DISTRIBUTION AND HABITAT OF COLUMBIA TORRENT SALAMANDERS AT MULTIPLE SPATIAL SCALES IN MANAGED FORESTS OF NORTHWESTERN OREGON

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***Abstract*:** We examined relationships between Columbia torrent salamanders (*Rhyacotriton kezeri*) and biotic and abiotic habitat attributes at landscape and reach (within-stream) scales in managed forests of northwestern Oregon, USA. In 2000, we found 851 torrent salamanders in 58% of 119 headwater (first-order) streams from randomly selected 2.58-km^2 sections of the study area. Landscape-level variation in torrent salamander distribution and relative abundance was related to abiotic landform features that included parent geology, elevation, and aspect, but variation was not related to age or composition of adjacent riparian forests. In 2001, we conducted a more detailed study of salamander occurrence and abundance within 179 10-m stream reaches stratified by geology and gradient. The stream reaches were randomly selected from 40 streams known to contain salamanders. We recorded 1,224 salamanders from 92 (51%) of the stream reaches. Akaike's Information Criterion (AIC) model selection indicated that the global model containing all 23 variables best explained salamander occupancy in stream reaches, but a model containing only stream gradient also received empirical support. The stream-gradient model was the best candidate model explaining reach-level salamander abundance. Three other models explaining abundance (an abiotic landform model, the global model, and a physical substrate model) also received empirical support. Overall, our study suggests that variation in physical features of stream habitats may have an important influence on distribution and abundance of Columbia torrent salamanders at multiple spatial scales.

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Managers of federal, state, and private forests are increasingly challenged to balance timber harvest with protecting and enhancing biological diversity (Tuchmann et al. 1996, Moore and Allen 1999, Aubry 2000). Previous studies in the Pacific Northwest (PNW) suggest that amphibians, in particular, are at risk from timber harvest because of an apparent association with old-growth forests (Bury and Corn 1988, Bury et al. 1991, Adams and Bury 2002). However, few studies have been conducted on amphibian communities in commercially managed, second-growth forests in the PNW (Aubry 2000). Although extensive research on amphibian community–vegetation relationships in unmanaged, late-seral Douglas-fir (*Pseudotsuga menziesii*) forests of the PNW was conducted in the mid-1980s (e.g., Ruggiero et al. 1991, Welsh and Lind 2002), applicability of those studies to intensively managed forest landscapes is limited (Aubry 2000).

Current understanding of forest management effects on amphibians also may be limited by the historical paradigm that condition of stand-level vegetation is equivalent to habitat suitability (Hansen and Rotella 1999). Most studies evaluating responses of amphibians to forest management in the PNW and elsewhere have related species presence and abundance to variation in stand age or other vegetation characteristics (deMaynadier and Hunter 1995). Although periodic disturbance of vegetation often influences amphibian populations (deMaynadier and Hunter 1995), recent studies suggest that the importance of abiotic habitat features (e.g., geology, topography, climate) has not been sufficiently recognized (Diller and Wallace 1996, 1999; Wilkins and Peterson 2000; Sutherland and Bunnell 2001). Further, responses of amphibians to timber harvest likely are influenced by interactions of abiotic and biotic features occurring at multiple spatial scales (Wilkins and Peterson 2000), emphasizing the need to better match scales of amphibian sampling and habitat attributes of interest (Diller and Wallace 1996, Hayes et al. 2002).

Torrent salamanders (*Rhyacotriton* spp.) are among PNW stream amphibians reported to be most at risk from timber harvest (Bury and Corn 1988, Corn and Bury 1989, Welsh and Lind 1996).

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Torrent salamanders are considered obligates of clear, cold streams (e.g., 5–16 °C; Brattstrom 1963, Nussbaum et al. 1983, Diller and Wallace 1996), with an aquatic larval stage lasting perhaps 2–4 years (Nussbaum and Tait 1977, Nussbaum et al. 1983). Transformed individuals generally occur in the same headwater streams, springs, and seeps as the larvae but occasionally are found in adjacent upland forests during periods of precipitation (Nussbaum and Tait 1977, Nussbaum et al. 1983).

The Columbia torrent salamander is restricted to headwater streams of the Coast Range Mountains of southwestern Washington and northwestern Oregon (Good and Wake 1992). Although other torrent salamander species have significant ranges in federal lands with long-term management objectives for old-growth forest conditions (Tuchmann et al. 1996), over 95% of the known distribution of Columbia torrent salamanders lies within private and state lands subject to intensive timber harvest (Good and Wake 1992, McAllister 1995). No studies have addressed the ecology of Columbia torrent salamanders, but like other torrent salamanders, this species is presumed to require habitats best provided by old-growth forests (e.g., cold, shaded streams with clean gravel and cobble substrates; Bury et al. 1991, Corn and Bury 1989, Welsh and Lind 1996). Timber harvest is thought to extirpate torrent salamanders from streams for decades by (1) depositing sediments that degrade microhabitats and (2) removing canopy cover resulting in elevated stream temperatures (Bury and Corn 1988, Corn and Bury 1989, Welsh and Lind 1996). Recolonization of streams is expected to be rare because torrent salamanders are thought to have limited dispersal abilities and small home ranges (Nussbaum et al. 1983).

Studies are needed that not only characterize amphibian populations within intensively managed forest landscapes of the PNW (Aubry 2000), but also explore how vegetation, physical features, and forest management interact at different spatial scales to influence habitat relationships (Hansen and Rotella 1999). We examined habitat relationships of Columbia torrent salamanders at 2 spatial scales within intensively managed forests of northwestern Oregon. Our specific objectives were to (1) establish broad patterns of torrent salamander distribution and abundance in relation to major landscape-level habitat variables, (2) use results from our landscape sampling and an information–theoretic modeling approach (Burnham and Anderson 1998) to examine habitat relationships at the stream-reach scale, and (3) evaluate the relative importance of biotic versus abiotic paradigms for explaining torrent salamander occurrence and abundance in commercially managed forests.

