Evaluating Abiotic and Biotic Predictors of Coastal Giant Salamander (Dicamptodon tenebrosus) Populations in Fish-Bearing Headwaters of the Oregon Coast Range

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Evaluating Abiotic and Biotic Predictors of Coastal Giant Salamander (*Dicamptodon tenebrosus*) Populations in Fish-bearing Headwaters of the Oregon Coast Range

Abstract

From British Columbia to northern California, coastal giant salamanders (*Dicamptodon tenebrosus*) are a dominant vertebrate predator in forested headwater streams. Though widespread, body condition and abundance of coastal giant salamanders can differ substantially among locations, provoking the question of which factors may influence this variation and to what degree habitat features versus biotic variables drive variability. In this study, we collected data on coastal giant salamander populations along with four biotic factors and eight abiotic factors across 24 different study streams adjacent to mature second-growth forests in western Oregon, USA. We used single and multi-parameter linear mixed-effects models to explore the factors individually and in combination to functionally represent alternative hypotheses accounting for variation in salamander biomass density, population density, and condition. We established a set of 25 models and employed Akaike's Information Criterion (AIC) selection for comparison. We expected food resources and the abundance of coastal giant salamander competitors to have comparable and complementary influences with stream habitat metrics. However, biotic metrics did not appear in our top models. Two abiotic variables, pool area and substrate size, best predicted the biomass and population densities of coastal giant salamanders across our study streams. Substrate size and pool area were negatively related to salamander density, in contrast to our expectations. Overall, our results suggest that habitat metrics in summer months influence the population density and biomass density of coastal giant salamanders in western headwater streams, and therefore habitat availability warrants particular consideration in conservation efforts.

Keywords: abiotic factors, Akaike Information Criterion, biotic factors, managed forests, mixed-effects models

Introduction

Coastal giant salamanders (*Dicamptodon tenebrosus*) are the dominant aquatic apex predator in fishless headwaters of the Oregon Coast Range, USA, and when sympatric with fish can still comprise up to 90% of vertebrate biomass (Parker 1994, Kaylor et al. 2017). Given their prevalence, coastal giant salamanders are an important focal taxon for evaluating the status and functionality of forested headwaters. Yet, there is not widespread information about the relationships between their populations and the ecological factors that may shape or be shaped by them. This study aims to assess the respective roles of abiotic and biotic factors in accounting for variation in salamander populations across similarly sized, small to medium fish-bearing streams in second-growth timberland forests nearing harvest age.

The range of coastal giant salamanders in the Oregon Coast Range overlaps with some of the most productive forests in western North America and therefore the species inevitably occurs throughout stream networks on managed forest landscapes. There has been increasing interest in updating riparian buffer rules to enhance protection for salamanders and other amphibians (McIntyre et al. 2018, Oregon Department of Forestry 2022); however, studies assessing forest management

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effects on salamanders have been equivocal. DeMaynadier and Hunter (1995) documented short-term negative effects of timber harvest on salamanders, but other studies have found mixed relationships between clear-cutting and coastal giant salamander populations (Curtis and Taylor 2004, Leuthold et al. 2012, Auteri et al. 2022). A key step in addressing these inconsistences is to improve our understanding of relationships between salamander populations and the structural and food web conditions of headwater streams in which they occur.

Previous studies exploring environmental factors associated with salamander populations in streams are varied, but in general, they emphasize the importance of abiotic features and streamflow (Olson and Ares 2022). A study in southern Oregon and northern California, for example, found salamanders preferred "relatively narrow, shady channels, with medium-coarse substrate, slow water, and pools, at less disturbed forest sites" (Welsh and Lind 2002). The importance of pools to *Dicamptodon* spp. was also noted in a study of 30 streams in Washington State where the average size of western *Dicamptodon* spp. salamanders was larger in pools than in other areas of the stream (Roni 2002).

In addition to pools, multiple studies have identified substrate size as an important factor influencing the biomass density of coastal giant salamanders in forested headwaters (Hawkins et al. 1983, Welsh and Lind 2002, Leuthold et al. 2012). Olson and Ares (2022) reported that coastal giant salamanders were most commonly associated with perennial flow regimes, which had a greater percent of large gravel substrate and proportion of pools, and less percent fines across their sites. Coastal giant salamander biomass density is generally greater in streams with larger substrate sizes that provide cover from threats and ideal habitat for laying eggs (Hawkins et al. 1983, Rundio and Olson 2003). Although several studies found positive associations between substrate size and coastal giant salamanders, a study on the closely related Idaho giant salamander (*D. aterrimus*) led to a different conclusion. In a series of 40 Idaho streams, biomass density of *D. aterrimus* was positively related to embedded substrate and presence of fine sediment (Sepulveda and Lowe 2009). Contrasting predictions within the same genus may be a result of critical differences between species and localized adaptations, but also allude to generalist behavior. On a broader habitat scale, higher stream gradient has been tied to the presence of coastal giant salamanders, although not necessarily population density (Dudaneic and Richardson 2012).

