Herpetological Conservation and Biology 7(1):1-15
Submitted: 25 October 2011; Accepted: 22 March 2012; Published: 6 May 2012.

# HABITAT ASSOCIATIONS OF THE COASTAL GIANT SALAMANDER (*DICAMPTODON TENEBROSUS*) AT ITS NORTHERN RANGE LIMIT

***RACHAEL Y. DUDANIEC*[1] *AND JOHN S. RICHARDSON***

*Department of Forest Sciences, 2424-3041 Main Mall, University of British Columbia,*
*Vancouver, British Columbia V6T 1Z4, Canada*
[1]*Current Address: The University of Queensland, School of Geography, Planning and Environmental Management,*
*Brisbane, Queensland 4072, Australia*; *e-mail: rachael.dudaniec@gmail.com*

*Abstract.*—**Knowledge of species-environment associations is critical for the management of threatened amphibian populations facing habitat fragmentation and a restricted range. The Coastal Giant Salamander (*Dicamptodon tenebrosus*) is subject to habitat degradation from logging and human development and is classified as Threatened at its northern range limit in British Columbia, Canada. We examined habitat associations for *D. tenebrosus* in relation to relative abundance and presence/absence for 32 streams sampled across the approximately 100 km$^2$ range of the species in British Columbia. Of 12 environmental variables we measured at 100-m stream reaches and the adjacent riparian zone, *D. tenebrosus* relative abundance was positively associated with stream elevation, forest age, and the percentage of boulders within streams. A higher stream gradient was the best predictor of *D. tenebrosus* presence within a stream reach, with present sites having a 91% higher gradient than absent sites. When excluding sites with low relative abundance, *D. tenebrosus* presence was also predicted by greater forest age surrounding streams and higher site elevation. Our study highlights that conservation planning for stream-associated amphibians with patchy distributions may be improved by an understanding of species-specific habitat associations at the stream-reach scale.**

*Key Words.*—conservation; Coastal Giant Salamander; *Dicamptodon tenebrosus*; habitat associations; range limit; stream reach

## INTRODUCTION

Efforts to manage species of conservation concern depend on knowledge of a species' habitat requirements across multiple spatial scales. Non-field based, broad-scale, modeling approaches can be beneficial due to their relatively low costs and time effectiveness (Rotenberry et al. 2006), leading to questions on the importance of field-based habitat data for predicting species-environment associations in smaller, localized sites (Saveraid et al. 2001; Tingely et al. 2010). However, variations in site-level habitat relationships may become particularly relevant at local spatial scales, which are frequently the subject of species recovery plans and land management activities. In addition, understanding habitat relationships at species' range margins is particularly pertinent as these areas are typically of lower habitat quality, yet may be valuable for conserving evolutionary processes that generate diversity (Lesica and Allendorf 1995; Gibson et al. 2009).

The distribution of stream-associated species is not only influenced by broad-scale (e.g., catchment level) landscape characteristics, but is also closely coupled with riparian vegetation and hydrological and physical structure at the scale of stream reaches (Richardson et al. 2009). Landscape, stream reach, and microhabitat attributes may co-influence species assembly and consequent ecological processes within a stream (Lecerf and Richardson 2010), leading to patchy species distributions within an otherwise apparently continuous habitat type. Because stream amphibians occupy physically diverse and dynamic environments, models of species distributions that encompass local (e.g., stream reach) habitat features may outperform models based on regional geographic data alone (Welsh and Lind 2002; Tingely et al. 2010). Such models are particularly relevant for cryptic amphibians with specialized habitat requirements, a patchy distribution, poor dispersal capacity, and a limited range.

Although relatively abundant and widespread in the coastal Pacific United States, the Coastal Giant Salamander (*Dicamptodon tenebrosus*) is recognized as Threatened by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC), primarily due to habitat fragmentation from forestry practices, human recreation, and urban encroachment on its small Canadian range (Ferguson 2000; Curtis and Taylor 2003). The estimated 100 km$^2$ that the species occupies in Canada falls at the northern limits of its range (Fig. 1), which represents the forefront of northward range expansion under predicted climate change scenarios (Hamann and Wang 2006). Although numerous studies of habitat associations in *D. tenebrosus* have been conducted in the south and central parts of the species' range (e.g., Corn and Bury 1989; Parker 1991; Steele et al. 2002; Welsh and Lind 2002; Kroll et al. 2008), little is known of associations for populations at the northern range margin (Richardson and Neill 1998; Ferguson

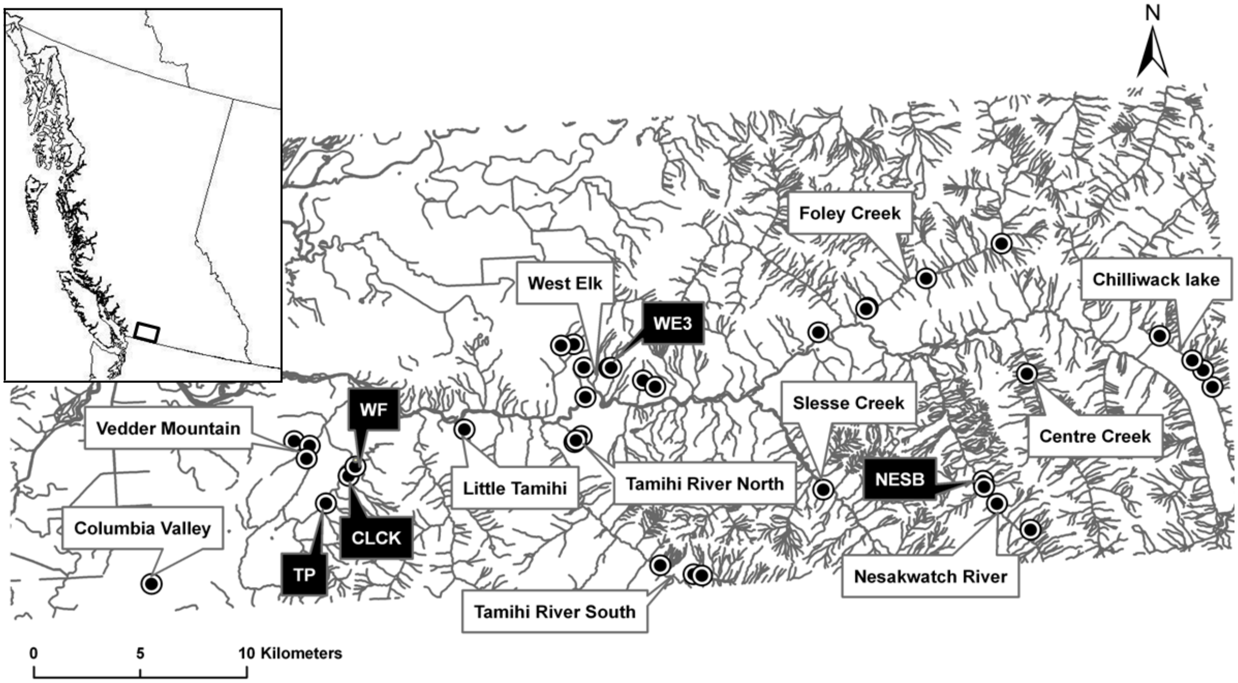


**FIGURE 1.** Inset showing location of sampling area in British Columbia (BC), Canada (rectangle). Large map shows locations of streams sampled in the Chilliwack Valley. Circles indicate sample sites. White labels indicate drainage names and black labels indicate streams where *D. tenebrosus* were absent. A complete listing of site names and abbreviations is provided in Appendix 1.

2000; Wilkins and Peterson 2000; Johnston and Frid 2002; Curtis and Taylor 2003). The threatened Canadian population is genetically differentiated from populations further south in Washington State, USA, and also exhibits different landscape genetic patterns and a smaller effective population size (Dudaniec et al. 2010; Dudaniec et al. in press). These patterns are likely reflective of the species' phylogeographic history in combination with contemporary landscape change. Therefore, *D. tenebrosus* is likely diverging due to genetic drift and natural selection at its periphery, so this area may be important for the species' evolutionary potential (Lesica and Allendorf 1995).

Logging activities have been linked to negative impacts on amphibians throughout the Pacific Northwest of North America (Hawkins et al. 1983; Curtis and Taylor 2003; Jackson et al. 2007; Olson et al. 2007; Kroll 2009). In Canada, forested habitat used by *D. tenebrosus* is declining, with timber harvesting having occurred in more than 25 km$^2$ within its range since 1985 (Ministry of Forests and Range, Chilliwack Forest District, pers. comm.). Here we tease apart the stream-reach habitat characteristics that are best able to predict *D. tenebrosus* presence/absence and abundance, which has direct implications for habitat management within the species' threatened range. For example, sustainable forestry practices in the region require specific recommendations regarding local, site-specific conservation needs, so that logging practices may be altered accordingly in sensitive areas (e.g., thinning versus clear-cutting, leaving buffer zones around highly productive streams).

We predict that relative abundance at sites will increase with time since forest harvest due to population recovery (e.g., as found in Corn and Bury 1989; Jackson et al. 2007) and that *D. tenebrous* presence, relative abundance, and body condition will be predicted by habitat characteristics at the stream-reach scale, using a combination of in-stream, topographical, and land use variables. By providing field-based data on how *D. tenebrous* distribution and abundance varies with environmental characteristics, better informed conservation planning will be made possible throughout the species' threatened range. This information will also be relevant to the conservation of other stream-associated amphibians that are subject to anthropogenic impacts.