STUDY AREA

Our study area was approximately 94,600 ha of private timberlands on both the western and eastern slopes of the Coast Range Mountains in the counties of Clatsop, Tillamook, Washington, and Yamhill in northwestern Oregon, USA (Fig. 1). Most of our study area was ≤35 km from the coast but extended up to 68 km inland in places. The Pacific Ocean creates a cool, wet climate across the area, with mean annual precipitation ranging from 90 cm at inland sites to 380 cm along the coast (Taylor 1993). Most precipitation occurs between October and May, with winter snow accumulation common above 500 m. Minimum and maximum temperatures averaged 0 °C in January and 25 °C in August.

Two vegetation zones, Sitka spruce (*Picea sitchensis*) and western hemlock (*Tsuga heterophylla*) occurred within the study area (Franklin and Dyrness 1973). Sitka spruce dominated the narrow (5–15 km) fog belt along the Pacific Ocean. Inland of the spruce zone was the western hemlock zone, representing an east–west gradient of western hemlock near the coast to Douglas-fir at more inland sites. Historically, fires allowed Douglas-fir to dominate much of the western hemlock zone, particularly east of the Coast Range Crest (Agee 1993).

Timber harvesting in the study area began in the early 1900s, when entire drainages were clearcut from the coast inland or westward from the eastern slope of the Coast Range. Our study area currently is comprised of zero to 80-year-old second- and third-growth stands of Douglas-fir, western hemlock, and Sitka spruce that were regenerated naturally (pre-1950s) or artificially. Conifers of minor abundance included western redcedar (*Thuja plicata*), grand fir (*Abies grandis*), and noble fir (*A. procera*). Hardwoods, including bigleaf maple (*Acer macrophyllum*) and red alder (*Alnus rubra*), also were significant stand components. Dominant plants in the shrub layer included ocean spray (*Holodiscus discolor*), vine maple (*Acer cirinatum*), red huckleberry (*Vaccinium* spp.), rhododendron (*Rhododendron macrophyllum*), young red alder, sword fern (*Polystichum munitum*), and salal (*Galutheria shallon*).

Elevations across the study area range from 5 to 780 m. Parent geology is dominated by 2 major divisions of lithology: basalt and marine sediment

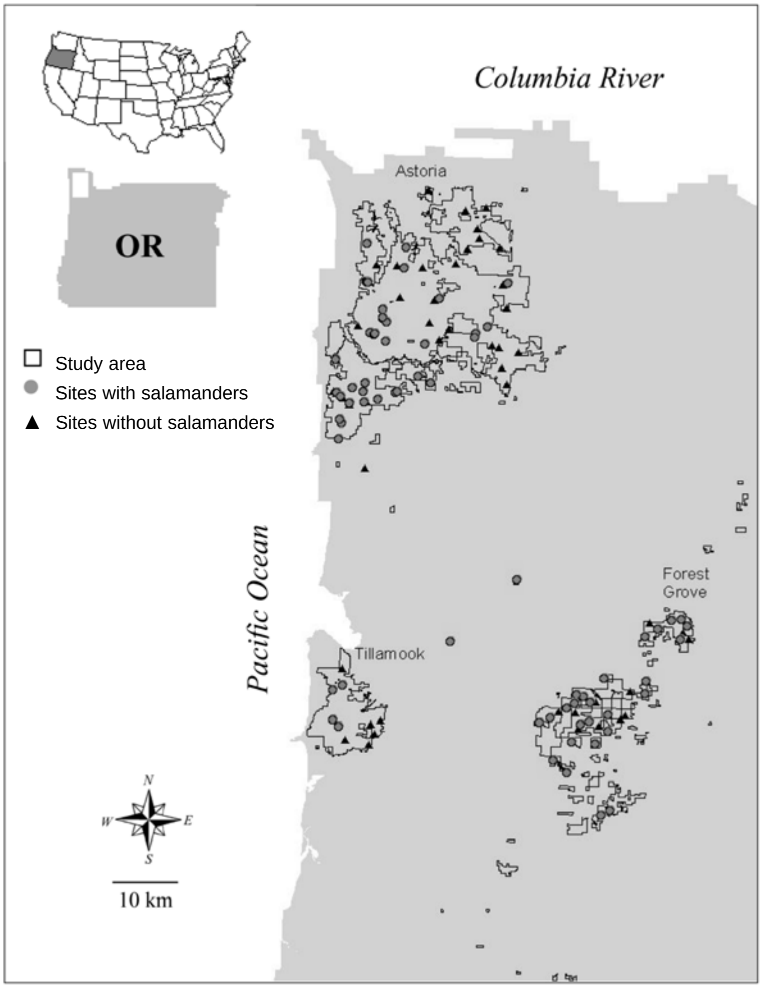

Fig. 1. Map of study area showing locations of 119 streams with and without Columbia torrent salamanders, northwestern Oregon, USA, 2000.

(Franklin and Dyrness 1973). The area's bedrock is of volcanic basalt origin overlaid with marine sediments. Layers of sandstone, siltstone, and clay vary in thickness from 1 to ≥30 m. Surficial geology is a complex matrix of uplifted marine sediment with outcroppings of basalt that are close to the surface at higher elevations.

METHODS

Landscape Sampling and Analyses

Between June and October 2000, we conducted systematic surveys to explore patterns of torrent salamander occurrence and relative abundance in relation to major landscape variables. To ensure broad geographic coverage, we used a stratified sampling design to randomly select up to 4 sections per township in the study area from a Geographic Information System (GIS) database (Diller and Wallace 1996). Sampling was designed to select 1 section (2.58 km^2) per quarter township (9 sections), but the number of sections per township was reduced if the entire township was not located in the study area. We required each section chosen to include ≥50% study area and have road access. The only exception to this selection procedure occurred in the Forest Grove portion of our study area (Fig. 1), where the property is fragmented. In Forest Grove, we sampled all sections with ≥50% study area.

We selected 119 sections for the landscape-level surveys. We sampled the first headwater (first-order) stream that we encountered along the major road through the section (Diller and Wallace 1996). Relatively short (≤50 m) random sample reaches may be insufficient to determine torrent salamander occurrence reliably (Diller and Wallace 1996, Hayes et al. 2002). We therefore used long, continuous searches and located the starting point of each survey a minimum of 100 m, but typically no more than about 500 m, from the upstream origin. We searched all habitat within the stream channel by turning over larger substrates with a rake and sifting through finer substrates by hand. If torrent salamanders were detected, we continued the search for an additional 30 m (measured with a hip chain) to establish an index of relative abundance (salamanders/linear m searched; Diller and Wallace 1996). We recorded snout–vent length (SVL; mm), life-history category (larva, transformed), and sex of adults (inspection of cloacal lips, enlarged and squared in males). If no salamanders were found, we continued searching to the stream origin (headwater).

