RESEARCH LETTER

The endemic headwater stream amphibians of the American Northwest: associations with environmental gradients in a large forested preserve

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ABSTRACT

We used a large forested preserve (Olympic National Park, USA) to examine the habitat associations of a unique and environmentally sensitive stream amphibian fauna: *Ascaphus truei* Stegneger, *Rhyacotriton olympicus* (Gaige) and *Dicamptodon copei* Nussbaum. We quantified the relative abundance of stream amphibians and compared them to physical, topographic, climatic and landscape variables. All three species were associated with the south-west to north-east climate gradient, tending to be most abundant in the south-west. Although a habitat generalist relative to the other two species, *Dicamptodon copei* was absent from the north-eastern portion of the park. *Ascaphus truei* and *Rhyacotriton olympicus* were both associated with coarse substrates and steep gradients. Unlike studies in harvested forests, all stream amphibians were common in waters with unconsolidated surface geology (e.g. marine sediments that erode easily). Studies of ecological preserves can provide an important baseline for evaluating species associations with environmental gradients and can reveal patterns not evident in more disturbed landscapes.

Key words *Ascaphus truei*, *Dicamptodon copei*, environmental gradients, geology, headwater streams, North America, Olympic National Park, preserves, *Rhyacotriton olympicus*, substrate.

INTRODUCTION

The forests of the Pacific Northwest host a unique and environmentally sensitive stream-amphibian fauna (Nussbaum *et al.*, 1983; Bury, 1994). This endemic fauna includes *Ascaphus truei* Stejneger (tailed frog), which is the sole member of the family Ascaphidae and considered the most primitive extant anuran in the world (Ford & Cannatella, 1993), and the salamander families Dicamptodontidae and Rhyacotritonidae. Several workers have described habitat associations for these species but have based their work predominately (Dupuis *et al.*, 2000) or entirely (Diller & Wallace, 1996, 1999; Wilkins & Peterson, 2000) in harvested forests. Few studies have examined patterns in unharvested forests and these have focused on the role of stand age (Welsh, 1990; Bury *et al.*, 1991). Here, we describe habitat associations for stream amphibians in the relatively pristine forests of Olympic National Park (ONP).

ONP provides an opportunity for the study of ecological patterns along pronounced environmental gradients. It is situated on the Olympic Peninsula in Washington State, USA, and is surrounded by the Pacific Ocean to the west, the Straight of Juan de Fuca to the north and Hood Canal and Puget Sound to the east (Fig. 1). ONP is 370 000 ha and contains the bulk of the Olympic Mountains, which are isolated by water and low elevation areas from other ranges such as the Cascade Mountains (*c.* 80 km east) and the Willipa Hills (*c.* 60 km south). The Olympic Mountains rise to 2400 m and produce a pronounced rain shadow: average annual precipitation ranges from 6000 mm on the south-west side to 450 mm on the north-east side. The relative isolation and marked environmental gradients of ONP are ideal for describing environmental limits and associations. Moreover, almost no logging has ever occurred inside the park's boundaries, offering a marked contrast with the intensively harvested forests of much of the Pacific Northwest.

Three species of stream-breeding amphibian occur in ONP: *Ascaphus truei*, *Rhyacotriton olympicus* (Gaige) (Olympic torrent salamander) and *Dicamptodon copei* Nussbaum (Cope's giant salamander). All require permanent water for their

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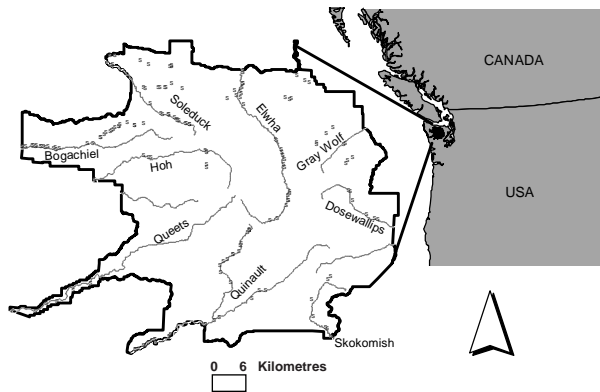
Fig. I Stream survey sites (*N* = 141) in Olympic National Park.

multi-year larval stages (Nussbaum & Tait, 1977; Bury & Adams, 1999). *D. copei* is almost obligately paedomorphic, and so may be especially reliant on permanent waters for survival (Nussbaum *et al.*, 1983). Ascaphidae and Rhyacotritonidae are two of the coldest adapted amphibians in the world (Brattstrom, 1963; de Vlaming & Bury, 1970). *A. truei*, *R. variegatus* Stebbins and Lowe and *D. tenebrosus* Good have each been shown to have positive associations with coarse cobble and boulder substrates (Corn & Bury, 1989; Diller & Wallace, 1996, 1999). All decreased in abundance with the input of fine sediments (Hawkins *et al.*, 1988; Welsh & Ollivier, 1998). The density of *D. tenebrosus* increased with the experimental input of large stones (Parker, 1991). Because of their association with coarse substrates and cold water temperatures, these species may be sensitive to timber harvest (Corn & Bury, 1989; Welsh, 1990; Dupuis & Steventon, 1999), although they persist in many managed forests (Diller & Wallace, 1996, 1999; Wilkins & Peterson, 2000).