Considering potential biotic factors that may affect coastal giant salamander populations, competition, predation, and food availability (their diets consist largely of macroinvertebrates but can include fish, snails, and other salamanders) are also potentially important in headwater ecosystems. Coastal giant salamanders rear in streams, with aquatic populations composed of larvae, mature neotenic adults, and metamorphosed adults that return to the stream to eat and lay eggs. In general, coastal giant salamanders remain as larvae for two to three years and do not reach complete maturity until almost seven years of age (Sagar et al. 2007). As young larvae, they are a common prey item of salmonids (Salmonidae), sculpin (*Cottus* spp.), and larger larval or mature salamanders, and are thought to use gaps between coarse substrate to avoid predation (Rundio and Olson 2003). As larvae mature, predation risk declines and they transition to being competitors with other vertebrates in these headwaters, including adult resident trout (*Salvelinus* spp.), juvenile salmonids (*Oncorhynchus* spp.), and sculpin (*Cottus* spp.) (Parker 1994, Cudmore and Bury 2014, Falke et al. 2020). Coastal giant salamanders compete most with sculpin, as they are both benthic generalist predators and strongly overlap in diet selection (Bond 1963, Daniels and Moyle 1978, Wells 2007, Cudmore and Bury 2014, Falke et al. 2020). Salmonid and coastal giant salamander distributions coincide throughout many headwater stream networks and both taxa overlap some in diet choice, but salmonids often prefer deeper pools, consuming drift (much of it terrestrial) from the water surface (Falke et al. 2020). Other studies on intraguild predation determined that coastal giant salamanders and salmonids exhibit no significant trophic niche partitioning when they co-occur (Roni 2002, Rundio and Olson 2003, Sepulveda et al. 2012).

In headwater streams in the Pacific Northwest, the dominant diet items for coastal giant salamanders (aquatic macroinvertebrates) are supported by a combination of in-stream primary producers and benthic organic matter entering the stream from the riparian forest. While standing stocks of organic matter are often high, benthic biofilms are a higher quality food resource (based on C:N ratios) and therefore a disproportionately important basal resource in headwater streams (Finlay 2001, McCutchan and Lewis 2002, Lau et al. 2009). Given the relative importance of benthic biofilms, factors that increase their production (particularly autotrophs within those biofilms) can have a strong influence on stream macroinvertebrates (Hawkins et al. 1983), which have in turn been hypothesized to increase apex predators such as salamanders through bottom-up processes (Kiffney and Roni 2007, Kaylor et al. 2017). So, in addition to habitat, food web resources are also important considerations in evaluating factors that could explain variation in coastal giant salamander populations across sites.

Although prior research has included ecological associations of coastal giant salamander populations, few have tested multi-parameter models of both abiotic and biotic variables. Inclusion of biotic factors along with established abiotic stream features may provide greater capacity to account for fluctuations in coastal giant salamander metrics. Resources can be scarce, therefore interspecies competition may control abundances, particularly between coastal giant salamanders and sculpin that consume similar diets and spend much of their time on the stream benthos. While there has been ample research on the ecology of coastal giant salamanders in headwaters, these studies exclude interactions with fishes either because salamanders occur in stream reaches above fish sections or because fish presence is overlooked or not clarified (Corn and Bury 1989, Wilkins and Peterson 2000, Ashton et al. 2006, except see Hawkins et al. 1983). Results from these and others identify habitat variables such as elevation, gradient, and coarse substrates as important predictors of density, which may emerge by nature of the watershed position of the study sites (Hunter 1998, Wilkins and Peterson 2000, Dudaneic and Richardson 2012). Gaps remain in our knowledge of how interspecies population dynamics influence abundances and how these compare to, or interact with, abiotic habitat factors in headwater sections where many vertebrate species cohabitate.

Beyond the Pacific Northwest, amphibians have endured some of the most precipitous global population and biodiversity declines of any vertebrate taxon over the past 30 years (Stuart et al. 2004, Grant et al. 2020). Stressors range from disease to habitat modification such as timber harvest, with 25% of species threatened and another 25% lacking sufficient data to assess their status (Stuart et al. 2004, González-del-Pliego et al. 2019). The conservation status of coastal giant salamanders is considered secure within its range of Oregon and Washington (IUCN 2022). However, future sustainability is not guaranteed, and comprehensive studies on population size and distribution are needed to gauge potential future threats and overall population health. Further, considering global amphibian decline, the consistent presence of coastal giant salamanders provides an example of a species that has been resilient to threats facing this group of organisms. Understanding which features relate to the abundance of coastal giant salamanders in systems affected by previous forest management may provide insight into the factors needed to continue support of this species.