We determined underlying geology of each stream from U.S. Geological Survey maps (1:48,000 scale) and soil surveys of the study area. Although multiple geological formations were identified, we grouped them into the 2 major divisions of Coast Range lithology: basalt and marine sediment. We derived age and overstory vegetation composition (Douglas-fir, Douglas-fir–western hemlock, western hemlock–Sitka spruce, conifer–hardwood, hardwood) of forest stands adjacent to streams, stream aspect, and elevation from the study area GIS database.

We tested for normality of data using Kolmogorov-Smirnov tests and used nonparametric analyses when data violated assumptions of normality. Elevation (m) and forest age (1–80 yr; $\bar{x}$ = 37.5 ± 1.50 SE) were considered continuous independent variables. Stream aspect was measured as a continuous variable (0–360°), but grouped into 45° octants and treated as a categorical variable (Diller and Wallace 1996). We treated all other variables as categorical.

We used chi-square tests to relate lithology, aspect, and overstory vegetation composition to salamander occurrence. We used Mann-Whitney *U*-tests to compare elevation and adjacent forest age of streams with and without salamanders. We also used Mann-Whitney *U*-tests to relate lithology and aspect to relative abundance of salamanders, and we used a Kruskal-Wallis test to determine relationships between salamander abundance and overstory vegetation composition. We used Spearman rank correlations to compare elevation and stand age with salamander relative abundance.

We divided the study area into western and eastern regions for further analysis because of increased precipitation and a more moderate climate west of the Coast Range Crest (Taylor 1993). We used chi-square and Mann-Whitney *U*-tests to compare occurrence and relative abundance of salamanders between eastern and western regions. All means are presented ±1 standard error (SE), and the significance level for all tests was $\alpha = 0.05$.

Stream-reach Sampling and Analyses

Data Collection.—For stream-reach sampling, we randomly selected 40 headwater streams known to have salamanders (from our landscape surveys or incidental sightings) for sampling in June and July 2001. Because landscape sampling suggested a strong influence of geology on torrent salamanders, we stratified our sample between marine sediment and basalt lithologies (n = 20 streams each). Prior studies also indicated stream slope to be an important correlate of torrent salamander occurrence (Diller and Wallace 1996, Wilkins and Peterson 2000). Therefore, we partitioned our sample streams into low (0–5°), medium (6–10°), and high gradient (≥15°) reaches (range = 1–35°) prior to sampling (Diller and Wallace 1996). We measured the gradient of each reach in degrees, using a clinometer. If available, we randomly selected 2 10-m reaches of each gradient class per stream. Because of obstacles in the stream, 14 reaches were shortened to a minimum of 5 m and not all gradient classes were available in all streams. We thoroughly searched each reach for torrent salamanders as previously described.

Within each reach, we measured biotic and abiotic parameters indicated by previous studies to be important habitat correlates of torrent salamanders (e.g., Nussbaum et al. 1983, Diller and Wallace 1996, Welsh and Lind 1996, Wilkins and Peterson 2000). We estimated percent canopy closure at the lower and upper ends of each reach with a spherical densiometer read at the 4 cardinal directions. We measured water temperature, dissolved oxygen, and conductivity using a YSI Model 85 (YSI, Inc., Yellow Springs, Ohio, USA) water chemistry meter and recorded pH (nearest 0.01; Oakton pH Test 3, Construction Safety Products, Inc., Shreveport, Louisiana, USA). We tallied large woody debris (LWD; ≥10-cm diameter and ≥2 m long) that broke the vertical plane of the bankfull along the entire reach (Wilkins and Peterson 2000). We established a 10 × 10-m riparian plot immediately adjacent to and centered on both sides of each reach, and we visually estimated percent cover of exposed soil, woody and herbaceous ground cover, understory shrubs and trees (conifer and hardwood), and overstory (conifer and hardwood) within each plot (Wilkins and Peterson 2000).

For each reach, we also sampled up to 6 cross-stream habitat transects. Transects were located at 2-m intervals and perpendicular to the flow of water (Cole et al. 2003). Each transect was assigned to 1 of 4 habitat types: cascade, riffle, run, or pool. We recorded channel dimensions at each transect (Cole et al. 2003). We estimated substrate composition at 15 equally spaced locations along each transect. At each location, we recorded the substrate type (bedrock, boulder, cobble, gravel, pebble, sand, silt, or wood).

Table 1. Biotic and abiotic habitat parameters measured from 179 10-m stream reaches, included in logistic and linear regression models explaining microhabitat relationships of Columbia torrent salamanders in northwestern Oregon, USA, 2001.

Variable	Units	Abbreviation	Additional description
Lithology		LI	Basalt or marine sediment parent geology
Gradient class	°	GC	Low (0–5°), medium (6–10°), or high (≥15°) 10-m reach
Distance to stream origin	m	DS	Distance of a 10-m reach from stream origin (headwater)
Stand age	yr	SA	Age of overstory trees adjacent to a 10-m reach
Overstory canopy	%	OC	Canopy closure of vegetation overhanging a 10-m reach
Riparian ground cover	%	RC	% ground cover in 100 m^2 plots adjacent to a 10-m reach
Water temperature	°C	WT	Water temperature of a 10-m reach
Dissolved oxygen	%	DO	Dissolved oxygen saturation in a 10-m reach
Wetted: bankfull width ratio		WB	Ratio of wetted and bankfull widths of a 10-m reach
Mean channel depth	m	MD	Mean depth of a 10-m reach channel
In-stream large wood	no.	LW	Tally of large wood (≥10-cm diameter, ≥2 m long) in a 10-m reach
Boulders	%	BO	% boulder habitat substrate in a 10-m reach
Cobble	%	CO	% cobble habitat substrate in a 10-m reach
Gravel	%	GR	% gravel habitat substrate in a 10-m reach
Fines	%	FI	% fines in a 10-m reach
Sand	%	SA	% sand in a 10-m reach
Wood	%	WO	% woody material in a 10-m reach
Pools-runs	%	PO	% pool and run habitat in a 10-m reach
Cascade	%	CA	% cascade habitat in a 10-m reach
Dicamptodon density	no./m^2	DD	Density of Pacific giant salamanders in a 10-m reach
Crayfish density	no.m^2	CD	Density of signal crayfish in a 10-m reach
Invertebrate prey	no./m^2	IP	Density of potential aquatic invertebrate prey of torrent salamanders in a 10-m reach
Invertebrate competitors	no./m^2	IC	Density of potential invertebrate competitors of torrent salamanders in a 10-m reach

In each reach, we tallied numbers of Pacific giant salamanders (*Dicamptodon tenebrosus*) and signal crayfish (*Pacifastacus leniusculus*), potential predators of torrent salamanders (Nussbaum et al. 1983, Haggerty et al. 2002). We also measured densities of aquatic invertebrates that potentially competed with torrent salamanders for food and served as prey (Bury and Martin 1967, Nussbaum et al. 1983), using methods in Cole et al. (2003).