## MATERIALS AND METHODS

***Study area and species.***—We studied *D. tenebrosus* distribution and abundance in headwater streams of the Chilliwack Valley of British Columbia, Canada, which falls within the coastal Western Hemlock (*Tsuga heterophylla*) biogeographic zone, otherwise known as 'temperate rainforest' (Krajina 1965). Elevation in the valley ranges from sea level to ~2500 m, and the dominant vegetation is coniferous forest consisting mainly of Western Red Cedar (*Thuja plicata*), Western Hemlock, and Douglas Fir (*Pseudotsuga menziesii*), with Big Leaf Maple (*Acer macrophyllum*) and Red Alder (*Alnus rubra*) common in riparian areas. The extent of our sampling area covered ~70 km$^2$ of the species' estimated 100 km$^2$ range within the Chilliwack Valley (Latitude: 121°39′48″, Longitude: 49°20′10″; Fig. 1). Larvae of *D. tenebrosus* are generally associated with coarse substrates in streams with intermediate to high gradient (range sampled: 10–50°), low amounts of fine sediments, and elevations ranging from 80–1,200 m (Corn and Bury 1989; Welsh and Ollivier 1998; Jackson et al. 2007). *Dicamptodon tenebrosus* may live up to 20 years or more and is facultatively paedomorphic. The aquatic, gill-breathing larval stage is estimated to last 3–4 y in British Columbia, followed by metamorphosis into the terrestrial adult or neotenic form (i.e., reproductive adults that remain gill-breathing, aquatic residents; Ferguson 1998). Both adult morphotypes may reach up to 35 cm in total length.

***Species sampling.***—We selected 48 study streams at elevations between 80 and 1,050 m, surrounded by forests ranging from 1 to 274 years old (mean ± SE = 74 ± 12.08; Appendix 1 and 2). We only chose streams that appeared permanent and avoided large streams (e.g., depth > 50 cm) that were less likely to contain *D. tenebrosus*, and where our search technique was less effective. A number of the chosen streams did not appear on maps. At each stream, in July and August of 2008 and 2009, 2–4 field technicians searched a 100 m reach (hereafter referred to as a 'site') along the entire wetted width in an upstream direction. We searched one, 100 m reach in each stream except for Fin Creek, where we searched two reaches that were approximately 500 m apart. Due to differences in elevation and habitat variables, these reaches are considered separate sites in the analysis (FIN01, FIN02; see Appendices 1–4). As the majority of streams crossed unpaved forestry access roads, we located reaches at least 20 m upstream from roads to minimize road disturbance effects on habitat stability and quality. We searched sites for 1–4 d (consecutively or over a one-week period) between 0900 and 1930, and calculated site relative abundance as a capture rate, being the total number of captured individuals at a site divided by the total number of search hours (summed for all searchers). We categorized streams as 'absent' if no *D. tenebrosus* were found after three total search hours of the entire 100 m stream reach. We found salamander larvae by gently poking and searching within all stream pools and crevices with a stick and using a flashlight to increase visibility. Small cobbles were gently overturned and replaced. This technique was effective in luring salamanders out of their refuges without disturbing the sediment, which can decrease visibility greatly and allow larvae to escape downstream. We swept all individuals into small aquarium dip nets held against the substrate and recorded the time of capture for each individual. We housed each salamander in a separate container of fresh stream water. Prior to processing, we anaesthetized each individual in a 0.5 g/L tricaine methanesulfonate (MS-222) solution (Fellers et al. 1994). We measured each individual for body mass (g), total length (mm), and snout-vent length (SVL; mm) and marked each individual on the lateral/ventral surface using visual implant elastomer (Northwest Marine Technology Inc., Shaw Island, Washington, USA) to prevent duplicate capture records between days and years. We took a 2 mm$^2$ tissue sample from the tail tip for use in a companion study. Following recovery from anaesthesia in fresh stream water (between 10–30 min), we returned individuals to their location of capture.

Adult morphotypes of *D. tenebrosus* show large variation in body size, so we refined our classifications using additional morphological indicators. We identified neotenes by a SVL ≥ 90 mm in combination with the presence of well-developed gills, an enlarged head, protruding eyes, and/or an enlarged cloaca. Transitioning metamorphs (those undergoing metamorphosis into terrestrial form) were identified by short gills (≤ 0.5 cm), protruding eyes, and little to no skin marbling. We conducted searches for terrestrial adults along stream reaches for 10 sites, up to 10 m to either side of the stream reach for 2–8 search hours (mean 4.33 ± 0.66) per stream. We thoroughly searched all potential refuges under vegetation, large wood, and bank crevices along each transect. We conducted searches primarily during rainy, cool days, in late afternoon, and at night. Terrestrial individuals were also found opportunistically.

***Habitat variables.***—Of the 48 sites searched, we measured stream reach habitat variables for 27 of the 35 sites in which *D. tenebrosus* was detected/present (consisting of 34 independent streams) and at five of the 14 sites where it was not detected/absent (total sites with habitat data = 32). We excluded the remaining sites from habitat data collection due to inaccessibility. We measured environmental variables based on those found to be relevant for *D. tenebrosus* movement, distribution, and abundance in previous studies (Corn and Bury 1989; Ferguson 2000; Welsh and Lind 2002; Kroll 2009; Dudaniec et al., unpubl. data). We collected data for 21 environmental variables encompassing topographical, in-stream, and riparian characteristics for each stream reach (Appendices 2–4). We chose sites that were accessible for measuring 100-m transects and that appeared to contain habitat that was suitable for *D. tenebrosus*, based on the available literature (e.g., larger substrates, pools, and riffles). Our study therefore tests and refines existing theory concerning the habitat associations of *D.*

*tenebrosus* at its northern range limit. We collected stream reach habitat data at 0, 25, 50, 75, and 100 m for the 32 sites sampled (Appendices 2–4). We used ArcMap 9.3.1 to determine forest age, elevation, site aspect, and gradient from vegetation layers and digital elevation models (GeoBase®; www. geobase.ca/ geobase/en/index.html. [Accessed July 2010]).

At each of the five reach points, we recorded the in-stream variables, water depth (cm), wetted width (cm), bank full width (cm), and substrate composition. We visually estimated substrate composition as the percentage of each substrate size class (boulder ≥ 25.6 cm, cobble = 6.5–25.6 cm, pebble = 3.2–6.4 cm, gravel = 0.2–3.1 cm, and sand and finer sediment ≤ 0.2 cm; Cummins 1974) within a 2-m strip (1 m upstream and 1 m downstream of the reach point; Appendix 3). We recorded riparian habitat characteristics along 10 m transects measured perpendicular to the stream at each reach point, using alternate sides of the stream at each point (Appendix 4). We recorded the following variables within a 5-m strip on either side of each 10 m transect: percentage shrub cover (visual estimate), tree species (number of each species and circumference at chest height for trees > 10 cm in circumference), number of pieces of large wood (LW: ≥ 1 m length and ≥ 20 cm diameter), and the percentage of large wood within three categories of decomposition (1 = recently fallen, wood firm and intact; 2 = partially decayed; 3 = late stage of decay, soft wood; Cummins 1974). All visual estimates were performed by the same individual (RYD) to reduce observer bias. We calculated tree species evenness and Shannon's Diversity Index (I) for tree species diversity at each site using an online calculator (Chang Bioscience, Shannon-Wiener Diversity Index Calculator; www.changbioscience.com/genetics/shannon.html, [Accessed August 2011]).

***Data analysis.***—We assessed relationships between salamander presence, abundance, and body condition score using several analytical approaches. We used correlation analysis first to test for co-linearity among explanatory variables (Appendix 5). If a pair of variables had a Pearson correlation coefficient greater than 0.5, we considered the two variables proxies of one another and one of the variables was removed from the analysis (Green 1979). We only used data collected during stream-reach searches for assessments of relative abundance and presence/absence at a site. For example, at one site a single terrestrial adult was encountered, but no aquatic *D. tenebrosus* were detected, and so this site was classified as absent as there was no evidence of breeding activity. We transformed all percentage data using arcsine square-root to meet normality assumptions.

We used a multivariate general linear model (GLM) with tests of between-subject effects (i.e., for each predictor variable against each of the two response variables: capture rate and body condition) to examine for effects of all environmental explanatory variables on relative abundance and body condition across sites (n = 27). To isolate the effects of habitat variables at the stream-reach scale, we excluded topographical variables within a second multivariate GLM for relative abundance and body condition. We averaged measurements for each habitat variable at each site for these analyses. We calculated salamander body condition from the residuals of an ordinary least squares regression of $\log_{10}$-transformed body mass and $\log_{10}$-transformed SVL (Schulte-Hostedde et al. 2005). We averaged body condition across all individuals at each site and excluded individual salamanders from body condition multivariate analyses if any variable was missing from the dataset. We also excluded missing data from stream habitat analyses.

We conducted presence/absence analyses using two models; including all sites, and including sites with > 1.5 individuals per hour (n = 12, Appendix 1) to ensure that only sites with larger populations were compared against sites without detections (n = 5). Thus for model 2, present sites only included those with high relative abundance to minimize potential bias in classification of a site as absent. To test which habitat characteristics were most powerful at predicting presence or absence at a site, we conducted two-group stepwise Discriminant Function Analysis (DFA). All variables were entered into DFA analyses (i.e., for models 1 and 2) to test for the strongest environmental predictor variables for *D. tenebrosus* presence or absence.

Detectability of amphibians may vary throughout the day due to fluctuating temperatures and activity levels, and surveys conducted across multiple days may exhibit a 'learning curve effect' among searchers, whereby estimated relative abundance increases according to the time spent searching (or number of visits per site; MacKenzie et al. 2003; Bailey et al. 2004). Therefore, we examined for temporal effects on our relative abundance estimates throughout the day and across search days. We calculated the percentage of individuals caught at each site (pooling all search days) for three time periods: morning (0900–1200), early afternoon (1201–1500), and late afternoon/evening (1501–1930). We then conducted ANOVA on the percentage of the total number of individuals caught at a site (response variable) with the fixed factors 'time period,' and 'number of days site was searched at each time period' (range = 1–4 days), which was included to examine for an interaction effect of sampling effort with relative abundance. We did not have data for hourly or per person search effort at every time period, as search hours were totalled for all searchers on a per day basis. A potential bias in animal surveys is higher detection with increasing sampling effort. Therefore, we also tested for an effect of 'search day number' on per day capture rates using simple linear regression to examine whether estimated relative abundance increased with the number of times a site was visited. We used PASW Statistics 18.0 for Mac (SPSS Inc. 2011) to conduct all analyses. Data are presented as mean ± 1 standard error (SE) and significance of tests was assessed using an alpha level of 0.05.