To improve conservation approaches and management, we investigated ecosystem associations of coastal giant salamanders. We evaluated how density and condition of coastal giant salamanders relate to a range of abiotic and biotic factors across 24 small to medium fish-bearing streams in the Oregon Coast Range, USA. We explored a suite of eight abiotic factors that reflect watershed, stream, and riparian conditions and four biotic factors that represent trophic and competition effects on coastal giant salamanders. Our objectives were to understand the relative importance of individual stream characteristics in accounting for salamander population variation across Coast Range headwaters, and more broadly, we sought to

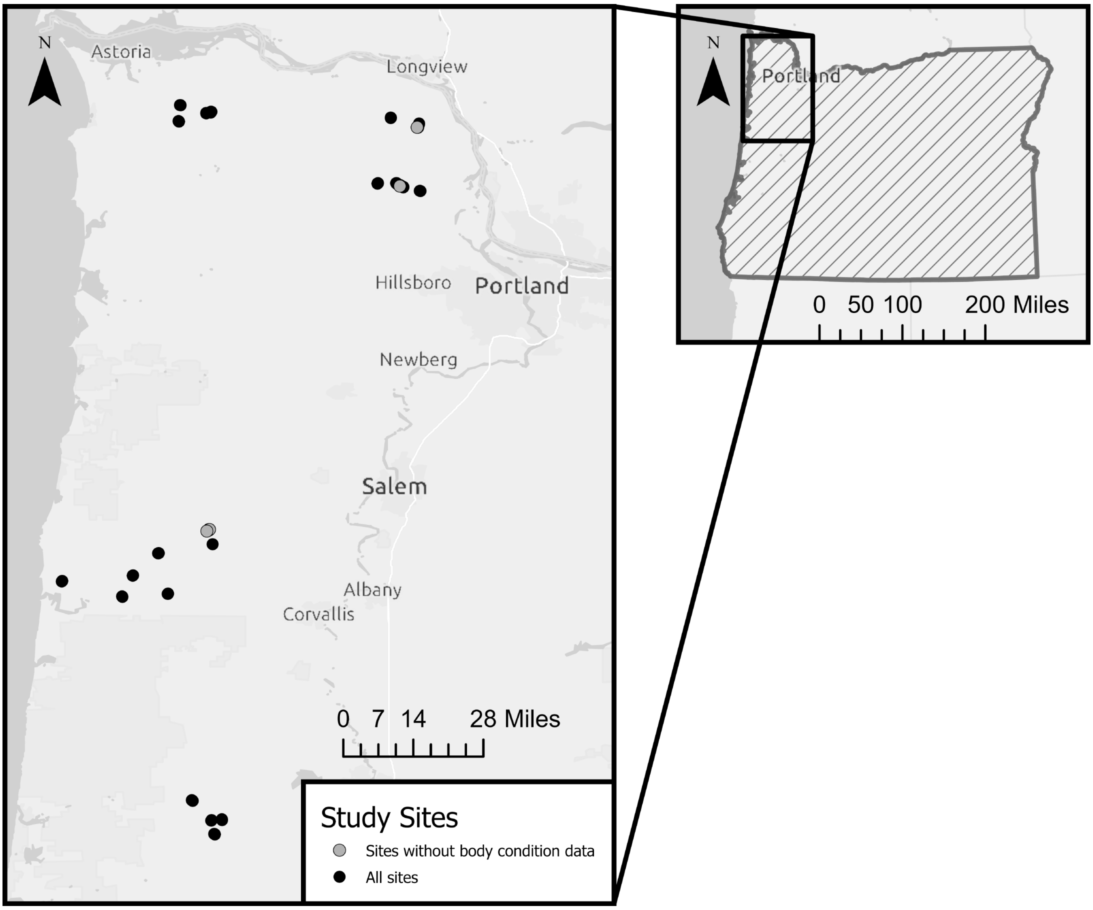

Figure 1. All 24 study sites were located in the Oregon Coast Range. Sites with fewer than three coastal giant salamander individuals were excluded from the body condition data and are marked as grey.

understand whether and to what degree including both biotic and abiotic factors in a model might improve our ability to account for variation, and therefore ultimately predict, salamander abundance and condition across headwater streams.

Methods

Our study included 24 streams across the northern half of the Oregon Coast Range (Figure 1). We selected streams in a block design with each of six blocks consisting of five streams of similar characteristics including geographic location, climate, and stream size classification. All sites were forested headwaters classified as "small" or "medium" fish-bearing streams (controlled within each block; Supplemental Appendix A, available online only). A total of six of the potential 30 total streams were excluded from electrofishing due to access constraints or forest harvest activity. All streams were located on privately owned timberland with adjacent riparian forests between 30 to 50 years old. These specific riparian forests were composed predominantly of Douglas-fir (*Pseudotsuga menziesii*) and red alder (*Alnus rubra*), with understory vegetation dominated by vine maple (*Acer circinatum*) and salmonberry (*Rubus spectabilis*). The Oregon Coast Range has a Mediterranean climate with cool, wet winters and warm, dry summers. All streams in our study support both coastal cutthroat trout (*Oncorhynchus clarkii clarkii*) and coastal giant salamanders.

Fifteen streams included unspecified sculpin species (*Cottus* spp.), and three streams also supported populations of juvenile coho salmon (*O. kisutch*).