Model Specification and Analyses.—Prior to model specification, we eliminated redundant variables (Spearman's $r^2 \geq 0.70$) and retained 23 parameters for inclusion in models (Tables 1, 2). We examined scatterplots and residual plots to ensure that variables met assumptions of analyses (i.e., linearity, normality, colinearity) and did not contain presumed outliers (>4 SE). We used the square-root transformation on salamander abundance to approximate normality. We used 2 approaches to specify a set of plausible a priori candidate models for explaining torrent salamander occurrence and abundance: (1) a review of published literature on torrent salamander habitat relationships, and (2) evaluation of our results from landscape sampling. We specified 15 models: a global model containing all 23 parameters and subset models representing potential influences of abiotic and biotic attributes on torrent salamanders (Tables 3, 5). We analyzed the model set separately for salamander occurrence and abundance using logistic and linear regression, respectively. Prior to model selection, we examined fit of global models following recommendations of Burnham and Anderson (1998) that included examining residuals, measures of fit (R^2 = 0.54 and 0.36, respectively, for logistic and linear models), classification tables (overall percentage for logistic regression = 80%), and histograms of expected probabilities.

Because the number of reaches sampled (n = 179) was small relative to the number of parameters (K) in most models (i.e., $n/K < 40$), we used Akaike's Information Criterion corrected for small sample size (AIC$_c$) for model selection (Burnham and Anderson 1998). We used the formulas presented in Burnham and Anderson (1998) to calculate AIC$_c$ for our maximum likelihood (logistic regression) and least-squares (linear regression) methods. We ranked all candidate models according to their AIC$_c$ values, and the best model (i.e., most parsimonious) was the model with the smallest AIC$_c$ value (Burnham and Anderson 1998). We drew primary inference from models within 2 units of AIC$_{cmin}$, although models within 4–7 units may have some empirical support (Burnham and Anderson 1998). We cal-

Table 2. Habitat characteristics (± SE), stratified by lithology (basalt and marine sediment) and 3 gradient classes (low: 0–5°, medium: 6–10°, and high: ≥15°) of 179 10-m stream reaches, included in logistic and linear regression models explaining microhabitat relationships of Columbia torrent salamanders in northwestern Oregon, USA, 2001.

	Basalt lithology			Marine sediment lithology		
Gradient	Low (*n* = 27)	Medium (*n* = 34)	High (*n* = 33)	Low (*n* = 29)	Medium (*n* = 35)	High (*n* = 21)
Variable	3.46 ± 0.29°	9.71 ± 0.26°	19.7 ± 0.59°	3.21 ± 0.24°	9.04 ± 0.36°	20.3 ± 1.19°
Distance to stream origin	125.4 ± 24.9	133.1 ± 22.7	62.2 ± 9.90	143.8 ± 27.1	118.7 ± 18.1	122.5 ± 38.2
Stand age	39.1 ± 2.12	39.6 ± 1.84	40.6 ± 1.81	41.9 ± 2.52	43.2 ± 2.13	40.9 ± 3.46
Overstory canopy	74.0 ± 2.28	74.8 ± 2.61	72.6 ± 2.51	63.9 ± 4.21	68.5 ± 3.27	59.7 ± 5.92
Riparian ground cover	92.7 ± 1.31	88.6 ± 1.83	87.5 ± 2.65	90.7 ± 1.61	88.8 ± 1.41	88.3 ± 2.62
Water temperature	10.3 ± 0.22	10.2 ± 0.17	9.9 ± 0.21	10.3 ± 0.18	10.7 ± 0.19	11.1 ± 0.25
Dissolved oxygen	81.0 ± 1.79	86.7 ± 1.42	87.6 ± 1.48	80.5 ± 2.69	84.3 ± 1.53	84.8 ± 2.27
Wetted: bankfull width ratio	0.72 ± 0.04	0.75 ± 0.03	0.78 ± 0.03	0.77 ± 0.04	0.77 ± 0.04	0.81 ± 0.06
Mean channel depth	1.86 ± 0.17	1.52 ± 0.12	1.15 ± 0.09	1.76 ± 0.12	1.73 ± 0.16	1.18 ± 0.18
In-stream large wood	6.48 ± 1.45	7.03 ± 0.80	7.83 ± 1.18	6.04 ± 0.83	7.47 ± 0.87	7.12 ± 0.92
Boulders	0.13 ± 0.13	1.36 ± 0.47	4.54 ± 1.69	2.40 ± 1.51	1.45 ± 0.49	7.06 ± 3.04
Cobble	2.73 ± 0.94	6.04 ± 1.26	11.3 ± 1.76	7.57 ± 2.14	10.9 ± 1.97	16.2 ± 3.75
Gravel	22.8 ± 3.53	33.5 ± 2.41	45.2 ± 3.31	25.5 ± 3.49	32.9 ± 3.41	34.2 ± 3.76
Fines	29.7 ± 3.58	19.8 ± 2.12	7.28 ± 1.39	28.9 ± 4.39	19.3 ± 3.21	12.4 ± 4.43
Sand	17.2 ± 2.34	14.4 ± 1.94	7.67 ± 1.18	11.4 ± 1.89	11.1 ± 1.75	7.74 ± 1.72
Wood	26.3 ± 2.99	24.3 ± 1.98	23.9 ± 2.58	23.5 ± 2.96	24.3 ± 2.27	21.9 ± 4.02
Pools-runs	24.3 ± 5.44	6.83 ± 2.52	1.11 ± 1.11	20.9 ± 4.78	9.95 ± 3.40	2.11 ± 2.11
Cascade	2.33 ± 1.32	19.2 ± 5.01	77.7 ± 6.21	3.45 ± 3.45	15.9 ± 5.37	79.4 ± 6.75
Dicamptodon density	0.08 ± 0.04	0.14 ± 0.05	0.20 ± 0.07	0.16 ± 0.05	0.10 ± 0.03	0.21 ± 0.09
Crayfish density	0.16 ± 0.05	0.44 ± 0.12	0.32 ± 0.11	0.17 ± 0.06	0.34 ± 0.07	0.34 ± 0.09
Invertebrate prey	2,902.4 ± 661.0	3,198.8 ± 979.4	3,239.2 ± 637.2	2,047.3 ± 715.8	1,707.8 ± 278.9	2,207.9 ± 834.8
Invertebrate competitors	1,475.9 ± 417.2	2,130.3 ± 699.1	1,641.9 ± 523.8	630.7 ± 137.3	679.6 ± 157.4	624.4 ± 356.6