## RESULTS

***Presence/absence and relative abundance.***—We detected *D. tenebrosus* in 34 out of 48 surveyed streams (70.8%) in the Chilliwack Valley. At these sites, the relative abundance of salamanders (excluding terrestrial adults) ranged from 0.09–4.20 individuals captured per hour (mean = 1.63 ± 0.20 SE individuals per hour). Across all streams we captured 856 salamanders, with 1–63 individuals per stream (Appendix 1). We recaptured only 12 larvae from seven sites in 2009 that had been tagged in 2008 (1–2 larvae per site), precluding mark-recapture analyses. These recaptured individuals were only analyzed for body size in 2008. Larvae and adult morphotypes of *D. tenebrosus* exhibited a wide range of body sizes (Table 1). We found only two terrestrial adults during timed riparian searches (22% of total), and found the remaining seven either within the stream during stream searches, or encountered them opportunistically on stream banks. The percentage of individuals caught at sites did not differ across the three time periods (mean ± SE: morning = 32.2 ± 3.1%; early afternoon = 39.9 ± 4.1%; late afternoon/evening = 27.4 ± 3.6%; $F_{2,60} = 1.86$, n = 20, $P > 0.1$; Fig. 2). There was no significant interaction effect of 'time period · number of days site searched at time period' on the percentage of captures at each time period ($F_{5,60} = 2.30$, $P = 0.059$). There was no significant effect of 'search day number' on 'per day capture rate' ($b = -0.056$, $P > 0.6$; $R^2 = 0.003$); therefore, detectability did not increase with site visitation.

***Habitat associations***.—Overall there was low to moderate colinearity across the 21 explanatory habitat variables (Appendix 5). However, nine variables showed consistently high colinearity with one or more variables ($r > 0.5$) and were randomly excluded, resulting in 12 variables for analysis (Appendix 5). Relative abundance was significantly higher in older forests and at higher elevation sites (Multivariate GLM: $R^2 = 0.69$; elevation: $F_{1,14} = 8.47$, $P < 0.02$; time since forest harvest: $F_{1,14} = 5.12$, $P < 0.04$; Fig. 3). There was no significant effect of any environmental variable on body condition (all $P > 0.1$). With topographical/forest age variables excluded from the regression, relative abundance increased with the percentage of boulders at a site (Multivariate GLM: $R^2 = 0.40$; % boulders: $F_{1,18} = 4.85$, $P < 0.05$). Again, no variables were significantly related to body condition. For DFA analyses stream gradient was identified as the best variable for classifying present from absent sites (all sites: $F_{1,30} = 14.11$, $P < 0.01$) with 81.3% of cases correctly classified (Table 2). When only the 12 high relative abundance sites were included, 88.2% of cases were correctly classified and gradient remained in the best model ($F_{1,15} = 6.49$, $P < 0.03$), with the additional effects of elevation ($F_{1,15} = 11.37$, $P < 0.01$), and time since forest harvest ($F_{1,15} = 6.41$, $P < 0.02$; Table 2).

**TABLE 1.** Measurements of snout-vent length (SVL) and body mass (g) for four life-stages of *D. tenebrosus* in the Chilliwack Valley, British Columbia, Canada. Values are range (mean ± SE). n = sample size.

| Life stage | n | SVL (cm) | Body mass (g) |
|---|---|---|---|
| Larva | 811 | 1.7–9.0<br>(4.5 ± 0.06) | 0.44–34<br>(5.7 ± 0.2) |
| Neotenes | 20 | 7.7–13.0<br>(9.8 ± 0.31) | 19.6–83.0<br>(38.9 ± 3.75) |
| In metamorphosis | 10 | 7.0–10.0<br>(8.2 ± 0.28) | 14.0–42.0<br>(21.9 ± 2.6) |
| Terrestrial adult | 9 | 7.4–14.7<br>(11.1 ± 0.99) | 16.0–118.0<br>(62.2 ± 14.8) |

## DISCUSSION

***Habitat associations and effects of forest harvest.***—We identified influential effects of environmental variables on presence/absence and abundance of *D. tenebrosus* within its threatened northern range. Negative impacts of forest harvest on *D. tenebrosus* relative abundance were evident, which is consistent with some (e.g., Corn and Bury 1989; Jackson et al. 2007; Kroll et al. 2008), but not all (Steele et al. 2002; Welsh and Lind 2002) previous studies. Relative abundance varied substantially in forests up to ~100 y of age, but increased in stands between 100–271 y, though our small sample size of older forests may underestimate the existing variation. However, studies in core locations of the species' range have found increases in abundance or occupancy of *D. tenebrosus* across a narrower range of forest ages (e.g., 14–40 y, Corn and Bury 1989; 0-70 y, Kroll et al. 2008). To our knowledge this study is the first to report changes in relative abundance with forest age in British Columbia, where lower genetic diversity in harvested sites and restricted dispersal from clear-cut streams has been found (Richardson and Neil 1998; Johnston and Frid 2002; Curtis and Taylor 2003).

In-stream (Welsh and Lind 2002) or ground surface (Kluber et al. 2008) conditions have been found to be better predictors of *D. tenebrosus* presence and abundance than the surrounding forest conditions. Site-specific variation in fine-scale habitat characteristics

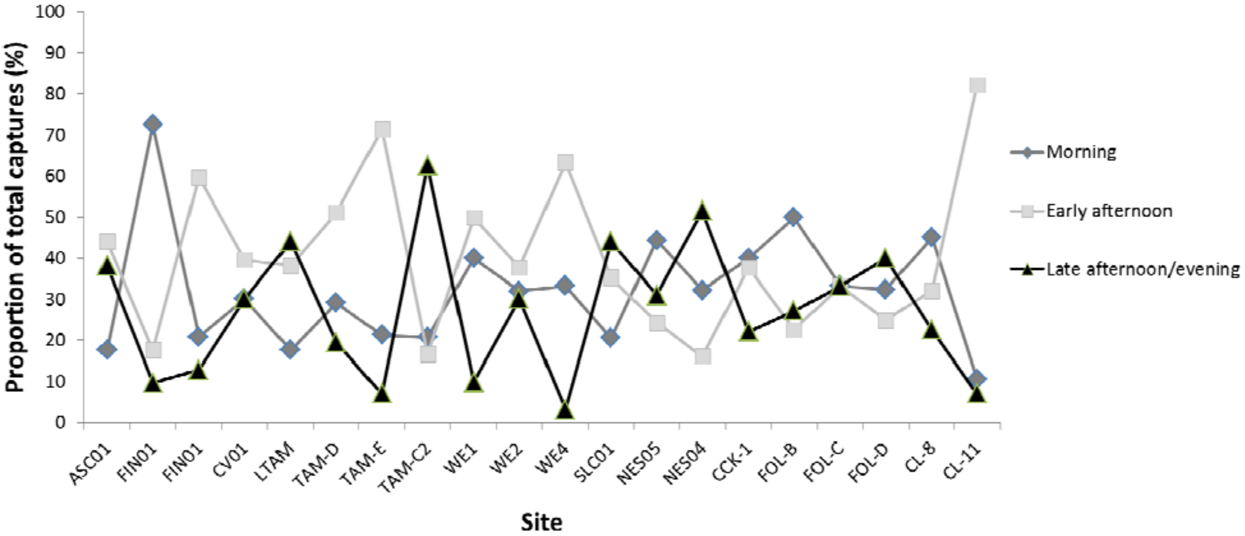


**FIGURE 2.** Time of day (morning, early afternoon, late afternoon/evening) in relation to the percentage of captures caught within each time period. Data are presented only for sites at which searches were conducted during all three time periods (n = 20 sites).

across a mosaic of harvested forest patches may therefore obscure any direct effect of forest age on stream-associated amphibians. However we found that topographical stream characteristics (i.e., elevation, gradient) and forest age were the best explanatory variables for site presence/absence and relative abundance. Yet when only in-stream and riparian variables are analyzed, the percentage of boulders within the stream has a positive effect on relative abundance, suggesting that substrate composition is indeed important for this species. Notably, we did not find any significant relationships between our measured habitat variables and salamander body condition.

Although some previous studies of *D. tenebrosus* have failed to find a difference in habitat between occupied and unoccupied sites (e.g., in the South Cascade Mountains; Steele et al. 2002), our data show that stream gradient is highly informative for classifying streams where salamanders were present or absent. This is consistent with previous descriptions of the species' habitat associations (e.g., Wilkins and Peterson 2000) despite our small sample size of absent sites; however, a larger sample size may reveal additional explanatory variables. Higher stream gradients may positively affect *D. tenebrosus* by facilitating the flushing of fine sediments that block refuge areas created by coarse substrates (Murphy and Hall 1981; Kroll 2009). Steep streams are also subject to structural failures (e.g., rock slides and avalanches), which increase in frequency with forest harvest and alter the transport of stream sediment (Church 2010). Previous studies have found that low stream sedimentation and course rocky substrates support a higher density of *D. tenebrosus* (Parker 1991; Welsh and Ollivier 1998).