We quantified eight abiotic metrics (large wood volume [LW, m^3], pool area [m^2], water depth [cm], canopy cover [%], substrate composition [D80], stream temperature [°C], elevation [m], and stream gradient [%]) and four biotic metrics (periphyton ash-free dry mass [AFDM, $mg \cdot cm^{-2}$], macroinvertebrate density [$individuals \cdot m^{-2}$], salmonid density [$g \cdot m^{-2}$], and sculpin density [$g \cdot m^{-2}$]). We examined relationships among these variables and coastal giant salamander population density ($individuals \cdot m^{-2}$), biomass density ($g \cdot m^{-2}$), and body condition ($g \cdot mm^{-3}$) at each respective site in a correlation matrix, and we used Pearson's correlation coefficients to describe linear correlations, detect collinearity, and inform *a priori* model selection. We then constructed single and multi-parameter linear regression models followed by Akaike's Information Criterion (AIC) analysis to test performance of various model sets to determine how abiotic and biotic variables describe the variation present in coastal giant salamander population density, biomass density, and body condition.

Data collection occurred from July to August 2021. Study sites were established for a separate forest management study and encompassed stream reaches 200–300 m in length. Vertebrate, large wood (LW), and geomorphological (pool area, wetted width, and stream depth) surveys occurred in 60–90 m reaches within each larger reach (defined as the "fishing reach"). Canopy cover and substrate size were measured every 20–25 m along the entire 200–300 m reach.

Abiotic Habitat Metrics

Large wood was defined as dead woody material greater than 1 m in length and greater than 0.1 m in diameter in the bankfull width of the 60–90 m fishing reach (Fetherston et al. 1995). The volume of each piece of LW was calculated with a truncated cone equation:

$$V_{LW} = (1/3) \times \pi \times L \times [r_1^2 + (r_1 \times r_2) + r_2^2] \qquad (1)$$

where L is the length of the piece and r_1 and r_2 are radii at each end of the piece of wood. The volumes at each stream were summed then standardized by reach length ($m^3 \cdot m^{-1}$).

We calculated pool area in the fishing reach by measuring the length and width of deep, depositional habitats along the longest axes. We multiplied these lengths and widths to calculate the area of each pool, summed values for each stream, then divided the total pool area by the length of the fishing reach ($m^2 \cdot m^{-1}$). Mean water depth was determined by measuring five equidistant water depths along 9–16 transects in each reach and averaging all values.

A spherical crown densiometer (Concave Model C; Forestry Suppliers, Jackson, MS) was used to estimate percent canopy cover directly above the stream at 9–16 reach locations. Measurements were taken in four cardinal directions at each location, then values were multiplied by 1.04, subtracted from 1, and averaged to obtain mean canopy cover. We used a gravelometer cobble scale (Wildco, Yulee, FL) to measure substrate size classes of ten particles along transects at 9–16 reach locations. The 80th percentile substrate size for each stream was determined and classified as the "D80" value.

We deployed temperature loggers (HOBO Pro v2, Onset Computer Corporation, Bourne, MA) encased in a PVC housing (to shade loggers) at the downstream end of the stream reach. These sensors recorded the water temperature (± 0.2 °C) at 1-hr intervals during the summer low flow period. Logger deployment and retrieval was staggered, therefore the stream temperatures for 20 streams were compiled for the week of 21 August to 28 August, while the stream temperature for five streams was compiled for the week of 14 August to 21 August. The recorded hourly temperature readings were averaged across each respective week to determine the average weekly August temperature.

We used ArcGIS Pro 2.9 (Esri Inc. 2022) to determine both the average elevation and percent gradient across the 200–300 m reach of each stream. This was accomplished by overlaying the GPS locations of the start and end points of each stream atop a LiDAR topographic map of Oregon (Hanser 2008). We calculated average elevation across five equidistant points along each stream reach and determined the percent gradient as the elevation difference between the upstream and downstream ends of the reach.

Biotic Metrics

We sampled standing stocks of epilithic algal communities (periphyton) using standard rock-scraping methods on natural substrates (Chételat et al. 1999). At five equidistant transects along the stream reach we selected three flat cobbles from thalweg riffles. We scrubbed rocks with wire brushes, then split the biofilm from their surfaces into two samples. We filtered scrubbate through pre-ashed 47 mm Whatman glass fiber (GF/F) filters, wrapped filters in foil, and stored on ice until frozen within six hours. To determine the surface area scrubbed, we traced each rock, and used rock tracings to determine surface area from a weight-to-area relationship. We determined ash-free dry mass (AFDM; $mg \cdot cm^{-2}$) using the EPA standard protocol (APHA 1995). We thawed filters, dried them at 60 ˚C, weighed them on an analytical balance, ashed at 500 ˚C for two hours, then we re-weighed each filter.

We used a 0.45 m^2 Surber sampler with a 500 µm mesh bag to collect benthic macroinvertebrates at five equidistant points throughout each stream reach (upstream of sample locations for substrate). We pooled macroinvertebrates into a single sample per site and immediately placed them in 95% ethanol. We completed a full census of macroinvertebrates in the sample and identified to genus (except for chironomids, which were identified to family) by Benthic Aquatic Research Services (Lawrence, KS).