culated Akaike weights (w_i) to determine the weight of evidence in favor of each model and to estimate the relative importance of individual parameters (Burnham and Anderson 1998). All analyses were conducted using SPSS software (SPSS 1999).

RESULTS

Landscape Scale

We recorded 851 Columbia torrent salamanders from 69 of 119 (57.9%) streams (Fig. 1). Relative abundance ranged from zero to 4.77 salamanders/linear m (overall = 0.47 salamanders/m), and larvae comprised 59.6% of captures. Only 32.0% (16 of 50) of streams flowing through marine sediment lithology contained salamanders compared to 76.8% (53 of 69) of streams flowing through basalt (χ^2 = 24.50, df = 1, $P < 0.0001$). Relative abundance of salamanders also was higher in basalt streams ($\bar{x}$ = 0.31 ± 0.07 salamanders/m) when compared to marine sediment streams ($\bar{x}$ = 0.07 ± 0.08 salamanders/m; Mann-Whitney *U*-test: Z = 2.20, P = 0.029). A greater proportion of streams with northerly aspects (35 of 51) contained salamanders compared to those with southerly aspects (32 of 68; χ^2 = 18.42, df = 1, $P < 0.010$), but relative abundance was similar between northerly ($\bar{x}$ = 0.29 ± 0.08 salamanders/m) and southerly aspects ($\bar{x}$ = 0.15 ± 0.07 salamanders/m; Z = 1.38, P = 0.184). Mean elevation of streams with salamanders ($\bar{x}$ = 367.5 ± 22.3 m) was higher than streams without salamanders ($\bar{x}$ = 262.9 ± 26.2 m; Z = 3.05, P = 0.002), but relative abundance was not related to elevation (Spearman r_s = 0.001, P = 0.732).

Forest age was similar between sites with ($\bar{x}$ = 39.8 ± 1.74 yr) and without salamanders ($\bar{x}$ = 34.4 ± 2.61 yr; Mann-Whitney *U*-test: Z =

Table 3. Logistic regression models explaining influence of biotic and abiotic habitat attributes on occurrence of Columbia torrent salamanders in managed headwater stream reaches (10 m; n = 179) of northwestern Oregon, USA, 2001. Model rankings were based on Akaike's Information Criterion corrected for small sample size (AIC_c).

Model[a]	K[b]	AIC_c	ΔAIC_c[c]	w_i[d]
Global {*LI, GC, DS, SA, OC, RC, WT, DO, WB, MD, LW, BO, CO, GR, FI, SA, WO, PO, CA, DD, CD, IP, IC*}	25	213.19	0.00	0.82
Gradient {*GC*}	3	216.51	3.32	0.16
Landform {*LI, GC, DS*}	5	220.42	7.24	0.02
Streambed substrate {*BO, CO, GR, FI, SA*}	6	226.58	13.39	0.00
Physical habitat {*LI, GC, DS, WB, MD, LW, BO, CO, GR, FI, SA, WO, PO, CA*}	16	228.86	15.68	0.00
Stream-reach habitat {*PO, CA*}	3	230.88	17.70	0.00
Water quality {*WT, DO*}	3	233.87	21.60	0.00
Predators {*DD, CD*}	3	242.07	28.88	0.00
Invertebrate prey density {*IP*}	2	248.37	35.18	0.00
Invertebrate competitors {*IC*}	2	248.67	35.48	0.00
Stand age {*SA*}	2	249.31	36.12	0.00
Stream channel {*WB, MD, DS*}	4	250.06	36.87	0.00
Lithology {*LI*}	2	250.86	37.67	0.00
Vegetation {*SA, OC, RC*}	4	251.25	38.07	0.00
Distance to stream origin {*DS*}	2	251.53	38.34	0.00

[a] Abbreviations in parentheses correspond to model parameters in Table 1.
[b] Number of estimable parameters in approximating model.
[c] Difference in value between AIC_c of the current model versus the best-approximating model (AIC_{cmin}).
[d] Akaike weight. Probability that the current model (i) is the best-approximating model among those considered.

1.93, P = 0.08), and was not related to relative abundance (Spearman r_s = 0.007, P = 0.338). Forest overstory composition was not related to salamander occupancy (χ^2 = 4.96, df = 1, P = 0.293) or relative abundance (Kruskal-Wallis H = 2.25, df = 114, P = 0.07).

A smaller proportion of streams west of the Coast Range Crest (53.1%, 43 of 81) contained salamanders when compared to those east of the Crest (68.4%, 26 of 38), but this difference was not significant (χ^2 = 2.54, df = 1, P = 0.111). Relative abundance was similar between western (0.25 ± 0.06 salamander/m) and eastern regions (0.12 ± 0.10 salamander/m) of the study area (Mann-Whitney U-test: Z = 2.54, P = 0.111).