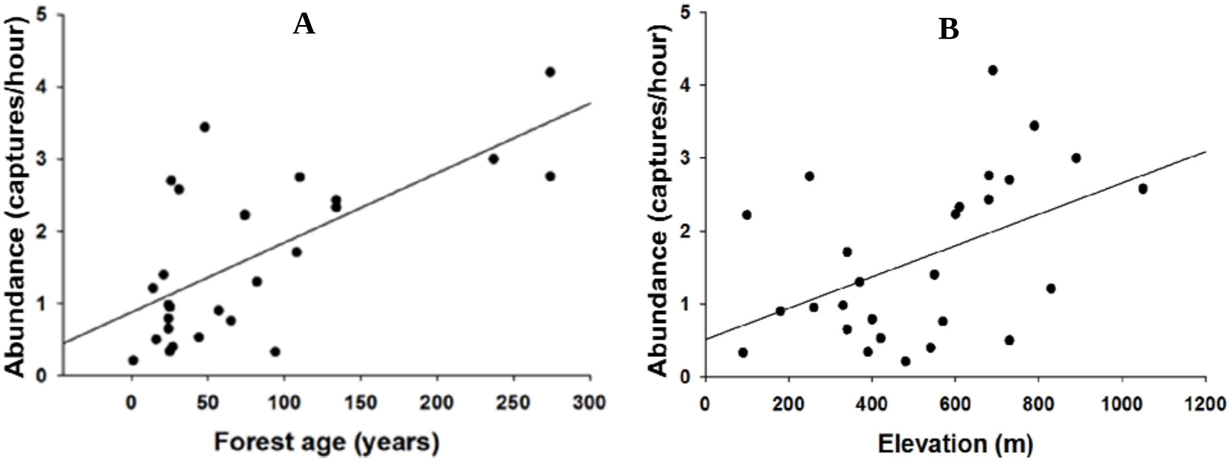


**FIGURE 3.** Relative abundance of *D. tenebrosus* within stream reaches, represented as captures/ search hour in relation to A) time since forest harvest (years), and B) elevation (meters; model $R^2 = 0.69$, n = 27 present sites).

**TABLE 2.** Values of landscape and habitat variables (mean ± SE) in sites where *D. tenebrosus* was present (sample sizes below) or absent (n = 5). Results are presented for two Discriminant Function Analysis (DFA) models. Values are presented for all sites where *D. tenebrosus* was present (Model 1, present n = 27 sites) and for those sites with high relative abundance (i.e., capture rates > 1.5 per hour; Model 2, abundant n = 12 sites). Exact F-values are presented for each model. Stream gradient (in bold) was significant at $P < 0.05$ in both Model 1 ($P = 0.001$) and Model 2 ($P = 0.022$). Italicized variables are those that were significant in addition to stream gradient in Model 2 only (for elevation $P = 0.001$; for years since forest harvest, $P = 0.011$).

| | | Mean ± SE | | | Exact F | |
|---|---|---|---|---|---|---|
| Classification | Variable | Any Presence Sites: Model 1 | High Abundance Sites: Model 2 | Undetected | Model 1 | Model 2 |
| Topographical/Land use | *elevation (m)* | *514 (20.7)* | *617.5 (33.5)* | *344 (69.2)* | *1.7* | *2.9* |
| | aspect (degrees) | 197.2 (8.2) | 274 (8.0) | 274 (8.0) | 2.2 | 2.5 |
| | stream gradient (deg) | 30.3 (0.9) | 28.7 (1.5) | 15.8 (1.0) | 14.1 | 6.5 |
| | *years since forest harvest* | *76.6 (6.5)* | *127 (11.1)* | *79.4 (6.8)* | *0.5* | *0.8* |
| Riparian/In-stream | tree species diversity (I) | 1.3 (0.0) | 1.3 (0.0) | 1.2 (0.1) | 1.4 | 3.9 |
| | tree species evenness (E) | 0.9 (0.0) | 0.9 (0.0) | 0.80(0.1) | 0.9 | 2.4 |
| | tree girth (cm) | 73.0 (7.3) | 79.5 (6.9) | 99.1 (18.1) | 2.0 | 0.7 |
| | # large wood | 6.5 (0.4) | 6.7 (0.6) | 4.7 (0.7) | 2.1 | 1.6 |
| | % large wood category 3 | 34.8 (2.6) | 41.0 (3.7) | 32.1 (5.5) | 0.0 | 0.5 |
| | % shrub cover | 42.8 (2.1) | 39.5 (3.4) | 53.2 (5.9) | 1.4 | 2.1 |
| | % boulders in stream | 27.1 (1.9) | 31.8 (3.0) | 17.4 (4.3) | 1.8 | 3.4 |
| | % stream bank full | 53.0 (1.7) | 51.1 (2.6) | 36.1 (3.8) | 7.2 | 4.4 |

The significant effect of ‘time since forest harvest’ was less intuitive, with absent sites being situated in slightly older forests than present sites. Although this indicates that forest age may not be a vital factor for *D. tenebrosus* presence, the opposite conclusion may be drawn from our results for relative abundance. This result is likely because three out of the five absent sites were situated close to developed areas where forest harvest has not occurred for many decades (i.e., Cultus Lake). Therefore, our results do not rule out an effect of forest age on site colonization and breeding activity. Notably, environmental predictors of presence or absence at species peripheries likely represent a snap shot in time, as peripheral populations may not be in equilibrium; they may be expanding or contracting. Therefore, unoccupied areas may not be unsuitable for colonization, but rather have not yet been colonized due to non-equilibrium population dynamics (Hoffman and Blows 1994; Lesica and Allendorf 1995; Kawecki 2008). Although Curtis and Taylor (2003) reported reduced genetic diversity in *D. tenebrosus* at high elevation sites within our study area, we found higher relative abundance at higher elevations. This suggests that environmental factors (e.g., higher stream productivity and resource availability) may support larger population sizes at higher elevation, but the number of breeding individuals may be fewer (e.g., effective population size), with less migration and gene flow compared with lower elevation streams (Dudaniec et al., unpubl. data).

As for most stream-associated amphibians, *D. tenebrosus* is highly sedentary and dependent on locally suitable aquatic conditions and substrate, with estimates of net larval movement rates of just 1–20 m per season (Ferguson 1998; Johnston and Frid 2002). Greater cover availability (i.e., in the form of cobbles, wood, etc.) and substrate size have been associated with higher larval densities and site occupancy in *D. tenebrosus* (Parker 1991) and can affect oviposition behavior and reproductive investment in other salamander species (Sadeh et al. 2009). Thus, anthropogenic impacts on habitat availability, such as modified stream hydrology from catchment disturbance, are likely to have profound effects on *D. tenebrosus* populations.

***Detection rates.***—The probability of detection is a clear concern in amphibian studies (MacKenzie et al. 2003; Kroll et al. 2008). Previous studies of *D. tenebrosus* estimate that a sizeable proportion of the larval population is missed on a given sampling occasion due to the complex three-dimensional structure of the stream habitat (Richardson and Neill 1998; Ferguson 2000). Our stream sampling was conducted over the summer months when flows were low, allowing better visibility and access to refuges. Our sampling technique also minimized habitat disturbance such that the stream water did not become turbid during searches, enabling all encountered individuals to be captured and measured.

**TABLE 3.** Description of explanatory variables (landscape, riparian, and in-stream) used within predictive models of relative abundance and presence/absence of *D. tenebrosus*. Ecological justification for each variable is presented with selected references referring to supporting evidence for *Dicamptodon* species.

| **Variable** | **Units** | **Description** | **Justification** |
|---|---|---|---|
| *Topographical/land use* | | | |
| elevation | meters | Elevation at midpoint of 100-m stream reach | Population connectivity and abundance can be reduced at high elevation streams[1] |
| aspect | degrees | Facing aspect of 100-m stream reach | Affects solar radiation exposure and site primary productivity[2] |
| gradient | degrees | Gradient measured between 0 and 100 m of stream reach | High gradient streams have decreased sedimentation and provide favorable habitat[2,3,4] |
| time since forest harvest | years | Average years since harvest of forest plots surrounding 100-m stream reach | Logging has negative effects on population abundance, connectivity, and genetic diversity[1,2,5,6] |
| *Riparian* | | | |
| tree species diversity | Shannon's I | Shannon's Diversity Index (I) for number of tree species within riparian transects | Affects site habitat structure, site productivity, and basal resource heterogeneity[4,5] |
| tree species evenness | | Relative distribution of tree species, calculated from Shannon-Wiener Index | Same as for tree species diversity[4,5] |
| tree girth | centimeters | Girth measured at chest height for trees in riparian transects | Larger trees are associated with older forest, which provides favorable habitat[1,7] |
| shrub cover | percent | Estimated percentage of shrubs covering ground in riparian transects | Shrubs provide refuge and dispersal cover for terrestrial individuals[2] |
| large wood | count | Number of large woody debris in riparian transects | Large wood is used for refuge by terrestrial individuals[2,8] |
| decomposed large wood | percent | Estimated percentage of large wood in late stage of decay (category 3) in riparian transects | Terrestrial individuals utilize decomposed, rotting wood as refuge habitat[2, 4,8] |
| *In-stream* | | | |
| boulders in stream | percent | Estimated percentage of boulders within the stream substrate | Aquatic individuals utilize large substrates for refuge[2, 4] |
| stream bank full | percent | Percentage of stream full of water calculated as wetted width/bank full width × 100 | Higher abundance of individuals in flowing, permanent streams with many pools and riffles[9] |

[1]Curtis and Taylor (2003); [2]Welsh and Lind (2002); [3]Richardson et al. (2009); [4]Hawkins et al. (1983); [5]Steele et al. (2002); [6]Johnston and Frid (2002); [7]Corn and Bury (1989); [8]Wilkins and Peterson (2000); [9]Ferguson (1998).