We employed a three-pass depletion method with a backpack electrofisher (Smith Root, Vancouver, WA) for the collection of salmonids, sculpins, and coastal giant salamanders. The length of the fishing reaches varied by block with a target of either 60 m (Astoria, Newport, Vernonia, and Scappoose) or 90 m (Valsetz and Walton). The 60 m fishing reaches were divided into two 30-m sections and the 90 m fishing reaches were divided into two 45-m sections. We placed block nets at the upstream and downstream ends of each fishing reach section for the duration of the survey to prevent movement in or out of the reach section, and fish from each pass were held out of the stream reach section until all passes were complete. All fish were anesthetized using Aqui-S 20E (approved for trial use through INAD AADAP, study number 11-741-21-112F, Lower Hutt, New Zealand), weighed (g) and measured (total length in mm). We did not anesthetize coastal giant salamanders, but we placed them in a plastic bag to measure length (snout–vent length, mm) and in a weigh boat for weight (g). We placed all salamanders, salmonids, and sculpins in recovery coolers separated by age class and species prior to releasing them back into the fish reaches where they were originally caught.

We used a maximum likelihood method (Carle and Strub 1978) computed by the "FSA" package (Ogle et al. 2023) to estimate vertebrate populations from the depletion of fishes and coastal giant salamanders over each of the three passes. Due to differences in capture probabilities, we estimated each species separately and divided salmonids into two size/age categories, age 0 (young-of-year) and age 1+ (juveniles and adults) based on length–frequency histograms (Hall et al. 2016). We then normalized the population estimates of each stream relative to wetted stream area (fishing reach length multiplied by average wetted width) to allow for population density estimate comparisons across streams ($individuals \cdot m^{-2}$). To calculate the total biomass (g) of sculpins, salmonids, and coastal giant salamanders, we multiplied the population estimate by the mean mass and then divided this number by the fishing reach area to calculate the biomass density ($g \cdot m^{-2}$) of each stream. For coastal giant salamanders, we additionally determined average condition ($g \cdot mm^{-3}$) using the following formula (Kaylor et al. 2019):

$$C = [M / SVL^3\ ] \times 100 \tag{2}$$

where C is body condition, M is mass (g), and SVL is snout-to-vent length (mm).

Data Analysis

Our analyses focused on single and multi-parameter linear mixed-effects regression models representative of alternative hypotheses to account for variation in coastal giant salamander biomass density, population density, and condition across our 24 study sites. We created an *a priori* model set (Supplemental Appendix B, available online only) with 12 predictor variables in our models: salmonid biomass density, sculpin biomass density, pool area, LW density, mean depth, mean canopy cover, D80 substrate, percent gradient, mean elevation, mean weekly August temperature, AFDM, and macroinvertebrate density. Linear mixed-effects models were constructed using the "lme" function from the "nlme" package (Pinheiro et al. 2021). To account for variation in geography, climate, stream size, and length of electrofishing reaches, we included "block" as a random effect in each model. Variables were checked for normality with the "shapiro.test" function of the "stats" package (R Core Team 2022) and log transformed as necessary to meet the assumptions of a normal distribution (Wickham et al. 2022). Linear mixed-effects model assumptions were assessed through residual plots and qqplots. To ensure models were not overfit, we restricted the number of candidate models by limiting models to a maximum of two predictor variables except in the case of the full biotic, full abiotic, and global models, which were included to compare the factor categories more broadly, thereby limiting the total candidate models to 25. A correlation matrix was generated using the "corr" function of the "corrplot" package (Wei and Simko 2021) to inform model set design for multiparameter regression models and to identify collinearity (Burnham and Anderson 2002). We excluded four sites from condition factor analyses because there were too few coastal giant salamanders (fewer than three individuals) to capture population variation in condition.

To select the best models, we used AIC correction for small sample sizes (AICc) and retained models within two units of AICc separation (delta AICc) of the best model (Zuur et al. 2010). Of these models, we determined AIC weights. AICc was performed using the "aictab" function in the "AICcmodavg" package to calculate the AICc values and delta AICc values (Mazerolle 2020). The "r2_nakagawa" function from the "performance" package was employed to calculate the conditional R^2 (proportion of variance explained by fixed and random effects) and marginal R^2 (proportion of variance explained by fixed effects) values outlined for use in linear mixed-effects models (Nakagawa and Schielzeth 2013, Lüdecke et al. 2021).