Here, we report results of a 3-year survey that determined the distribution and abundance of stream-breeding amphibians across environmental gradients in ONP. We examined in-stream habitat features, topographical features and climate gradients that might be affected by global change or timber harvest. We contrast our findings with those of studies in other parts of this region where intensive timber harvest occurs.

METHODS

We surveyed 141 headwater streams in 12 of 13 major drainages in ONP (Fig. 1). Each stream was sampled once during the summer months (June–August), 1996–98. Because off-trail access to ONP is difficult, we used trails and a few roads as a network of nonrandom transects covering the park. The population of streams from which study sites were chosen was determined by hiking the roads and trails in late summer or fall and recording the location of streams that still had water flowing. Many of these streams did not appear on maps. We

then selected randomly one-third to one-half of the streams within each drainage that were crossed by main trails and roads. The proportion varied due to changes in logistical constraints. We only chose from streams that appeared permanent. We did not survey large streams (average depths > 30 cm) because our survey technique was less effective in larger waters and our subject species occur predominantly in headwater habitats (Nussbaum *et al.*, 1983). In a few cases, adverse weather and access problems precluded surveys of some selected streams, and part of one watershed (upper Queets River). The streams we surveyed were generally ≥ 50 m apart and we considered all to be independent. Because our sampling frame included only areas adjacent to trails and roads, we cannot provide broad inference to the entire park. Rather, our conclusions are limited to the stream reaches directly above trails. Because tadpoles and metamorphic frogs are present during the entire season (summer) in which we sampled, we did not attempt to correct for any seasonal changes in abundance.

A crew of two or four people visited randomly chosen streams and established a starting point for the survey 30 m upstream of the trail. Then they chose randomly 10 1-m long segments out of the next 100 metres of stream. Each segment spanned the entire wetted width of the stream. If dangerous conditions prevented sampling of a randomly chosen segment, the beginning of this segment was moved to the closest safe position. The crew searched for amphibians in each segment by overturning rocks and debris directly upstream from a dip net that was held against the substrate. Amphibians disturbed during the search were then swept into the dip net by the current or were hand-captured (Bury & Corn, 1991). All animals were released at point of capture.

Environmental variables

In addition to the relative abundance of amphibians, we also measured habitat characteristics (Table 1). We recorded gradient at three points within each 100-m survey. We also recorded aspect and elevation at the start of the survey. We recorded the following variables at each segment: (1) stream width; (2) depth; (3) dominant and subdominant substrate types; and (4) four variables indicating the percent of the segment covered by coarse woody debris, organic debris other than coarse wood, undercut bank and overhanging vegetative structure.

We used a geographical information system (Arcview 3.2) to obtain two additional variables: surface geology (from a 1 : 125000 USGS geological map that was digitized by the Olympic National Forest) and primary vegetation (from an image-based vegetation classification by Pacific Meridian Resources). Surface geology was placed into two categories: consolidated (basalt) and unconsolidated (mainly marine sediment origin). Vegetation was placed into six categories:

Table 1 Habitat variables from stream amphibian surveys in Olympic National Park

Name	Description
Elevation (Elev)	From USGS 1 : 62500 maps. Range = 15–1350 m.
Width	Averaged over all segments surveyed in each stream. Range = 55–530 cm.
Gradient (Grad)	Measured the 25, 50 and 75 m points within each 100 m reach, then averaged.
	Gradient was measured between the tops of two stakes of equal height using a clinometer.
	The stakes were placed in the lowest point in the channel, 5-m apart. Range = 2–70%.
Depth	Measured at three equidistant points spanning the width of the stream at each segment,
	then averaged. Range = 1–35 cm.
Coarse Wood (CW)	The percentage of each segment covered by wood with > 10 cm diameter.
	Visually estimated for each segment, then averaged. Range = 0–45%.
Organic Debris (OD)	The percentage of each segment covered by organic debris other than coarse wood.
	Visually estimated for each segment, then averaged. Range = 0–70%.
Undercut Bank (UB)	The percentage of each segment covered by an undercut bank.
	Visually estimated for each segment, then averaged. Range = 0–60%.
Canopy	The percentage of each segment covered by overhanging vegetation.
	Visually estimated for each segment, then averaged. Range = 0–100%.
Substrate	Following the Cummins (1962) modification of the Wentworth scale (Wentworth, 1922),
	11 categories for inorganic substrates from silt/sand to boulder that correspond to particle size.
	We used five additional categories for wood, bark, soil, vegetation and leaf litter.
	Dominant and subdominant categories were recorded for each segment.
Aspect	Deviation from a north aspect. Range = 0–180°.

cedar (*Thuja plicata* Donn. or *Chamaecyparis nootkatensis* (D. Don)), deciduous, Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco), western hemlock (*Tsuga heterophylla* (Raf.)), unforested and other (mixed forest or rare categories).