Stream-reach Scale

We recorded 1,224 Columbia torrent salamanders from 92 of 179 stream reaches (51.4%) that we surveyed. Abundance ranged from zero to 68.3 salamanders/m^2 ($\bar{x}$ = 2.24 ± 0.89 salamanders/m^2), and larvae comprised 62.6% of captures. Of the 15 models explaining occurrence of salamanders in stream reaches, the global model was selected as the best-approximating model (Table 3). The second-best model was the single abiotic parameter "gradient class" (ΔAIC_c = 3.32; Tables 3, 4). The remaining 13 model sets, including the stand age and vegetation models, received no empirical support (Table 3). Although the weight of evidence supporting the global model was about 5 times greater than that of the gradient class model ($w_{\text{global}}/w_{\text{gradient class}}$; Burnham and Anderson 1998), we found at least limited evidence

Table 4. Parameter estimates from the gradient and landform models explaining influence of biotic and abiotic habitat attributes on occurrence and abundance of Columbia torrent salamanders in managed headwater stream reaches (10 m; n = 179) of northwestern Oregon, USA, 2001. Coefficients of the categorical variables (gradient, lithology) were calculated relative to high gradient and marine sediment (lithology) reaches.

Model[a]	B	SE	R^2
Gradient {*GC*}[b]			0.253
Constant	1.482	0.350	
Gradient = low	–2.580	0.467	
Gradient = medium	–1.511	0.425	
Gradient {*GC*}[c]			0.143
Intercept	1.053	0.120	
Gradient = low	–0.857	0.168	
Gradient = medium	–0.680	0.160	
Landform {*LI, GC, DS*}[c]			0.159
Intercept	1.207	0.152	
Lithology = basalt	–0.127	0.132	
Gradient = low	–0.839	0.169	
Gradient = medium	–0.662	0.161	
Distance to stream origin	–0.001	0.001	

[a] Abbreviations in parentheses correspond to model parameters in Table 1.
[b] Model from logistic regression explaining occurrence of torrent salamanders.
[c] Model from linear regression explaining abundance of torrent salamanders.

Table 5. Linear regression models explaining influence of biotic and abiotic habitat attributes on density of Columbia torrent salamanders in managed headwater stream reaches (10 m; n = 179) of northwestern Oregon, USA, 2001. Model rankings were based on Akaike's Information Criterion corrected for sample size (AIC_c).

Model[a]	RSS[b]	K[c]	AIC_c	ΔAIC_c[c]	w_i[d]
Gradient {*GC*}	135.9	4	–41.06	0.00	0.47
Landform {*LI, GC, DS*}	133.3	6	–40.22	0.84	0.31
Global {*LI, GC, DS, SA, OC, RC, WT, DO, WB, MD, LW, BO, CO, GR, FI, SA, WO, PO, CA, DD, CD, IP, IC*}	102.0	26	–39.36	1.71	0.20
Physical habitat {*LI, GC, DS, WB, MD, LW, BO, CO, GR, FI, SA, WO, PO, CA*}	119.6	17	–34.42	6.64	0.02
Stream-reach habitat {*PO, CA*}	142.2	4	–33.01	8.04	0.01
Streambed substrate {*BO, CO, GR, FI, SA*}	145.2	7	–22.78	18.29	0.00
Stream channel {*WB, MD, DS*}	149.8	5	–21.57	19.49	0.00
Distance to stream origin {*DS*}	154.4	3	–20.32	20.74	0.00
Predators {*DD, CD*}	154.2	4	–18.41	22.65	0.00
Water quality {*WT, DO*}	154.4	4	–18.27	22.79	0.00
Invertebrate prey competitors {*IC*}	157.1	3	–17.21	23.85	0.00
Vegetation {*SA, OC, RC*}	153.9	5	–16.69	24.37	0.00
Invertebrate prey density {*IP*}	157.8	3	–16.40	24.66	0.00
Lithology {*LI*}	158.5	3	–15.62	25.44	0.00
Stand age {*SA*}	158.6	3	–15.55	25.51	0.00

[a] Abbreviations in parentheses correspond to model parameters in Table 1.

[b] Residual sum of squared.

[c] Number of estimable parameters in approximating model.

[d] Difference in value between AIC_c of the current model versus the best-approximating model (AIC_{cmin}).

[e] Akaike weight. Probability that the current model (i) is the best-approximating model among those considered.

of a positive relationship between gradient and presence of torrent salamanders in stream reaches.

The best-approximating model explaining abundance of Columbia torrent salamanders in stream reaches was the single parameter gradient class (Tables 4, 5). Salamander abundance increased with stream reach gradient (Fig. 2). The second-best model, "landform," contained lithology, gradient class, and distance to origin and also received strong empirical support (ΔAIC_c = 0.84; Tables 4, 5). This model indicated that in addition to gradient, both basalt geology and closer proximity to stream channel origin had positive effects on salamander abundance. Weight of evidence in favor of the gradient-class model was only about 1.5 times greater than that of the landform model, indicating some uncertainty in selection of the best candidate model (Burnham and Anderson 1998). Overall, evidence for a gradient effect was strong in that the sum of Akaike weights for the 2 models containing this parameter was 0.78. Summing Akaike weights of parameters across all models also provided evidence for the importance of gradient class (0.99) over lithology (0.52) and distance to origin (0.52). The third-best model, the global model, received limited support (Table 5). Weight of evidence in favor of the gradient class model was about 2.3 times greater than that of the global model. A fourth model, "physical habitat," received only marginal support (ΔAIC_c = 6.64; Table 5). The remaining 11 model sets received no empirical support ($\Delta AIC_c > 7$, $w_i \leq 0.01$; Table 5).

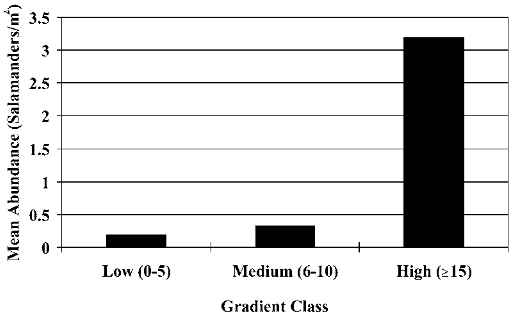

Fig. 2. Mean abundance of Columbia torrent salamanders within low- (0–5°), medium- (6–10°), and high- (≥15°) gradient 10-m stream reaches randomly sampled from 40 headwater streams in northwestern Oregon, USA, 2001.