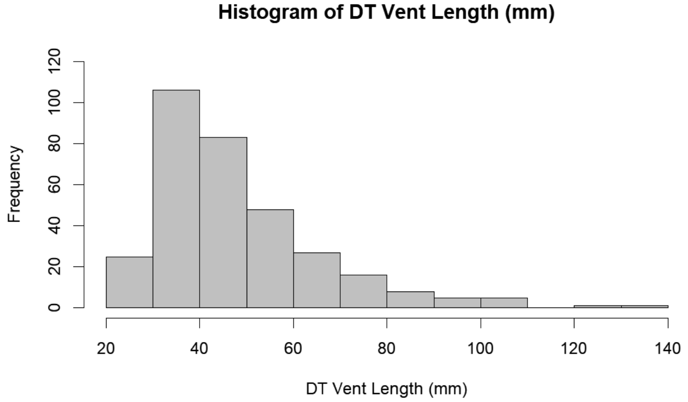

Figure 2. Frequency distribution of snout-vent length (mm) measurements across the 317 collected coastal giant salamanders.

Results

Dataset

Across the 24 stream sites sampled, we collected 317 coastal giant salamanders with snout-vent lengths ranging from 27 to 135 mm (Figure 2). The median snout-vent length across sites was 45 mm and the mean was 48.3 mm, indicating a higher composition of smaller individuals collected in this study compared to large larval or mature salamanders (Figure 2). Mean coastal giant salamander biomass density ranged from 0.027 to 2.67 $g{\cdot}m^{-2}$ and mean salamander population density ranged from 0.009 to 0.498 $individuals{\cdot}m^{-2}$. The mean body condition of the coastal giant salamander ranged from 0.00382 to 0.00464 $g{\cdot}mm^{-3}$.

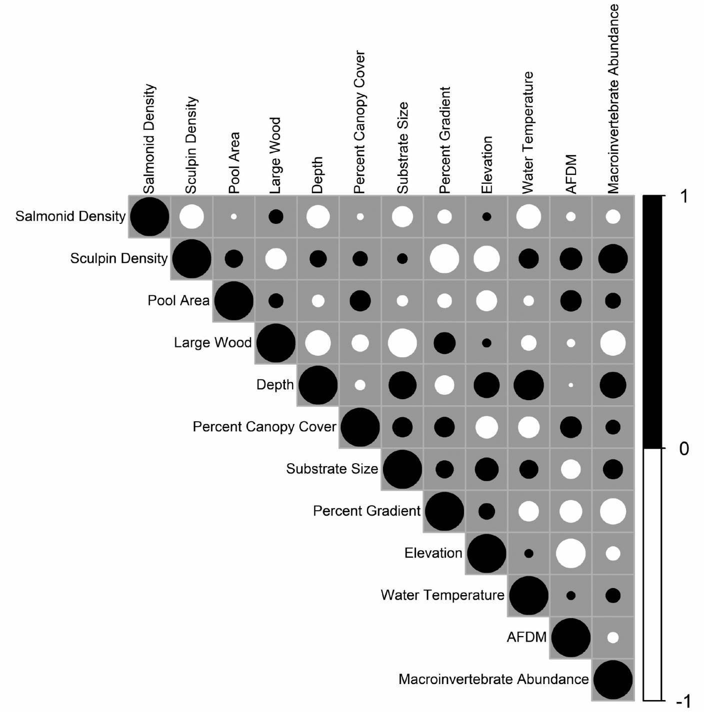

Figure 3. Correlation matrix of the 12 response variables collected at 24 small fish-bearing headwater streams in the Oregon Coast Range. Positive correlations are denoted as black circles, while negative correlations are white circles; circle size is relative to correlation strength. Ash-free dry mass is abbreviated as AFDM.

Model Selection

The correlation matrix encompassing all 12 explanatory variables yielded several moderate to strong relationships. We set a correlation value limit of $r = 0.45$ and excluded parameters from multivariate models where $r > 0.45$; this applied to nine pairs of variables. The variable pairs excluded were: mean temperature + mean depth, macroinvertebrate density + sculpin density, macroinvertebrate density + mean depth, D80 substrate + mean depth, mean temperature + salmonid density, mean elevation + sculpin density, percent gradient + sculpin density, D80 substrate + LW, and AFDM + mean elevation (Figure 3). All models included in the *a priori* model set included the random effect of "Block".

When considering the relative influence of individual metrics based on cumulative AICc weights, the abiotic metrics pool area and substrate size were most important when compared to the entire suite of 12 explanatory variables (Figure 4). The cumulative AICc weight of each had clear separation from other individual metrics regarding biomass density (cumulative AICc weights: pool area = 0.51, substrate size = 0.35) and population density (cumulative AICc weights: pool area = 0.41, substrate size = 0.17).

The most parsimonious model, as identified by AICc, in predicting coastal giant salamander biomass density ($g{\cdot}m^{-2}$) was the combined model of pool area + substrate size (Table 1). Only one other model (pool area alone) was within two units of the best AICc model. AICc analysis was performed again using only these two models (AICc weights: pool area + substrate size = 0.57, pool area = 0.43) (Figure 5). The pool area + substrate model explained 32% of variability in coastal giant salamander biomass density (conditional $R^2 = 0.321$, marginal $R^2 = 0.321$), while pool area alone explained 20% of variability (conditional $R^2 = 0.200$, marginal $R^2 = 0.200$); pool area in both models was significant (*P*-values: pool area + substrate size = 0.021, pool area = 0.035). However, substrate size in the multivariate model of pool area + substrate size was not significant (*P*-value = 0.075). The conditional R^2 and marginal R^2 values were the same for each respective top model, therefore the proportion of variance explained by the model did not change with or without the inclusion of the random effect of "Block".