Statistical analysis

These surveys produced nine continuous stream variables plus substrate (Table 1). The 16 substrate categories were made into 32 separate variables by counting the number of segments in each stream where each category was dominant and subdominant. These were standardized and then reduced using a principal components analysis. We used equamax rotation and maximized the variance explained by the first three factors (λ = 3.4, 2.7, and 3.0). The first factor represented a gradient from large cobbles and boulders (negative) to silt, sand and soil (positive). Silt loaded the most strongly (0.71), followed by fine sand (0.70), coarse sand (0.61) and large cobble (−0.42). This factor (hereafter 'substrate') represented 11.0% of the total variance in the 32 substrate variables. The other factors were difficult to interpret and were not used in subsequent analysis. Thus, 10 stream variables were available for analysis. After inspecting the correlations among these variables, we elected to eliminate depth, organic debris and undercut bank from subsequent analysis due to high correlation with other variables (e.g. width and substrate).

We explored the relationship of density (number captured/ m²) of each species of stream amphibian to the remaining seven continuous stream variables using generalized linear modelling techniques. For each species, we determined the most parsimonious model describing its relationship to the stream variables, treating each variable separately. Stream amphibian density was treated as a Poisson random variable because zeros and low values were numerous while larger values were increasingly rare. A log link (log transformation) made the models linear. After plotting the relationship between a species of amphibian and a stream characteristic, we explored the relationship by modelling the first and second order quadratic terms. If the second order term was not significant it was removed and only the log-linear relationship was modelled. If it was significant, both terms were left in whether the first was significant or not. Higher order quadratics were then tested until an insignificant term was encountered. If neither the first nor second order terms were significant, we reported the model with the lowest overall *P*-value (sometimes this meant leaving the second-order term in the model). We also used log-linear models with Poisson error to model amphibian associations with two additional variables: vegetation (six categories) and surface geology (two categories).

We used an *F*-test, rather than chi-square, to compensate for over- or underdispersion (Crawley, 1993). Terms were considered significant at α = 0.05. Our approach lacked strict adherence to significance tests and, rather, sought the most parsimonious models to describe relationships. Because predation by *D. copei* could have a negative effect on other species, we also tested whether *A. truei* or *R. olympicus* density had a negative association with *D. copei* density using the same form of model.

To determine the association between stream amphibian distributions and climate gradients, we used climate predictions from PRISM climate models. PRISM generates gridded estimates of climate parameters based on point data and a digital elevation model (Daly *et al.*, 1994). It is designed to account for the effect that mountainous terrain has on climate. We used the average density of amphibians for each PRISM grid cell (2×2 km) as the response variable for each species of stream amphibian. The climate variables we analysed were the means of annual precipitation, annual temperature and growing season length. These climate predictions were based on data collected from 1961 to 1990. Similar to the other analyses, we used a log-linear model with Poisson error for the analysis, but weighted each grid cell by the number of streams surveyed. We used stepwise forward selection to determine the best model and included interactions and quadratic terms until no more significant factors could be found.

Because *D. copei* was not detected in PRISM grid cells from five drainages on the north-east side of the park in historic records (McAllister, 1995) or in our surveys, we hypothesized that its absence from this region was due to climate. This hypothesis predicts that *D. copei*'s relationship to climate is the same with or without the data from the north-east side of the park. In other words, we hypothesized no significant difference in the form of the models derived with (hereafter 'ALLDATA') and without (hereafter 'SUBSET') the zeros from the five drainages where *D. copei* was absent. To test this hypothesis, we fit the significant climate variables from ALLDATA into SUBSET. We then compared the parameter coefficients using *t*-tests.

RESULTS

All three species had large differences in abundance among drainages (Table 2). *D. copei* was not detected in any of the five north-east drainages. *R. olympicus* was rare in the north-east and was not detected in the Gray Wolf Basin. *A. truei* had the broadest distribution and was detected in all drainages surveyed.

Our analysis suggested that multiple topographical variables were associated with stream amphibian density but only elevation appeared important for all three species (Table 3). *A. truei* had the weakest association with elevation and we did not detect an upper limit (Fig. 2). Both *R. olympicus* and *D. copei* densities had quadratic associations with elevation and both were absent at higher elevations (Fig. 2). *D. copei* was the only species that had a strong association with stream width; decreasing in density as width increased. *R. olympicus* exhibited a similar but nonsignificant trend. Both *R. olympicus* and *A. truei* peaked in density at moderate stream gradients and second order quadratic terms suggested they increase in abundance again at steep gradients (> 50%; Fig. 2). *A. truei* and *R. olympicus* were more abundant in streams with northern aspects while *D. copei* showed no association with aspect.