Terrestrial searches were done primarily during rainy days to capitalize on the higher surface activity of amphibians. We also compared results when excluding sites with low relative abundance in a separate analysis, with almost identical findings. We found little evidence for temporal effects on estimated relative abundance, with no significant difference between morning, early afternoon, and late afternoon. Furthermore, per day estimates of relative abundance were unrelated to the number of days a site was searched. Although these results are clear, we acknowledge that several unmeasured variables may have increased the variation in our estimates of relative abundance, such as weather conditions, site accessibility, the number of searchers at each time period, and the duration of searches at each time period.

***Conclusions.***—Dicamptodontid salamanders often represent the highest predator biomass within small headwater streams of the Pacific Northwest, particularly in the absence of fish (Hawkins et al. 1983; Corn and Bury 1989). Therefore, conservation of *D. tenebrosus* is in the interests of maintaining top-down food web processes and ecosystem services within streams (Lecerf and Richardson 2010). Our study suggests that field-based data at small spatial scales (e.g., the stream reach) are informative for predicting habitat features that support *D.tenebrosus,* though the explanatory power of these data in relation to broad-scale models and measures of landscape connectivity remains to be examined (e.g., Zanini et al 2009). For example, Lowe and Bolger (2002) found that landscape-level population connectivity may 'buffer' negative impacts of stream-scale habitat perturbations in Plethodontid salamanders. However, our results emphasize the importance of high gradient, high elevation streams for *D. tenebrosus* presence and abundance, with evidence for larger populations in older forest. Combined with the information on the distribution and relative abundance of *D. tenebrosus*, our study provides a strong reference point for prioritizing conservation actions at local spatial scales within the species' range limit where it is threatened.

*Acknowledgments.*—This research was conducted with approval of the Animal Care Committee of the University of British Columbia (permit A08-0241) in accordance with the Canadian Council on Animal Care. We thank all field assistants who helped with data collection for this project, in particular, Xavier Pinto, Silven Read, Kirsty Quinlan, Timothy Clark, Diane Boyd, Purnima Govindarajulu, Azadeh Faghihi, Graeme Grant, Stefanie Hartmann, and Daniel Hudson. We thank Eric Taylor, Kim Welstead, and Denis Knopp for helpful discussions. We thank the Canadian Department of National Defence (Chilliwack), Cultus Lake Provincial Park, the Ministry of Forests and Range, and the Chilliwack Hatchery for permission to work on private lands.

## LITERATURE CITED

Bailey, L., T.R. Simons, and K.H. Pollock. 2004. Estimating site occupancy and species detection probability parameters for terrestrial salamanders. Ecological Applications 14:692–702.

Church, M. 2010. Chapter 2: Mountains and montane channels. Pp. 17–53 *In* Sediment Cascades: an Integrated Approach. Burt, T., and R. Allison (Eds.). John Wiley & Sons, Inc., Sussex, UK.

Corn, P.S., and R.B. Bury. 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. Forest Ecology and Management 29:39–57.

Cummins, K.W. 1974. Structure and function of stream ecosystems. Bioscience 24:631–641.

Curtis, J.M.R., and E.B. Taylor. 2003. The genetic structure of Coastal Giant Salamanders (*Dicamptodon tenebrosus*) in a managed forest. Biological Conservation 115:45–54.

Dudaniec, R.Y., S.F. Spear, J.S. Richardson, and Storfer A. in press. Current and historical drivers of landscape genetic patterns differ in core and peripheral salamander populations. PLoS ONE.

Dudaniec, R.Y., A. Storfer, S.F. Spear, and J.S. Richardson. 2010. New microsatellite markers for examining genetic variation in peripheral and core populations of the Coastal Giant Salamander (*Dicamptodon tenebrosus*). PLoS ONE 5:e14333.

Fellers, G.M., C.A. Drost, and W.R. Heyer. 1994. Appendix 1: Handling live amphibians. Pp. 275–276 *In* Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians. Heyer, W.R., M.A. Donnelly, R.W. McDiarmid, L.C. Hayek, and M.S. Foster (Eds.). Smithsonian Books, Washington, D.C., USA.

Ferguson, H.M. 1998. Demography, dispersal and colonisation of larvae of Pacific Giant Salamanders (*Dicamptodon tenebrosus*) at the northern extent of their range. M.Sc. Thesis, University of British Columbia, Vancouver, Canada.

Ferguson, H.M. 2000. Larval colonisation and recruitment in the Pacific Giant Salamander (*Dicamptodon tenebrosus*) in British Columbia. Canadian Journal of Zoology 78:1238–1242.

Gibson, S.Y., R.C. Van der Marel, and B.M. Starzomski. 2009. Climate change and conservation of leading-edge peripheral populations. Conservation Biology 23:1369–1373.

Green, R.H. 1979. Sampling Design and Statistical Methods for Environmental Biologists. Wiley, New York, New York, USA.

Hamann, A., and T. Wang. 2006. Potential effects of climate change on ecosystem and tree species distribution in British Columbia. Ecology 87:2773–2786.

Hawkins, C.P., M.L. Murphy, N.H. Anderson, and M.A. Wilzbach. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the north-western United States. Canadian Journal of Fisheries and Aquatic Sciences 40:1173–1185.

Hoffmann, A.A., and M.W. Blows. 1994. Species borders: ecological and evolutionary perspectives. Trends in Ecology and Evolution 9:223–227.

Jackson, C.R., D.P. Batzer, S.S. Cross, S.M. Haggarty, and C.A. Sturm. 2007. Headwater streams and timber harvest: channel, macroinvertebrate, and amphibian response and recovery. Forest Science 53:356–370.

Johnston, B., and L. Frid. 2002. Clearcut logging restricts the movement of terrestrial Pacific Giant Salamanders (*Dicamptodon tenebrosus* Good). Canadian Journal of Zoology 80:2170–2177.

Kawecki, T.J. 2008. Adaptation to marginal habitats. Annual Review of Ecology, Evolution, and Systematics 39:321–342.

Kluber, M.R., D.H. Olson, and K.J. Puettmann. 2008. Amphibian distributions in riparian and upslope areas and their habitat associations on managed forest landscapes in the Oregon coast range. Forest Ecology and Management 256:529–535.

Krajina, V.J 1965. Biogeoclimatic zones and classification of British Columbia. Ecology of Western North America 1:1–17.

Kroll, A.J. 2009. Sources of uncertainty in stream-associated amphibian ecology and responses to forest management in the Pacific Northwest, USA: a review.

Forest Ecology and Management 257:1188–1199.

Kroll, A.J., K. Risenhoover, T. McBride, E. Beach, and B.J. Kernohan. 2008. Factors influencing stream occupancy and detection probability parameters of stream-associated amphibians in commercial forests of Oregon and Washington, USA. Forest Ecology and Management 255:3726–3735.

Lecerf, A., and J.S. Richardson. 2010. Biodiversity-ecosystem function research: insights gained from streams. River Research and Applications 26:45–54.

Lesica, P., and F.W. Allendorf. 1995. When are peripheral populations valuable for conservation? Conservation Biology 9:753–760.

Lowe, W.H., and G.T. Bolger. 2002. Local and landscape scale predictors of salamander abundance in New Hampshire headwater streams. Conservation Biology 16:183–193.

MacKenzie, D.I., J.D. Nichols, J.E. Hines, M.G. Knutson, and A.B. Franklin. 2003. Estimating site occupancy, colonization and local extinction when a species is detected imperfectly. Ecology 84:2200–2207.

Murphy, M.L., and J.D. Hall. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences 38:137–145.

Olson, D.H., P.D. Anderson, C.A. Frissell, H.H. Welsh, and D.F. Bradford. 2007. Biodiversity management approaches for stream-riparian areas: perspectives for Pacific Northwest headwater forests, microclimates, and amphibians. Forest Ecology and Management 246:81–107.

Parker, M.S. 1991. Relationship between cover availability and larval Pacific Giant Salamander density. Journal of Herpetology 25:355–357.

SPSS Inc. 2011. PASW Statistics 18.0 for Mac. Chicago, Illinois, USA.

Richardson, J.S., T.M. Hoover, and A. Lecerf. 2009. Coarse particulate organic matter dynamics in small streams: towards linking function to physical structure. Freshwater Biology 54:2116–2126.

Richardson, J.S., and W.E. Neill. 1998. Headwater amphibians and forestry in British Columbia: Pacific Giant Salamanders and Tailed Frogs. Northwest Science 72:122–123.

Rotenberry, J.T., K.L. Preston, and S.T. Knick. 2006. GIS-based niche modelling for mapping species' habitat. Ecology 87:1458–1464.

Sadeh, A., M. Mangel, and L. Blaustein. 2009. Context-dependent reproductive habitat selection: the interactive roles of structural complexity and cannibalistic conspecifics. Ecology Letters 12:1158–1164.

Saveraid, E.H., D.M. Debinski, K. Kindscher, and M.E. Jakubauskas. 2001. A comparison of satellite data and landscape variables in predicting bird species occurrences in the Greater Yellowstone Ecosystem, USA. Landscape Ecology 16:71–83.

Schulte-Hostedde, A.I., B. Zinner, J.S. Millar, and G.J. Hickling. 2005. Restitution of mass-size residuals: validating body condition indices. Ecology 86:155–163.

Steele, C.A., E.D.J. Brodie, and J.G. MacCracken. 2002. Influence of forest age on densities of Cope's and Pacific Giant Salamanders. Northwest Science 76:347–352.

Tingely, R., T.B. Herman, M.D. Pulsifer, D.G. McCurdy, and J.P. Stephens. 2010. Intra-specific niche partitioning obscures the importance of fine-scale habitat data in species distribution models. Biodiversity and Conservation 19:2455–2467.