DISCUSSION

Landscape-scale Habitat

Columbia torrent salamanders were widely distributed at the landscape level and found in approximately 60% of sampled headwater streams. Because different sampling scales and methods were used, direct comparisons of our occupancy data with those from other studies should be viewed cautiously. Wilkins and Peterson (2000) found Columbia torrent salamanders in 52.5% of managed headwater streams from the Coast Range of southwestern Washington, and estimates of the proportion of streams occupied by southern torrent salamanders (*Rhyacotriton variegatus*) have varied from 28.5 to 80.3% (Carey 1989, Corn and Bury 1989, Diller and Wallace 1996, Welsh and Lind 1996).

At the landscape level, occupancy and relative abundance of Columbia torrent salamanders were not related to age or composition of riparian vegetation but rather to abiotic landform features. In our study area, torrent salamanders were strongly tied to basalt parent geology. Diller and Wallace (1996) reported that the landscape-level distribution of southern torrent salamanders in coastal northwestern California also was associated with consolidated geological formations. In contrast, Adams and Bury (2002) found no relationships between geological type and abundance of Olympic torrent salamanders (*Rhyacotriton olympicus*) from 1-m^2 reaches in Washington, but only 9 of the 141 streams they sampled had basalt geology. Wilkins and Peterson (2000) also found little variation in Columbia torrent salamander occupancy or abundance between basalt and marine sediment stream reaches (5-m length) in southwestern Washington, despite differences in habitat substrates related to the 2 geological types. We think associations between torrent salamanders and landform features may be most evident when animals are sampled at larger scales, as did Diller and Wallace (1996), even though the influence of these features on habitat relationships may be manifested at smaller scales.

The trend for occupied streams to be associated with north-facing aspects was similar to patterns previously reported for torrent salamander populations in Washington (Wilkins and Peterson 2000, Adams and Bury 2002) and California (Diller and Wallace 1996) and suggests that warm and dry southerly exposures may limit the presence of salamanders across our study area (Diller and Wallace 1996, Wilkins and Peterson 2000). We think the positive association between presence of torrent salamanders and elevation reflects relationships with other parameters rather than an effect of elevation per se. In our study area, uplifted areas of basalt are more common and closer to the surface at higher elevations. Further, these areas possess steeper topography and cooler water temperatures that appear to influence habitat relationships of torrent salamanders at smaller scales (Diller and Wallace 1996, Hunter 1998, Wilkins and Peterson 2000).

Stream-reach Scale Habitat

Occurrence.—Among the candidate models explaining salamander occupancy at the stream-reach scale, the global model received the strongest support. The only other model to receive empirical support was the gradient class model, indicating a potential association between the presence of torrent salamanders and steeper slopes. Good and Wake (1992) noted that torrent salamanders were associated with areas of substantial physical relief and generally were absent from areas with low relief. Diller and Wallace (1996) and Wilkins and Peterson (2000) also reported positive associations between stream-reach gradient and presence of torrent salamanders, suggesting that topography influences the distribution of these species.

Because individual parameters were associated with the landscape-level occurrence of salamanders, and AIC typically favors parsimonious models (Burnham and Anderson 1998), we were surprised that the global model received the most support. Although we evaluated a relatively large number of plausible models based on previous research of torrent salamanders, we avoided specification of all possible models (i.e., "data dredging;" Burnham and Anderson 1998:19). Support for the global model may indicate the importance of individual parameters, or parameter combinations, that we did not consider as models. For example, post hoc inclusion of a model with the parameters "gradient class" and "water temperature" would result in a best-approximating model with strong empirical support (w_i = 1.0), suggesting that salamander occupancy of reaches may be positively related to both steeper slopes and lower water temperatures. We cite this model only as an example and make no inferences about its biological merit for 2 reasons. First, we detected little variation in water temperatures across the reaches we sampled (Table 2). Second, post hoc AIC model specification is undesirable, and support for any new models would need to be evaluated with additional data (Burnham and Anderson 1998).

Although the gradient class model received some support, we think that the lack of strong evidence for other parsimonious (i.e., useful) models explaining stream-reach occupancy of torrent salamanders also was related to the scale of sampling. When surveys were confined to the reach scale in streams where we already had established occupancy, salamanders were still found in only 51.4% of the randomly selected reaches. Thus, we agree with Diller and Wallace (1996) and Hayes et al. (2002) that presence of torrent salamanders in streams may not be reliably determined by sampling methods limited to relatively short randomly selected reaches, and we urge caution when using presence data from particularly short reaches (e.g., ≤5 m) to infer larger-scale habitat relationships (Stoddard 2001, Welsh and Lind 2002).

Abundance.—At the stream-reach scale, we found that abundance of Columbia torrent salamanders was highly variable both among streams and reaches within streams (0.00–68.3 individuals/m^2). A similar pattern has been observed for southern torrent salamanders (Diller and Wallace 1996, Welsh and Lind 1996). Previous estimates of torrent salamander abundance have ranged from 0.01 to 41.2 individuals/m^2 (Nussbaum and Tait 1977, Corn and Bury 1989, Diller and Wallace 1996, Welsh and Lind 1996). The mean abundance we recorded from 10-m stream reaches across our study area (2.24 salamanders/m^2) was higher than mean abundances of southern torrent salamanders reported from older, unmanaged forests (0.29–0.68 salamanders/m^2; Corn and Bury 1989, Welsh and Lind 1996, Welsh et al. 2000), and the maximum abundance we found is the highest reported for any torrent salamander species.

The best-approximating model explaining abundance of Columbia torrent salamanders included the single variable gradient class. Salamander abundance increased with stream gradient, particularly within high-gradient reaches. Several studies have reported positive associations between abundance of torrent salamanders and higher stream gradients (e.g., ≥15°; Corn and Bury 1989, Diller and Wallace 1996, Wilkins and Peterson 2000, Adams and Bury 2002). Diller and Wallace (1996) suggested that steeper-gradient reaches are favorable habitats because these reaches represent transport areas where finer sediments do not accumulate and thus interstitial spaces within gravel and cobble substrates used by torrent salamanders do not become filled. In contrast, Welsh and Lind (1996) and Welsh et al. (2000) did not find an association between torrent salamanders and stream gradient. However, Welsh and Lind (1996:387) avoided "high-gradient/discharge habitats" and Welsh et al. (2000) also sampled only low- to medium-gradient stream reaches (≤8°).