Stream amphibians were also associated with physical stream variables (Table 3). *A. truei* and *R. olympicus* had strong

Table 2 The mean and standard deviation (SD) of captures per m^2 for stream amphibian surveys in Olympic National Park, 1996−98. N = number of streams sampled. Only larvae and paedomorphs are included. Drainages are listed in order going counter-clockwise from the north-west corner around Olympic National Park

Drainage	N	*Ascaphus truei* Stegneger		*Rhyacotriton olympicus* (Gaige)		*Dicamptodon copei* Nussbaum	
		mean	SD	mean	SD	mean	SD
North Fork Soleduck	8	0.522	1.279	0.147	0.368	0.401	0.669
Soleduck	13	0.049	0.158	0.106	0.449	0.106	0.360
Bogachiel	26	0.289	0.811	0.390	0.917	0.208	0.539
Hoh	6	0.204	0.741	0.041	0.196	0.013	0.072
Queets	5	0.012	0.070	0.207	0.565	0.159	0.446
Lake Quinault	11	0.049	0.168	0.010	0.062	0.063	0.202
North Fork Quinault	12	0.229	0.673	0.204	0.514	0.277	0.668
East Fork Quinault	6	0.091	0.306	0.241	0.388	0.161	0.568
Skokomish	4	0.205	0.672	0.157	0.417	0.147	0.438
Dosewallips	5	0.379	0.704	0.015	0.113	0.000	0.000
Gray Wolf	8	0.897	1.383	0.000	0.000	0.000	0.000
Morse	5	1.341	2.104	0.070	0.206	0.000	0.000
Elwha	27	0.403	0.835	0.352	0.658	0.000	0.000
Lyre	5	2.568	3.167	0.376	1.011	0.000	0.000
All drainages combined	141	0.390	1.089	0.200	0.583	0.110	0.402

Table 3 The most parsimonious models relating stream variables to the density of stream amphibians (captures/m^2) in Olympic National Park. See Table 1 for definition of variables. Models are log-linear with Poisson error

Variable	Model	d.f.	Deviance explained	P
Rhyacotriton olympicus (Gaige) (total deviance/d.f. = 89.269/140)				
Elevation (m)	$\exp(-2.349) \times \exp(0.007X) \times \exp(-8 \times 10^{-6}X^2)$	2, 138	14.212	< 0.001
Width (cm)	$\exp(-0.804) \times \exp(-0.002X)$	1, 139	1.555	0.119
Gradient (%)	$\exp(-6.043) \times \exp(0.3978X)$ $\times \exp(-0.009503X^2) \times \exp(7.242 \times 10^{-5}X^3)$	3, 137	25.58	< 0.001
Aspect	$\exp(-0.369) \times \exp(-0.010X)$	1, 139	13.68	< 0.001
CW[1]	$\exp(-2.169) \times \exp(0.1536X) \times \exp(0.003828X^2)$	2, 136	7.614	< 0.001
Canopy cover (%)	$\exp(-1.559) \times \exp(0.007X)$	1, 139	1.295	0.155
Substrate	$\exp(-1.455) \times \exp(-1.373X) \times \exp(-0.698X^2)$	2, 138	14.305	< 0.001
Ascaphus truei Stegneger (total deviance/d.f. = 130.66/140)				
Elevation (m)	$\exp(-1.734) \times \exp(0.003X) \times \exp(-2 \times 10^{-6}X^2)$	2, 138	8.847	0.007
Width (cm)	$\exp(-1.854) \times \exp(0.009X) \times \exp(-2 \times 10^{-5}X^2)$	2, 138	2.459	0.270
Gradient (%)	$\exp(-2.967) \times \exp(0.2519X)$ $\times \exp(-0.007657X^2) \times \exp(0.0000661X^3)$	3, 137	12.012	0.004
Aspect	$\exp(-0.073) \times \exp(-0.009X)$	1, 139	15.520	< 0.001
CW	$\exp(-1.051) \times \exp(0.083X) \times \exp(-0.004X^2)$	2, 138	4.827	0.074
Canopy cover (%)	$\exp(-2.104) \times \exp(0.054X) \times \exp(-0.0005X^2)$	2, 138	6.397	0.031
Substrate	$\exp(-1.3) \times \exp(-2.339X) \times \exp(-1.468X^2)$	2, 138	26.922	< 0.001
Dicamptodon copei Nussbaum (total deviance/d.f. = 44.994/140)				
Elevation (m)	$\exp(-3.366) \times \exp(0.007X) \times \exp(-7 \times 10^{-6}X^2)$	2, 138	5.548	0.001
Width (cm)	$\exp(-1.308) \times \exp(-0.004X)$	1, 139	2.371	0.006
Gradient (%)	$\exp(-2.792) \times \exp(0.064X) \times \exp(-0.001X^2)$	1, 138	1.313	0.130
Aspect	$\exp(-2.492) \times \exp(0.0035X)$	1, 139	0.596	0.174
CW	$\exp(-2.512) \times \exp(0.168X) \times \exp(-0.010X^2)$	1, 138	3.061	0.008
Canopy cover (%)	$\exp(-1.653) \times \exp(-0.010X)$	1, 139	1.303	0.044
Substrate	$\exp(-1.998) \times \exp(0.4797X) \times \exp(-0.1599X^2)$	1, 138	1.074	0.189

[1] Two data points were excluded due to high Cook's distance. Total deviance/d.f. = 83.711/138.