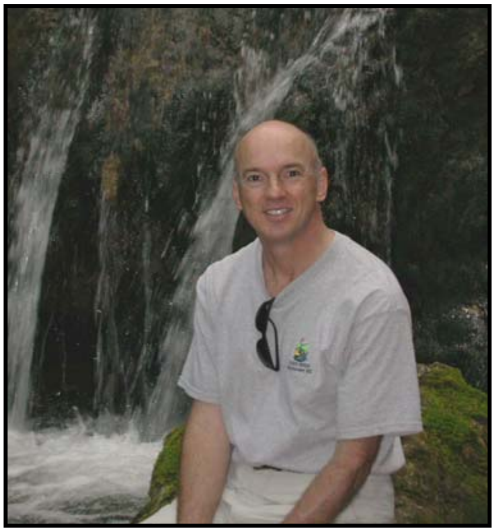
Welsh, H.H., and A.J. Lind. 2002. Multiscale habitat relationships of stream amphibians in the Klamath-Siskiyou region of California and Oregon. Journal of Wildlife Management 66:581–602.

Welsh, H.H., and L.M. Ollivier. 1998. Stream amphibians as indicators of ecosystem stress: a case study from California's redwoods. Ecological Applications 8:1118–1132.

Wilkins, R.N., and N.P. Peterson. 2000. Factors related to amphibian occurrence and abundance in headwater streams draining second-growth Douglas-fir forests in southwestern Washington. Forest Ecology and Management 139:79–91.

Zanini, F., J. Pellet, and B.R. Schmidt. 2009. The transferability of distribution models across regions: an amphibian case study. Diversity and Distributions 15:469–480.

**RACHAEL Y. DUDANIEC** is a Conservation Geneticist who is involved in research on a range of taxa, including birds, parasites, salamanders, and mammals. She received her Bachelor of Science (Honours) and Ph.D. from Flinders University in South Australia. Her Ph.D. research investigated the impact and genetic structure of an introduced parasitic fly (*Philornis downsi*) to the Galapagos Islands, Ecuador, which causes very high mortality in Darwin's finches. In British Columbia, Canada, her post-doctoral research investigated landscape genetic patterns and habitat associations of the Coastal Giant Salamander, which is provincially listed as threatened. Rachael is also interested in the evolutionary divergence of island and mainland species and the impacts of biological invasions. She is currently a post-doctoral researcher at the University of Queensland, Australia, where she conducts projects in landscape and conservation genetics for Australian native mammals. (Photographed by Kirsty Quinlan)



**JOHN S. RICHARDSON** is a Professor at the University of British Columbia. His research program addresses questions related to the mechanisms that structure stream and riparian area communities, and how various land-use practices affect those systems. He is on the editorial boards of two international journals and sits on two endangered amphibian recovery teams. He teaches about aquatic and riparian ecosystems and the organisms they sustain. More on his work can be found at http://faculty.forestry.ubc.ca/richardson/. (Photographed by John Richardson)

# Appendices

**Appendix 1**. Sample size (n) of larvae, adult morphotypes, and capture rates (relative abundance) for aquatic *Dicamptodon tenebrosus* within 34 detected sites in the Chilliwack Valley. Abbreviations are n larvae = number of larvae; n neo = number of neotenes; n tran = number of transitioning metamorphs.

| Drainage/Location | Site ID | n larvae | n neo | n tran | Captures/ hour |
|---|---|---|---|---|---|
| Vedder Mountain | ASC | 32 | 1 | 1 | 0.33 |
| | FIN01 | 51 | 0 | 1 | 2.22 |
| | FIN02 | 60 | 2 | 1 | 1.30 |
| Columbia Valley | CV01 | 49 | 3 | 2 | 2.75 |
| Little Tamihi | LTAM | 34 | 0 | 3 | 0.95 |
| Tamihi River North | TAM-D | 38 | 0 | 1 | 0.65 |
| | TAM-E | 28 | 0 | 0 | 0.98 |
| | TAM-F | 35 | 0 | 0 | 1.71 |
| Tamihi River South | TAM01† | 1 | 0 | 0 | 0.20 |
| | TAM03† | 1 | 0 | 0 | 0.09 |
| | TAM-C1† | 2 | 0 | 0 | 0.50 |
| | TAM-C2 | 22 | 2 | 0 | 0.50 |
| West Elk | WE-C | 2 | 0 | 0 | 0.21 |
| | WE1 | 20 | 0 | 0 | 0.76 |
| | WE2 | 52 | 1 | 0 | 2.33 |
| | WE3* | 0 | 0 | 0 | 0.00 |
| | WE4 | 29 | 1 | 0 | 2.22 |
| | WE5 | 1 | 0 | 0 | 0.40 |
| | WE6† | 3 | 0 | 0 | 0.75 |
| | SP01 | 18 | 0 | 0 | 0.90 |
| Slesse Creek | SLC01 | 34 | 0 | 0 | 0.79 |
| Nesakwatch River | NES05 | 35 | 0 | 0 | 3.00 |
| | NES04 | 32 | 0 | 0 | 2.58 |
| | NES-C | 17 | 2 | 0 | 1.21 |
| Center Creek | CCK-1 | 43 | 1 | 0 | 3.44 |
| Foley Creek | FOL-B | 21 | 0 | 0 | 0.53 |
| | FOL-C | 9 | 0 | 1 | 0.33 |
| | FOL-D | 38 | 1 | 0 | 2.70 |
| | FOL-F | 7 | 0 | 0 | 1.40 |
| | FOL-G† | 16 | 0 | 0 | 1.71 |
| Chilliwack Lake | CL-1 | 41 | 1 | 0 | 4.20 |
| | CL-5† | 1 | 0 | 0 | 0.50 |
| | CL-8 | 31 | 0 | 0 | 2.76 |
| | CL-11 | 28 | 0 | 0 | 2.43 |

† Stream habitat data were not recorded due to inaccessibility.
* One terrestrial adult was found at this stream.

**Appendix 2. Summary of topographical/land use variables for 32 stream reaches (100 m) that were searched for Dicamptodon tenebrosus.**

| Site name | Elevation (m) | Time since forest harvest (years) | Aspect (degrees) | Stream gradient (degrees) |
|---|---|---|---|---|
| ASC | 90 | 94 | 85 | 28 |
| CCK | 790 | 48 | 80 | 34 |
| CL-1 | 690 | 274 | 230 | 17 |
| CL-8 | 680 | 274 | 230 | 19 |
| CL-11 | 680 | 134 | 230 | 32 |
| CV01 | 250 | 110 | 130 | 40 |
| FIN01 | 100 | 74 | 85 | 54 |
| FIN02 | 370 | 82 | 100 | 29 |
| FOL-B | 420 | 44 | 160 | 33 |
| FOL-C | 390 | 25 | 160 | 32 |
| FOL-D | 720 | 26 | 315 | 36 |
| FOL-F | 550 | 21 | 345 | 25 |
| LTAM | 260 | 25 | 0 | 45 |
| NES-C | 830 | 14 | 250 | 27 |
| NES4 | 1050 | 31 | 240 | 40 |
| NES05 | 890 | 237 | 240 | 14 |
| SLC | 400 | 24 | 25 | 28 |
| SP01 | 180 | 57 | 165 | 22 |
| TAM-D | 340 | 24 | 350 | 26 |
| TAM-E | 330 | 24 | 50 | 34 |
| TAM-F | 340 | 108 | 200 | 18 |
| TAM-C2 | 730 | 16 | 350 | 61 |
| WE-C | 480 | 1 | 200 | 32 |
| WE1 | 20 | 65 | 210 | 22 |
| WE2 | 610 | 134 | 210 | 22 |
| WE4 | 600 | 74 | 205 | 18 |
| WE5 | 540 | 27 | 180 | 29 |
| †TP | 80 | 104 | 290 | 13 |
| †WE3 | 580 | 65 | 210 | 11 |
| †NESB | 900 | 20 | 250 | 17 |
| †CLCK | 80 | 104 | 320 | 13 |
| †WF | 80 | 104 | 300 | 25 |

† *D. tenebrosus* was not detected at this site.

**Appendix 3.** Summary of in-stream habitat variables for 32 stream reaches (100 m) that were searched for *Dicamptodon tenebrosus*. Values are mean (± SE) for five points sampled every 50 m on 100-m transects at each site.

