data (Steen et al., 2023). However, to our knowledge this is the first application of this model parameterization within the context of measuring the response of fauna to forest management. We opted to fit standard two-state occupancy models for *R. kezeri* because of the relatively low capture rates. We suspect these low capture rates are likely due to our sampling scheme, which largely focused on sampling the main channel instead of the seeps near the stream bank that this species tends to use. Overall, we found our ability to detect each species and detect large numbers of individuals when present was imperfect and related to the environmental conditions during sampling despite having exhaustive and consistent sampling protocols in relatively small sample units. Thus, our results confirm that estimators that account for the sampling process are needed to reliably interpret patterns in monitoring data when evaluating management effects on headwater stream amphibians.

4.4. Habitat associations

Patterns in occupancy in relation to habitat conditions were consistent with habitat associations observed elsewhere. The positive relationship between occupancy probability and coarse substrates across species generally supports the findings of other studies (Diller and Wallace, 1999; Wilkins and Peterson, 2000; Adams and Bury, 2002; Wahbe and Bunnell, 2003; Leuthold et al., 2012). However, Adams and Bury (2002) found *D. tenebrosus* can occur in a broader array of substrate conditions and our findings indicate this species had the strongest positive association with coarse substrates. Although we observed negative associations with stream gradient for *A. truei*, there was support for a positive relationship with gradient for *R. kezeri*. This positive relationship is consistent with patterns of occurrence of its congener, *R. variegatus* (Diller and Wallace, 1996). Finally, we found a strong positive relationship between the surface area of the plot and occupancy across species. This pattern is unsurprising and is likely related to the species-area relationship (e.g., Connor and McCoy, 1979).

5. Conclusions

Using catch data from a temporally and spatially rich BACI sampling design, we provided a nuanced picture of adjacent and downstream effects of forest harvest on three headwater stream amphibians that are endemic to the North American Pacific Northwest. Although we found the direction and magnitude of the response varied by species, our study confirms that clearcut logging in riparian habitats can have negative impacts to amphibians that inhabit the adjacent stream areas. Perhaps more importantly, we also found that this forest management practice can have negative effects on stream amphibians downstream of the harvested area and that the use of a larger 12-m buffer did not necessarily diminish impacts on stream amphibians in adjacent and downstream areas. To our knowledge, no other studies have considered downstream effects of forest harvest on headwater stream amphibian occupancy and abundance. Our findings demonstrate that forest management practices should consider downstream effects when assessing the potential impact of harvesting trees near headwater streams on aquatic taxa. Furthermore, the detection of downstream effects on occupancy and abundance of these species following forest harvest raises the possibility of cumulative effects. Thus, studies that further investigate the population consequences of downstream effects of forest harvest on headwater stream amphibians over a longer timespan are a fruitful area of further research.

CRediT authorship contribution statement

Adam Duarte: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft. **Nathan D. Chelgren:** Conceptualization, Data curation, Investigation, Methodology, Writing – original draft. **Jennifer C. Rowe:** Data curation, Visualization, Writing – original draft. **Christopher A. Pearl:** Writing – review & editing. **Sherri L. Johnson:** Conceptualization, Funding acquisition, Project administration, Supervision, Writing – review & editing. **Michael J. Adams:** Conceptualization, Funding acquisition, Investigation, Methodology, Supervision, Project administration, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available through a ScienceBase data release: https://doi.org/10.5066/P9QGQRB7.

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