The landform model also received empirical support and provided additional evidence of a gradient effect on salamander abundance. This model also provided support for the positive influence of basalt geology on salamander abundance that we observed at the landscape scale. Basalt parent material generally produces more of the coarse substrates (e.g., gravel and cobble) favored by torrent salamanders, whereas marine sediments naturally produce more fine sediments and sands (Table 2; Dupuis et al. 2000, Wilkins and Peterson 2000, Sutherland and Bunnell 2001).

Although they did not include geology or steep-gradient reaches in their study, Welsh and Lind (1996:396) hypothesized that purported ecological relationships among torrent salamanders, geology, and stream gradients actually represented the extirpation of salamanders from low-gradient reaches after logging-induced sedimentation. Prior to logging, Columbia torrent salamanders were possibly more widely distributed and abundant in streams traversing marine sediment lithologies and in low-gradient reaches. For example, Corn and Bury (1989) did not find a relationship between abundance of torrent salamanders and gradient of streams flowing through uncut forests. However, Adams and Bury (2002) found that Olympic torrent salamanders were strongly associated with steep gradients even in an unharvested (i.e., old growth) forest preserve (Olympic National Park, Washington, USA).

The landform model suggested a potential effect of within-stream location on salamander abundance. Previous studies have reported higher occupancy rates and abundance of torrent salamanders in headwater streams when compared to downstream reaches (Hunter 1998, Wilkins and Peterson 2000, Stoddard 2001), and our data indicate that within headwater reaches, abundance was higher closer to the channel origin. In our study area, these channel heads often exhibited steeper gradients and larger accumulations of cobble and gravel substrates considered favorable for torrent salamanders.

Point samples conducted at the microhabitat scale by Diller and Wallace (1996) indicated strong positive associations between southern torrent salamanders and percentage of gravel substrates with low amounts of fine sediments. Welsh and Lind (1996) and Adams and Bury (2002) also reported that torrent salamander abundance increased when substrates were composed of gravel and cobble. Although our physical habitat model received marginal support, we found no strong evidence for an influence of streambed substrate on salamander abundance. We suspect that our sampling at the stream-reach scale probably masked smaller variations in microhabitats, and we think that conducting point samples similar to Diller and Wallace (1996) may have revealed stronger weight of evidence in favor of models with physical substrate parameters.

Several studies have reported associations between stand age or vegetation characteristics and stream-breeding amphibians, including torrent salamanders, in other regions of the PNW (e.g., Corn and Bury 1989; Bury et al. 1991; Welsh and Lind 1996, 2002). Given the management history of our study area, we were unable to include the full range of variation in stand ages and structures (e.g., old growth) historically found in the region. However, at least within the full range of stand characteristics that existed in our intensively managed landscape, we found that attributes of overstory or understory vegetation were not related to the distribution and density of Columbia torrent salamanders at either the landscape or stream-reach scales. At least 2 factors may explain the possible insensitivity of torrent salamanders (i.e., wide distribution and high abundance) to variation in vegetative conditions across our study area. First, in the Oregon Coast Range, plant growth is so rapid that post-harvest vegetation often grows as high as the base of tree crowns in adjacent, unharvested stands in as little as 10 years (Hibbs and Bower 2001). Thus, direct solar radiation and air flows quickly become limited and moist, humid microclimates similar to those of unharvested areas are quickly reestablished (Hibbs and Bower 2001). Deep (1–2 m) accumulations of post-logging debris (slash) across small stream channels also are common in recently harvested areas and may adequately buffer temperatures for stream salamanders (Jackson et al. 2001).

Second, we think the cool, moist climate across our study area—particularly near the coast—mitigates effects of periodic canopy removal on water temperatures (Diller and Wallace 1996; Welsh and Lind 1996, 2002). The narrow range of water temperatures measured in all streams during June and July (≤12 °C; Table 2) would suggest that existing vegetation and moderate climate of the area are sufficient to maintain favorable water temperatures for torrent salamanders (≤16 °C; Brattstrom 1963, Diller and Wallace 1996, Welsh and Lind 1996). However, within the more extreme climates associated with interior physiographic provinces (e.g., Cascade and Klamath-Siskiyou Ranges), removal of riparian vegetation may have more pronounced effects on the distribution and abundance of other torrent salamander species (Welsh and Lind 1996, Hunter 1998, Welsh et al. 2000, Steele 2001).

MANAGEMENT IMPLICATIONS

Our study suggests that abiotic parameters, operating at multiple spatial scales, may exert an important influence on the distribution and abundance of Columbia torrent salamanders. Similarly, in southeastern British Columbia, Sutherland and Bunnell (2001) found that physical habitat features had a greater influence than did riparian vegetation management on occurrence and abundance of larval tailed frogs (*Ascaphus truei*), a species with habitat requirements roughly similar to torrent salamanders. We agree with Hansen and Rotella (1999) that evaluations of forestry effects on wildlife need to move beyond the traditional focus on composition and structure of vegetation and integrate abiotic factors into research, management, and conservation plans. For example, in areas where abiotic features have much greater influence on habitat than human-induced changes in vegetation, existing practices designed to conserve headwater amphibian populations (e.g., riparian buffers) may be well-intentioned but ineffective (Sutherland and Bunnell 2001).

If torrent salamanders are indeed sensitive to sedimentation and physical substrate composition, and inherent differences exist in these characteristics related to gradient or parent geology (Table 2; Dupuis et al. 2000, Wilkins and Peterson 2000, Sutherland and Bunnell 2001), we suggest that low-gradient, marine sediment streams could represent less favorable habitats for torrent salamanders regardless of management regime. If this is the case, torrent salamanders may not benefit from protective measures implemented in low-gradient marine sediment streams (Sutherland and Bunnell 2001). Manipulative comparisons between streams in our study area and those traversing unmanaged, old-growth stands (e.g., Adams and Bury 2002) that have been properly stratified both by gradient and geology could provide insights into these questions.

Finally, our study highlights the complexity of elucidating habitat relationships of torrent salamanders and other PNW stream amphibians. For example, although multiple models indicated the importance of gradient, much of the variation in torrent salamander occurrence and abundance remained unexplained. Our study indicates that not only should abiotic features be included in future research, but different spatial scales of animal sampling and habitat parameters may be needed to appropriately evaluate patterns of occurrence and abundance (Diller and Wallace 1996, Hayes et al. 2002).

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