| Site | water depth | wetted width (m) | bank width (m) | % bank full | % boulder | % cobble | % pebble | % gravel | % sand |
|---|---|---|---|---|---|---|---|---|---|
| ASC | 7.5 (1.4) | 1.7 (0.2) | 3.3 (0.2) | 52.0 (6.4) | 32.0 (6.44) | 27.0 (3.0) | 23.6 (6.6) | 13.2 (3.2) | 4.2 (0.6) |
| CCK | 20.1 (4.1) | 2.8 (0.4) | 6.1 (0.8) | 45.9 (3.9) | 41.0 (8.0) | 29.0 (8.4) | 18.0 (4.1) | 11.6 (3.5) | 0.4 (0.4) |
| CL-1 | 22.4 (2.8) | 2.1 (0.4) | 6.1 (0.8) | 34.3 (4.1) | 50.0 (6.9) | 20.0 (4.5) | 18.0 (3.7) | 9.0 (1.9) | 3.0 (1.2) |
| CL-8 | 15.7 (1.4) | 2.2 (0.1) | 4.6 (0.3) | 48.8 (3.6) | 36.0 (9.8) | 26.0 (4.0) | 21.0 (4.0) | 15.0 (2.2) | 2.0 (2.0) |
| CL-11 | 15.0 (1.5) | 2.3 (0.6) | 4.9 (0.2) | 48.8 (13.1) | 28.0 (13.2) | 12.0 (5.2) | 12.0 (5.2) | 5.0 (1.6) | *1.3 (1.3) |
| CV01 | 4.9 (0.6) | 2.6 (0.5) | 4.2 (0.7) | 62.2 (6.9) | 37.0 (9.8) | 25.0 (4.5) | 21.0 (5.1) | 11.2 (1.6) | 3.8 (0.7) |
| FIN01 | 6.8 (0.7) | 3.6 (0.3) | 5.1 (0.4) | 69.7 (2.9) | 21.0 (7.0) | 28.0 (3.4) | 30.0 (3.2) | 15.6 (2.7) | 5.4 (1.3) |
| FIN02 | 7.7 (1.6) | 2.1 (0.6) | 3.2 (0.7) | 65.8 (9.3) | 26.0 (10.3) | 30.0 (1.6) | 30.0 (8.8) | 10.8 (3.7) | 3.2 (0.8) |
| FOL-B | 16.2 (3.4) | 1.8 (0.1) | 4.5 (0.3) | 40.4 (3.9) | 39.0 (12.7) | 21.6 (1.4) | 21.4 (6.5) | 11.0 (4.9) | 7.0 (2.0) |
| FOL-C | 8.6 (2.3) | 2.2 (0.2) | 3.6 (0.3) | 60.8 (2.8) | 30.0 (14.4) | 17.0 (4.6) | 31.0 (10.3) | 15.0 (3.5) | 7.0 (2.6) |
| FOL-D | 22.2 (3.3) | 1.8 (0.4) | 6.1 (1.7) | 33.7 (5.4) | 53.0 (13.8) | 19.0 (6.6) | 4.4 (0.6) | 3.7 (1.7) | 1.9 (0.9) |
| FOL-F | 11.2 (2.8) | 1.9 (0.5) | 4.4 (0.5) | 42.2 (4.8) | 10.0 (5.2) | 30.0 (4.7) | 29.0 (5.6) | 18.0 (3.7) | 13.0 (2.0) |
| LTAM | 3.0 (0.6) | 0.9 (0.1) | 2.1 (0.) | 43.5 (8.5) | 6.0 (4.0) | 16.0 (4.0) | 42.0 (9.2) | 26.0 (4.0) | 10.0 (0.0) |
| NES-C | 12.0 (1.0) | 1.4 (0.3) | 5.2 (0.7) | 27.3 (3.3) | 52.0 (7.5) | 22.0 (4.1) | 18.6 (3.6) | 6.2 (1.2) | 1.2 (0.5) |
| NES4 | 11.9 (2.6) | 2.4 (0.6) | 4.7 (0.8) | 48.0 (5.2) | 50.0 (12.7) | 26.0 (6.0) | 12.00 (3.4) | 8.0 (2.9) | 4.0 (0.6) |
| NES05 | 12.2 (2.2) | 1.0 (0.2) | 1.5 (0.3) | 72.7 (9.1) | 23.0 (8.6) | 24.0 (4.3) | 11.0 (2.9) | 30.0 (4.5) | 12.0 (1.2) |
| SLC | 6.8 (2.3) | 1.2 (0.2) | 2.1 (0.2) | 55.9 (6.6) | 9.0 (4.0) | 25.0 (5.0) | 12.0 (2.6) | 30.0 (6.9) | 10.0 (2.7) |
| SP01 | 17.5 (7.3) | 4.0 (0.7) | 6.5 (0.7) | 59.6 (5.4) | 44.0 (6.8) | 28.0 (7.4) | 14.0 (2.5) | 6.0 (1.0) | 8.0 (2.0) |
| TAM-D | 10.6 (1.9) | 2.2 (0.4) | 4.2 (1.0) | 60.4 (8.5) | 25.0 (7.1) | 33.0 (3.0) | 20.0 (2.7) | 13.5 (5.0) | 8.5 (1.9) |
| TAM-E | 10.2 (1.6) | 1.6 (0.4) | 3.1 (0.3) | 51.7 (12.7) | 20.0 (6.52) | 26.0 (2.5) | 29.0 (5.6) | 19.0 (5.8) | 6.0 (1.0) |
| TAM-F | 6.2 (1.5) | 2.0 (0.6) | 14.2 (9.6) | 45.9 (12.8) | 9.0 (4.0) | 35.0 (6.7) | 27.0 (3.7) | 20.0 (2.2) | 9.0 (2.9) |
| TAM-C2 | 8.0 (0.7) | 1.1 (0.1) | 1.5 (0.1) | 75.1 (6.4) | 21.0 (8.0) | 21.0 (3.3) | 32.0 (7.4) | 18.0 (3.4) | 8.0 (1.2) |
| WE-C | 4.6 (0.5) | 1.0 (0.2) | 2.0 (0.3) | 49.1 (7.4) | 0.0 (0) | 4.0 (1.9) | 46.0 (8.1) | 33.0 (7.4) | 17.0 (2.0) |
| WE1 | 10.7 (1.8) | 1.5 (0.2) | 2.4 (0.3) | 63.6 (3.6) | 36.0 (7.5) | 22.0 (5.8) | 24.0 (5.1) | 17.0 (4.9) | 1.0 (1.0) |
| WE2 | 7.3 (0.9) | 1.7 (0.4) | 2.6 (0.5) | 66.1 (6.8) | 18.0 (6.0) | 26.0 (4.0) | 32.0 (5.8) | 17.0 (2.0) | 7.0 (1.2) |
| WE4 | 7.9 (0.3) | 1.4 (0.3) | 3.9 (0.4) | 37.7 (9.8) | 15.0 (5.0) | 29.0 (6.8) | 30.0 (2.7) | 18.0 (5.6) | 8.0 (3.0) |
| WE5 | 9.1 (1.7) | 0.5 (0.1) | 0.8 (0.2) | 71.0 (12.6) | 0.0 (0) | 8.0 (5.8) | 39.0 (6.4) | 34.0 (8.1) | 19.0 (3.3) |
| †TP | 5.7 (1.6) | 1.7 (0.5) | 5.0 (0.8) | 34.6 (9.5) | 0.0 (0) | 7.0 (5.8) | 55.0 (7.1) | 31.0 (3.3) | 7.0 (1.2) |
| †WE3 | 8.9 (1.9) | 0.9 (0.1) | 4.6 (0.4) | 19.6 (3.6) | 12.0 (3.7) | 19.0 (4.0) | 28.0 (6.4) | 28.0 (4.6) | 13.0 (1.2) |
| †NESB | 14.1 (1.5) | 2.3 (0.6) | 6.3 (1.0) | 37.4 (6.7) | 48.0 (10.2) | 21.0 (4.6) | 10.0 (2.7) | 9.0 (2.9) | 12.0 (3.4) |
| †CLCK | 15.3 (2.0) | 2.3 (0.6) | 7.2 (0.7) | 32.4 (8.1) | 27.0 (5.2) | 31.0 (4.9) | 24.0 (4.3) | 14.0 (4.0) | 4.0 (1.9) |
| †WF | 9.6 (2.2) | 1.2 (0.2) | 2.1 (0.3) | 56.4 (6.3) | 0.0 (0.0) | 13.0 (3.7) | 39.0 (10.8) | 16.6 (4.9) | 6.4 (3.5) |

*mean(± 1 SE) for 4 points along 100-m reach.

† *D. tenebrosus* larvae, neotenes, or transitioning metamorphs were not detected at this stream.

**APPENDIX 4.** Summary of riparian habitat variables for 32 stream reaches (100 m) that were searched for *Dicamptodon tenebrosus*. Values are means (± SE) for five points sampled every 50 m on 100-m transects at each site (except where indicated due to inaccessibility). All variables were measured at each point within a 10×5 m transect perpendicular to the stream. Tree species diversity (Shannon's I) and tree species evenness are calculated for all trees identified at each site. LW refers to large wood.