positive associations with cobble substrates. Substrate was the best predictor of density for both species. *A. truei* and *D. copei* had predicted peaks in density with 10% of the substrate covered by coarse woody debris. *R. olympicus* increased in density with increasing coarse woody debris but this pattern was highly influenced by two outlier streams (both had relatively high Cook's distance values). When these two points were removed, fitted *R. olympicus* density peaked at 20% substrate cover by coarse woody debris (Fig. 3). All three species differed in their relationship to canopy cover: *R. olympicus* was not associated with canopy, *A. truei* peaked at 50% cover and *D. copei* decreased with increasing cover. The density of *A. truei* was unrelated to the density of *D. copei* ($F_{1,139} = 0.839$, $P = 0.361$). *R. olympicus* was positively associated with the density of *D. copei* ($F_{1,139} = 5.608$, $P = 0.019$).

Only nine ONP streams (6.4%) were in areas with consolidated surface geology; the remainder were on unconsolidated substrates (Table 4). All three species differed in their relationship to surface geology. *A. truei* was more abundant in consolidated than in unconsolidated rock types ($F_{1,162} = 20.99$, $P < 0.001$). *D. copei* was detected only in unconsolidated rock types. Density did not differ between geological types for *R. olympicus* ($F_{1,162} = 0.094$, $P = 0.760$).

A. truei was the species with the strongest association with forest type ($F_{5,158} = 5.022$, $P < 0.001$) and was most abundant in Douglas fir forests (*P. menziesii*). They were also relatively abundant in western hemlock (*T. heterophylla*) and unforested areas. *R. olympicus* density showed little variation among forest types ($F_{5,158} = 2.169$, $P = 0.060$) but appeared least abundant in unforested and 'other' areas. *D. copei* was the only species to show a strong association with cedar (*T. plicata* and *C. nootkatensis*; $F_{5,158} = 3.677$, $P = 0.004$).

Average *A. truei* density increased as temperature and precipitation decreased (Table 5). *R. olympicus* and *D. copei* both had quadratic associations with growing-season length. Their predicted density peaked in PRISM grid cells with an average growing season of 170 days. *D. copei* was also more abundant in cells with higher precipitation. Precipitation was not
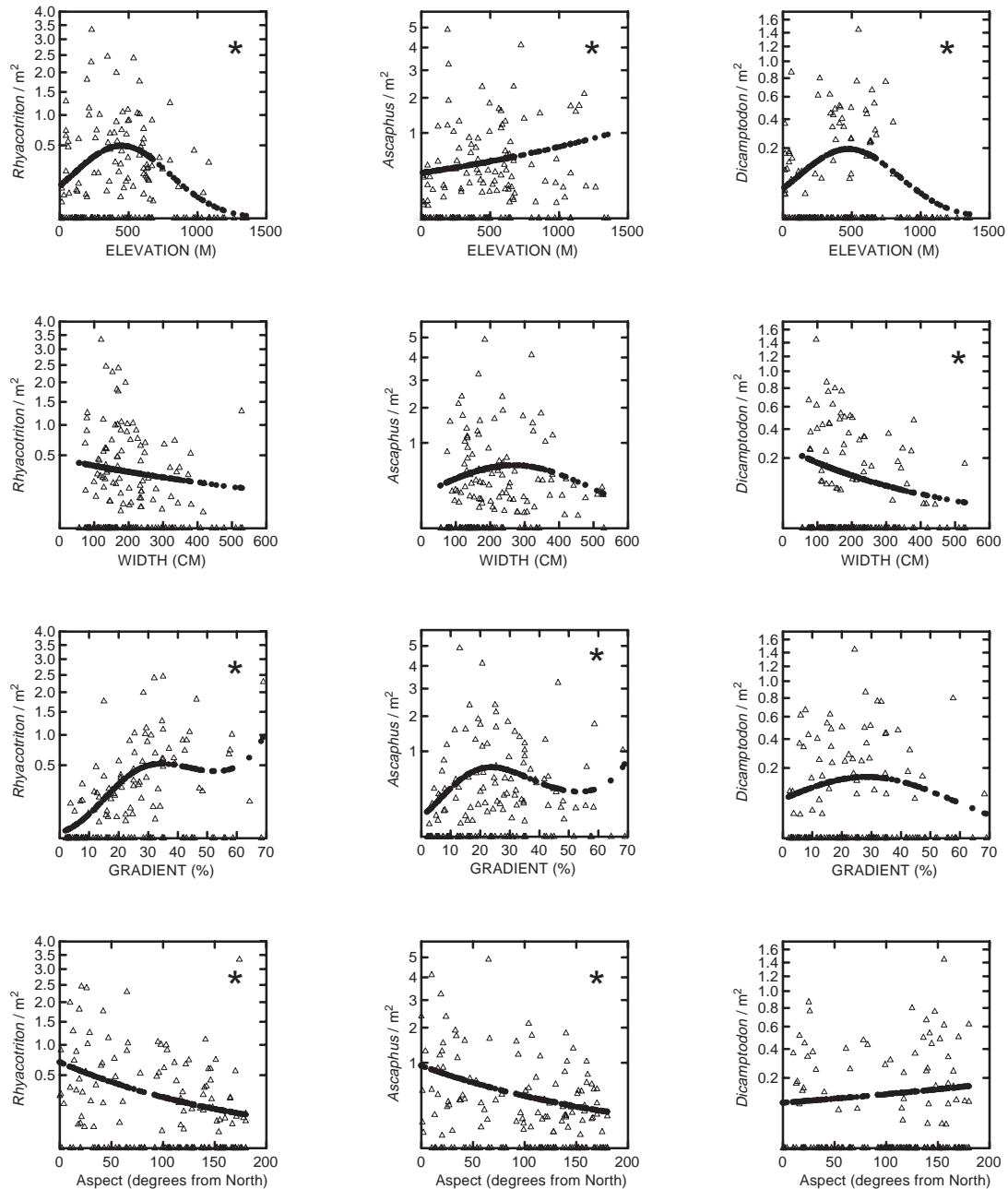
Fig. 2 Association of stream amphibians with topographic variables in Olympic National Park. Triangles are observed densities. Black dots are densities predicted by the most parsimonious model. An asterisk indicates $P < 0.05$ for the model.