Across our study streams, the model best accounting for coastal giant salamander population density (individuals$\cdot m^{-2}$) was the model of pool area (Table 2, Figure 5). Only one other model was within two units of the best AICc model, and this was a multivariate model of pool area + substrate size. For these models, AICc weights were pool area = 0.71 and pool area + substrate size = 0.29.

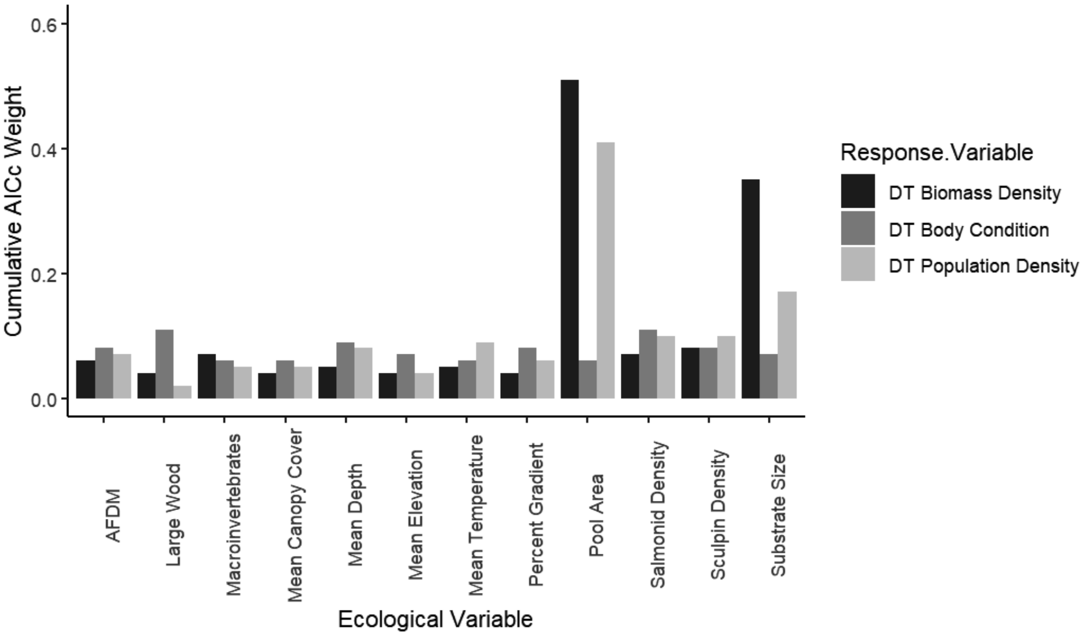

Figure 4. The clustered bar graph includes the cumulative corrected Akaike's Information Criterion (AICc) weight for each of the 12 ecosystem metrics examined in this study. Ash-free dry mass is abbreviated as AFDM and *Dicamptodon tenebrosus* is abbreviated as DT.

Table 1. All models within 2 units of AICc from the top model best predicting coastal giant salamander biomass density ($g{\cdot}m^{-2}$), AICc weight, delta AICc, conditional R^2, and marginal R^2 are calculated per model, while a *P*-value is only calculated for each respective variable in multivariate models; dashes indicate values not assessed. Significance is denoted by an asterisk on *P*-values lower than the 0.05 cutoff used.

Model	AICc weight	Delta AICc	Conditional R^2	Marginal R^2	*P*-value
Pool area + substrate	0.27	0.00	0.321	0.321	–
Pool area	–	–	–	–	0.021*
Substrate	–	–	–	–	0.075
Pool area	0.20	0.60	0.200	0.200	0.035*

For the top model of pool area alone, the conditional $R^2 = 0.490$ and the marginal $R^2 = 0.177$ and this model was statistically significant (*P*-value = 0.020). For the multivariate model of pool area + substrate size, the conditional $R^2 = 0.393$ and the marginal $R^2 = 0.251$ and only pool area was significant within the model (*P*-values: pool area = 0.030, substrate size = 0.172). The conditional R^2 was consistently higher than the marginal R^2 values for each respective top model, therefore the proportion of variance explained by the model improved with the inclusion of the random effect of "Block".

In evaluating factors affecting coastal giant salamander condition, no models outperformed the null model, an intercept-only model (Table 3). Also, no models were significantly related to any of the response variables (*P*-value > 0.05).