| Site | Tree species diversity | Tree species evenness | Mean tree girth (cm) | % shrub cover | # pieces large wood | % LW Decomposed (category 1) | % LW decomposed (category 2) | % LW decomposed (category 3) |
|---|---|---|---|---|---|---|---|---|
| ASC | 1.26 | 0.91 | 49.7 (6.6) | 40.0 (6.9) | 3.0 (3.0) | *5.0 (5.0) | *82.5 (11.8) | *12.5 (12.5) |
| CCK | 1.61 | 0.90 | 48.1 (9.6) | 56.0 (16.6) | 2.4 (0.7) | 0.0 (0.0) | 60.0 (14.1) | 40.0 (14.1) |
| CL-1 | 1.28 | 0.79 | 29.3 (4.6) | 46.0 (17.0) | 4.2 (0.9) | 4.0 (2.5) | 48.0 (16.3) | 48.0 (16.6) |
| CL-8 | 1.25 | 0.90 | 154.2 (38.5) | 21.2 (7.6) | 14.2 (2.5) | 0.0 (0) | 42.0 (12.4) | 52.0 (8.0) |
| CL-11 | 1.47 | 0.92 | 65.6 (2.6) | 31.0 (9.0) | 3.6 (0.7) | 0.0 (0.0) | 40.0 (7.8) | 60.0 (7.8) |
| CV01 | 1.36 | 0.98 | 92.7 (16.0) | 42.0 (5.8) | 6.8 (1.1) | 18.0 (13.2) | 67.0 (12.4) | 15.0 (17.4) |
| FIN01 | 1.61 | 0.90 | 123.7 (20.3) | 45.0 (13.3) | 6.8 (1.8) | 10.0 (10.0) | 68.0 (7.4) | 22.0 (8.0) |
| FIN02 | 1.39 | 0.87 | 175.5 (36.7) | 45.0 (7.4) | 7.6 (1.2) | 2.0 (2.0) | 26.0 (26.0) | 72.0 (11.6) |
| FOL-B | 1.32 | 0.82 | 60.2 (12.7) | 29.0 (5.3) | 5.8 (1.7) | 9.0 (7.8) | 35.0 (8.7) | 56.0 (15.1) |
| FOL-C | 1.29 | 0.93 | 51.0 (2.9) | 64.0 (9.7) | 4.0 (1.3) | 20.0 (20.0) | 62.0 (62.0) | 18.0 (13.6) |
| FOL-D | 1.44 | 0.89 | 23.5 (4.1) | 29.4 (7.6) | 7.8 (2.5) | 3.0 (2.0) | 50.0 (18.5) | 47.0 (17.4) |
| FOL-F | 1.07 | 0.77 | 52.3 (4.2) | 49.0 (7.7) | 4.4 (0.7) | 6.0 (4.0) | 66.0 (5.1) | 28.0 (5.8) |
| LTAM | 1.50 | 0.93 | 77.6 (16.6) | 30.0 (3.5) | 3.4 (0.4) | 0.0 (0.0) | 78.0 (11.6) | 22.0 (11.6) |
| NES-C | 0.97 | 0.60 | 34.1 (11.9) | 54.0 (12.4) | 5.8 (0.7) | 8.0 (3.4) | 87.0 (2.6) | 5.0 (1.6) |
| NES4 | 1.26 | 0.91 | 41.1 (10.5) | 56.0 (11.9) | 6.2 (1.0) | 0.0 (0.0) | 92.0 (4.9) | 8.0 (4.9) |
| NES05 | 1.08 | 0.78 | 107.8 (11.9) | 35.0 (4.0) | 11.0 (1.8) | 5.0 (2.2) | 45.0 (11.4) | 50.0 (11.4) |
| SLC | 0.99 | 0.71 | 36.6 (2.5) | 69.0 (5.3) | 5.0 (1.1) | 3.0 (2.0) | 35.0 (12.9) | 62.0 (12.5) |
| SP01 | 1.03 | 0.94 | 95.1 (18.4) | 53.0 (18.2) | 4.0 (0.6) | 44.0 (14.1) | 40.0 (10.1) | 14.0 (11.7) |
| TAM-D | 0.98 | 0.70 | 96.9 (23.0) | *58.8 (13.3) | 9.8 (1.1) | 29.0 (13.0) | 42.0 (8.6) | 31.0 (12.4) |
| TAM-E | 1.35 | 0.84 | 53.5 (13.7) | 29.0 (4.3) | 6.0 (0.3) | 12.0 (3.7) | 58.0 (8.6) | 30.0 (11.4) |
| TAM-F | 1.15 | 0.83 | 61.8 (29.4) | 64.0 (16.2) | 3.4 (0.5) | 12.0 (9.7) | 46.0 (6.8) | 42.0 (12.0) |
| TAM-C2 | 1.33 | 0.96 | 26.9 (3.3) | 73.0 (5.2) | 11.6 (3.1) | 24.0 (11.7) | 60.0 (11.4) | 16.0 (6.8) |
| WE-C | 1.01 | 0.73 | 55.1 (16.0) | 29.0 (9.27) | [a]10.0 (5.0) | 77.0 (9.0) | 22.0 (8.2) | 1.0 (1.0) |
| WE1 | 1.04 | 0.95 | 66.3 (10.1) | 53.0 (9.7) | 9.0 (1.3) | 36.0 (12.5) | 34.0 (11.2) | 30.0 (10.0) |
| WE2 | 1.08 | 0.98 | 107.5 (20.5) | 14.0 (4.0) | 5.2 (1.7) | 10.0 (10.0) | 44.0 (11.7) | 46.0 (16.3) |
| WE4 | 1.34 | 0.75 | 98.6 (10.0) | 34.0 (5.6) | 8.2 (1.4) | 0.0 (0.0) | 38.0 (8.0) | 62.0 (8.0) |
| WE5 | 1.57 | 0.76 | 62.5 (16.4) | 9.6 (1.7) | 7.8 (1.6) | 2.0 (1.2) | 54.0 (10.3) | 44.0 (11.3) |
| †TP | 1.12 | 0.69 | 162.8 (24.2) | 49.0 (13.5) | 3.2 (0.9) | 32.0 (19.3) | 48.0 (17.7) | 20.0 (15.5) |
| †WE3 | 1.34 | 0.75 | 82.3 (13.6) | 35.0 (7.3) | 7.0 (2.6) | 15.0 (5.2) | 64.0 (4.0) | 21.0 (1.9) |
| †NES-B | 0.99 | 0.71 | 43.4 (16.0) | 68.0 (14.9) | *1.8 (1.2) | [a]5.0 (5.0) | [a]55.0 (5.0) | [a]40.0 (10.0) |
| †CLCK | 1.08 | 0.98 | 108.1 (18.0) | 81.0 (5.3) | 4.8 (1.1) | 0.0 (0.0) | 74.0 (10.3) | 26.0 (10.3) |
| †WF | 1.21 | 0.87 | 88.2 (6.2) | 33.0 (12.3) | 6.0 (1.1) | 2.0 (2.0) | 40.0 (10.5) | 58.0 (9.7) |

*mean(± 1 SE) for 4 points instead of 5 on 100-m reach.

[a] mean(± 1 SE) for 2 points on 100-m reach.

† *D. tenebrosus* larvae, neotenes, or transitioning metamorphs were not detected at this stream.

**Appendix 5.** Correlation matrix of Pearson's correlation coefficients (r) for all riparian and topographical/in-stream explanatory variables (Var). Variables with r > 0.50 are in bold and were excluded from the analysis.

| | Var | 1 | 2 | 3 | 4 | 5 | 6 | 7 | **8** | **9** | 10 | 11 | 12 | 13 | **14** | **15** | **16** | 17 | **18** | **19** | **20** |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| elevation | 1 | - | | | | | | | | | | | | | | | | | | | |
| gradient | 2 | -0.01 | - | | | | | | | | | | | | | | | | | | |
| aspect | 3 | 0.13 | -0.41 | - | | | | | | | | | | | | | | | | | |
| time since forest harvest | 4 | -0.12 | -0.42 | 0.03 | - | | | | | | | | | | | | | | | | |
| tree species diversity | 5 | -0.03 | 0.48 | -0.40 | 0.17 | - | | | | | | | | | | | | | | | |
| tree species evenness | 6 | -0.20 | 0.36 | -0.23 | 0.34 | 0.37 | - | | | | | | | | | | | | | | |
| tree girth | 7 | -0.40 | -0.35 | -0.01 | 0.47 | -0.01 | .007 | - | | | | | | | | | | | | | |
| **% large wood category 1** | **8** | -0.18 | -0.03 | 0.14 | **-0.51** | -0.45 | -0.20 | -0.03 | - | | | | | | | | | | | | |
| **% large wood category 2** | **9** | 0.06 | 0.27 | -0.09 | -0.06 | 0.22 | 0.20 | -0.31 | -0.35 | - | | | | | | | | | | | |
| % large wood category 3 | 10 | 0.23 | 0.08 | 0.13 | -0.06 | -0.04 | -0.01 | 0.23 | 0.06 | -0.17 | - | | | | | | | | | | |
| # large wood | 11 | 0.15 | -0.24 | 0.03 | 0.47 | 0.16 | -0.07 | 0.22 | 0.09 | **-0.62** | 0.15 | - | | | | | | | | | |
| % shrub cover | 12 | -0.04 | -0.06 | 0.07 | -0.10 | -0.37 | -0.01 | -0.28 | -0.28 | -0.21 | -0.17 | -0.14 | - | | | | | | | | |
| % stream bank full | 13 | -0.10 | 0.44 | -0.26 | 0.03 | 0.14 | 0.34 | 0.15 | 0.08 | 0.08 | -0.16 | -0.17 | -0.13 | - | | | | | | | |
| **water depth** | **14** | 0.48 | -0.15 | 0.29 | 0.24 | 0.12 | 0.03 | -0.31 | -0.07 | -0.07 | 0.11 | -0.00 | 0.05 | -0.19 | - | | | | | | |
| **wetted width** | **15** | -0.16 | 0.13 | -0.21 | 0.26 | 0.05 | 0.36 | 0.21 | -0.04 | -0.08 | -0.12 | 0.27 | 0.34 | 0.03 | 0.24 | - | | | | | |
| **bank width** | **16** | 0.03 | -0.27 | 0.25 | 0.22 | 0.04 | 0.02 | 0.03 | 0.06 | 0.05 | -0.12 | -0.13 | 0.09 | -0.40 | 0.15 | **0.70** | - | | | | |
| % boulders in stream | 17 | 0.42 | 0.09 | -0.01 | 0.20 | -0.03 | 0.24 | -0.24 | -0.06 | -0.06 | 0.29 | -0.02 | 0.16 | 0.06 | 0.32 | **0.55** | **0.58** | - | | | |
| **% cobble** | **18** | 0.02 | -0.02 | 0.01 | 0.31 | 0.12 | 0.24 | 0.07 | 0.00 | 0.19 | 0.15 | 0.00 | 0.40 | 0.01 | 0.12 | 0.44 | 0.30 | **0.52** | - | | |
| **% pebble** | **19** | **-0.51** | -0.01 | -0.05 | -0.18 | 0.08 | 0.24 | 0.36 | 0.32 | 0.07 | -0.26 | 0.04 | -0.21 | 0.11 | **-0.63** | -0.36 | -0.42 | **-0.75** | -0.40 | - | |
| **% gravel** | **20** | -0.21 | -0.23 | -0.13 | -0.16 | -0.09 | -0.29 | 0.21 | 0.28 | 0.17 | 0.07 | 0.21 | 0.17 | 0.21 | **0.59** | **-0.61** | **-0.62** | **-0.79** | -0.33 | **0.65** | - |
| **% sand** | **21** | -0.13 | -0.11 | 0.03 | -0.41 | -0.18 | -0.37 | -0.13 | -0.24 | **0.65** | -0.16 | 0.04 | -0.14 | 0.18 | **-0.54** | -0.40 | -0.43 | **-0.61** | -0.24 | 0.40 | **0.66** |