significant in SUBSET, but the relationship between *D. copei* abundance and precipitation was not significantly different from that derived with ALLDATA ($t_{93} = 0.227$, $P = 0.821$; Table 5). The change in the coefficient for growing season length also was not significant ($t_{93} = 0.115$, $P = 0.909$). The coefficient of (growing)^2 did not change.

DISCUSSION

Because of the size and undisturbed nature of Olympic National Park, we were able to contrast the environmental associations of the three stream-breeding amphibians without the complication of impacts from timber harvest. Also, our analysis
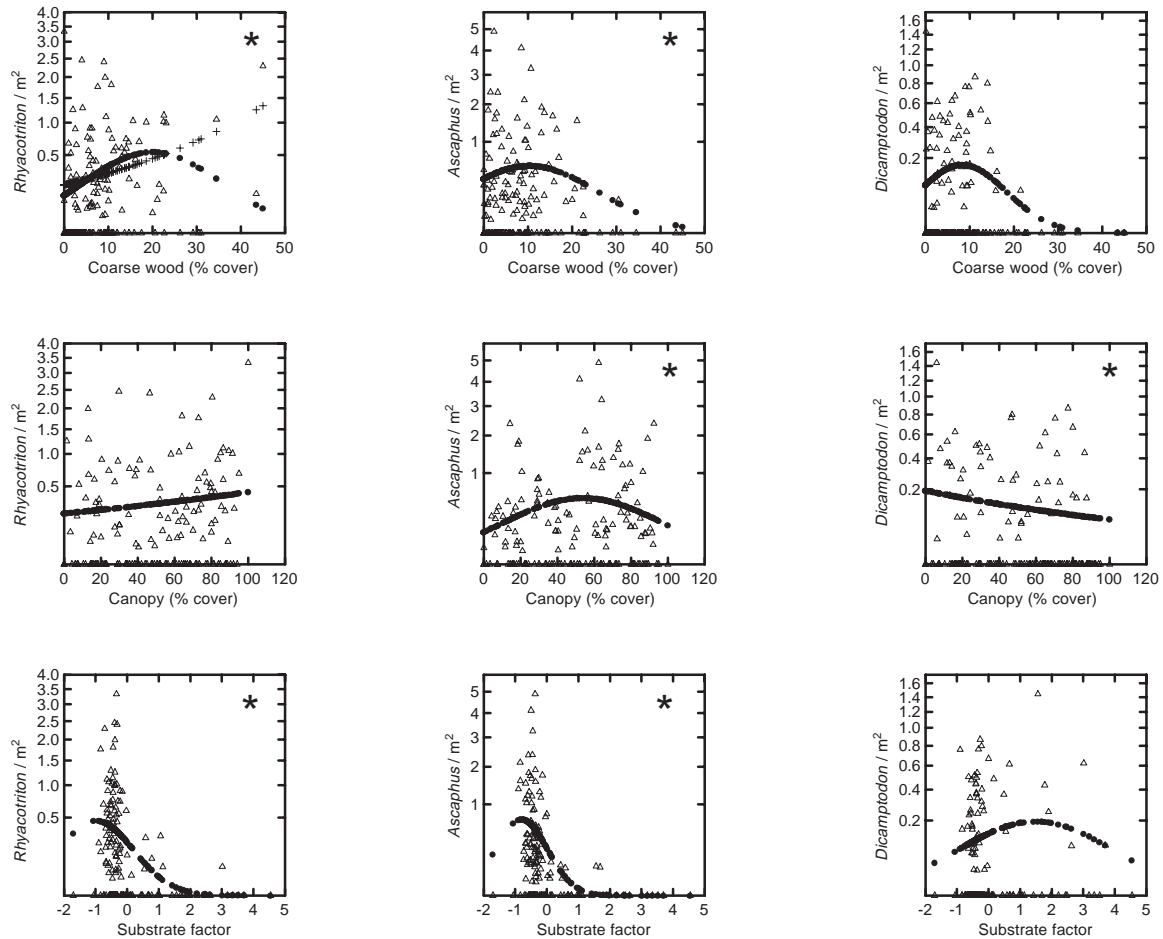
Fig. 3 Association of stream amphibians with physical variables in Olympic National Park. Triangles are observed densities. Black dots are densities predicted by the most parsimonious model. Plus signs indicate the most parsimonious model prior to removing outliers. An asterisk indicates that model $P < 0.05$.

revealed interspecific differences not evident in single species analyses. In general, we found patterns similar to those described in harvested forests, but some differences indicate a need for caution in implementing conservation recommendations based solely on studies in harvested forests. The strong association of *A. truei* and *R. olympicus* with coarse substrates and steep gradients is clearly established in other studies and was equally evident in our results. Cobble substrates provide smooth surfaces for *A. truei*'s suctorial tadpoles to cling to and feed on (Gradwell, 1971). They also provide interstices for cover (Feminella & Hawkins, 1994). Steep gradients help keep the interstices clear of fine sediment (Corn & Bury, 1989).

The association of *A. truei* with consolidated surface geology is consistent with their association with cobble substrates as consolidated rock tends to produce coarse substrates better than unconsolidated rock [our substrate score averaged 0.6

units smaller in consolidated than in unconsolidated substrates (95% CI = 0.1–1.1 units); a smaller score indicates coarser substrates, see Fig. 3]. Several other studies have documented a similar relationship for *A. truei* (Diller & Wallace, 1999; Dupuis *et al.*, 2000; Wilkins & Peterson, 2000), *D. copei* and *D. tenebrosus* (Wilkins & Peterson, 2000), *R. variegatus* (Diller & Wallace, 1996) and *R. kezeri* Good and Wake (Wilkins & Peterson, 2000). However, all studies in harvested forests tended to show a stronger association between stream amphibians and surface geology than found herein (Table 4). For example, Wilkins & Peterson (2000) never found *A. truei* in areas with unconsolidated surface geology in the coast range just south of the Olympic Peninsula. We found *A. truei* in 56% of such streams (*N* = 154). Also, while Diller & Wallace (1996) found that *R. variegatus* was associated with surface geology, we found no such pattern for *R. olympicus*, nor did Wilkins & Peterson (2000) for *R. kezeri*.

Table 4 Comparison of the proportion of streams occupied by *Ascaphus truei* Stegneger in two categories of surface geology among our and two other studies. Olympic National Park samples ranged from 15 to 1350 m elevation and stands were naturally regenerated. Willapa Hills samples were 76–463 m and in second growth forest (Wilkins & Peterson, 2000). Northern California samples were 24–1038 and in second growth forest (Diller & Wallace, 1996, 1999)

Region	Consolidated		Unconsolidated	
	% occupied	N	% occupied	N
Ascaphus truei Stegneger				
Olympic	67%	9	56%	154
Willapa	28%	18	0%	22
North. California	81%	67	0%	5
Rhyacotriton spp.				
Olympic	44%	9	44%	154
Willapa	61%	18	45%	22
North. California	88%	64	14%	7
Dicamptodon spp.				
Olympic	0%	9	34%	154
Willapa	100%	18	91%	22

The scarcity of stream amphibians in unconsolidated rock types found in previous studies caused Wilkins & Peterson (2000) to suggest that streams in such regions be a low priority for conservation of stream amphibians on harvested forests. However, no studies have examined the interaction of surface geology with timber harvest. Ours is the only study to examine surface geology in unlogged forests. The contrast of our findings with those from harvested forests (Table 4) suggests a hypothesis that unconsolidated rock types increase the sensitivity of stream amphibians to timber harvest. We suggest that Wilkins & Peterson's (2000) conclusion is premature and that a different conclusion could emerge after further testing. More specifically, we showed that unconsolidated surface geology can provide suitable habitat for stream amphibians. If the lack of amphibians in such rock types in harvested forests is due to logging, then unconsolidated rock types may require higher, rather than lower, prioritization for conservation strategies (e.g. wider buffer strips).

While Ascaphidae and Rhyacotritonidae consistently show strong and very similar associations with substrate, gradient and northern aspects, the two groups represent extremes in their distribution patterns: Ascaphidae is broadly distributed while the distribution of Rhyacotritonidae is much more narrow (Nussbaum *et al.*, 1983). The absence of Rhyacotritonidae in the northern Cascades suggests that this may not purely be a matter of geographical limitations on dispersal. Rather, despite the obvious importance of substrate and gradient, some other factor may act to limit the distribution of the Rhyacotritonidae.

D. copei differed from the other two species in most of its associations with stream characteristics. It was a generalist in terms of substrate, gradient and aspect. *D. copei* was associated with low canopy cover, *A. truei* with moderate cover and

Table 5 Analysis of deviance in density of stream amphibians in 2 × 2-km cells within Olympic National Park. Response variables are the mean number of stream amphibians captured/m^2 averaged over all streams in a cell. Models are log-linear with Poisson error and are weighted by the number of streams in each cell. Climate data are from PRISM climate models with input data from 1961 to 1990

Source	d.f.	Dev(cum)	F	P	coeff.	SE
Ascaphus truei Stegneger						
Temperature	1,58	10.49	7.123	0.010	-1.228×10^{-5}	4.172×10^{-6}
Precipitation	1,57	7.243	5.281	0.025	-3.721×10^{-6}	1.416×10^{-6}
Residual	57	78.176				
Rhyacotriton olympicus (Gaige)						
Growing	1,58	6.187	6.242	0.015	0.610	0.295
(Growing)^2	1,57	5.474	5.998	0.017	-0.0017	0.0009
Residual	57	52.019				
Dicamptodon copei Nussbaum (ALLDATA)						
Precipitation	1,58	7.127	19.863	< 0.001	1.0×10^{-5}	4.1×10^{-6}
Growing	1,57	6.459	18.001	< 0.001	1.055	0.6452
(Growing)^2	1,56	3.421	9.534	0.003	-0.003	0.0019
Residual	56	20.093				
Dicamptodon copei Nussbaum (SUBSET)						
Precipitation	1,41	0.870	1.891	0.177	8.6×10^{-6}	4.6×10^{-6}
Growing	1,40	3.300	7.174	0.011	0.950	0.650
(Growing)^2	1,39	2.662	5.787	0.021	-0.003	0.0019
Residual	39	17.940				

R. olympicus showed a nonsignificant trend towards higher densities with high cover. The relationship of these species to canopy cover and aspect is consistent with the low thermal preferences of *A. truei* and *R. olympicus* (Brattstrom, 1963). The absence of an association with aspect and the negative association with cover suggests that *D. copei* may be tolerant of a broader range of stream temperatures. Corn & Bury (1989) found that *D. tenebrosus* in young managed forests were more numerous in higher stream gradients compared to low gradients but, consistent with our results, found no association with gradient in unharvested forests. This finding, coupled with our data, suggests that timber harvest may limit the Dicamptodontidae to a narrower range of habitats than they occupy in unharvested forests.

The finding that, in general, *D. copei* tolerates the widest range of stream characteristics is at odds with the observed distribution of *D. copei* in ONP and, to a lesser extent, with the distribution of the Dicamptodontidae (Petranka, 1998). In ONP, *D. copei* had the narrowest distribution of the three stream-breeding species. As a family, the Dicamptodontidae are intermediate between the Ascaphidae and the Rhyacotritonidae in the breadth of their distribution. We found that *D. copei* had the strongest relationship to climate of the three species in ONP, suggesting a hypothesis that climate could be limiting its range (Table 5). *D. copei* density had a strong positive association with precipitation and its fitted density peaked in areas of ONP with a growing season of around 170 days.

Given the prevalence of amphibian declines globally (Wake, 1991; Corn, 1994), we considered whether *D. copei* may have formerly occurred in the north-eastern portion of ONP. This question is difficult to evaluate because of a lack of historic surveys. There is a single historic record of *D. copei* from a low elevation area north-east of ONP (Nussbaum *et al.*, 1983) but there are no records from inside the park in any of the drainages where we failed to detect *D. copei*. If accurate, this single low elevation record suggests that *D. copei* could conceivably invade suitable habitats in several north-eastern drainages of ONP. Aside from the obvious climatic gradient, the only other environmental difference we observed in the north-eastern portion of ONP is at higher elevations. *D. copei* and *R. olympicus* both had lower elevational limits than *A. truei*, and *D. copei* never occurred above 800 m. Of the 53 streams surveyed in the five drainages where *D. copei* was not detected, only nine were above 800 m. This is not representative of the relative amount of stream habitat above 800 m in that region of ONP, but suggests that we adequately sampled streams that were within the elevational range of *D. copei*. While we cannot infer cause and effect, our evidence suggests that local climate may be limiting *D. copei*'s distribution in ONP. We hypothesize that the paedomorphic life history of *D. copei* (Petranka, 1998) may increase its reliance on permanent streams and decrease its overland dispersal capabilities.

Precipitation is less in the north-east part of ONP and may result in fewer permanent streams in an area with higher summer temperatures. The north-east supports a more xeric-adapted flora, including patches of madrone (*Arbutus menziesii* Pursh) and a species of prickly pear on the coast (*Opuntia fragilis* (Nutt.) Haw. Buckingham *et al.*, 1995). Hydrological studies are needed to evaluate the density of suitable stream habitats at the landscape scale in the north-eastern portion of ONP.

The stream amphibian fauna in ONP is abundant and widespread, but the distribution of *D. copei* needs further study. The general association of stream amphibians with some of the pronounced climatic gradients in ONP coupled with the sensitivity of amphibians to environmental change (Welsh & Ollivier, 1998) suggests that they may be useful species in monitoring global climate change impacts. Moreover, the marked contrast of our findings in ONP with those in harvested forests highlight the importance of maintaining and studying ecological preserves. Patterns in preserves can provide a baseline for evaluating patterns in more impacted areas.

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