Discussion

Vertebrate presence and abundance in headwater streams are a function of many different ecosystem variables. Our study used linear and multiple

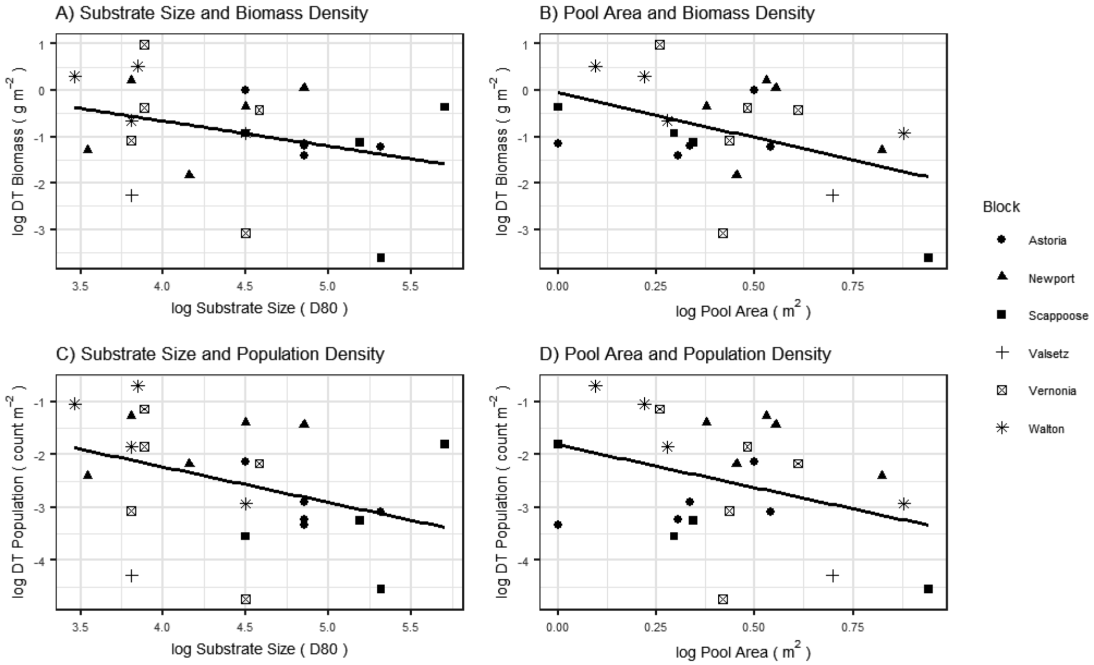

Figure 5. Linear regression models for the top-performing single fixed-effect variable models with shapes denoting each geographic block. *Dicamptodon tenebrosus* is abbreviated as DT. A) log substrate size (D80) and log DT biomass density (g·m^{-2}), B) log pool area (m^2) and log DT biomass density (g·m^{-2}), C) log substrate size (D80) and log DT population density (individuals·m^{-2}), and D) log pool area (m^2) and log DT population density (individuals·m^{-2}).

Table 2. All models within 2 units of AICc from the top model best predicting coastal giant salamander population density (individuals·m^{-2}). AICc weight, delta AICc, conditional R^2, and marginal R^2 are calculated per model, while a *P*-value is only calculated for each respective variable in multivariate models; dashes indicate values not assessed. Significance is denoted by an asterisk on *P*-values lower than the 0.05 cutoff used.

Model	AICc weight	Delta AICc	Conditional R^2	Marginal R^2	*P*-value
Pool area	0.25	0.00	0.490	0.177	0.020*
Pool area + substrate	0.11	1.75	0.393	0.251	–
Pool area	–	–	–	–	0.030*
Substrate	–-	–	–	–	0.172

regression models to identify the best predictors (among 12 variables) of coastal giant salamander population density, biomass density, and condition across 24 forested streams in the Oregon Coast Range. We found that the best predictors were two abiotic variables, pool area and substrate size. In contrast to previous findings, salamander biomass and population densities were greater when pool area and substrate size were smaller. In these fish-bearing streams, we expected that the addition of biotic variables including basal resources (periphyton AFDM), food resources (invertebrates), and densities of predators and competitors (sculpins and salmonids) would improve explanatory power, but none of these biotic variables were among the top variables to account for variation in coastal giant salamander populations. This finding suggests that fundamental habitat conditions appear relatively more important than competition or bottom-up food availability for coastal giant salamanders during the summer low flow period of these perennial streams. We note, however, that even after accounting for a

Table 3. All models within 2 units of AICc from the top model best predicting coastal giant salamander body condition ($g \cdot mm^{-3}$). AICc weight, delta AICc, conditional R^2, and marginal R^2 are calculated per model, while a P-value is only calculated for each respective variable in multivariate models; dashes indicate values not assessed. Significance is denoted by an asterisk on P-values lower than the 0.05 cutoff used.

Model	AICc weight	Delta AICc	Conditional R^2	Marginal R^2	P-value
Null	0.19	0.00	0.023	0.000	–
Salmonid density	0.08	1.79	0.064	0.064	0.284
Mean depth	0.07	1.90	0.059	0.059	0.305
Large wood	0.07	1.90	0.059	0.059	0.305

wide range of variables, there was a great deal of unexplained variation in the abundance, biomass, and condition of coastal giant salamanders across our study streams. This unexplained variation further underscores the complexity of modeling this species' relative abundance across stream reaches and demonstrates that there may be more large- or fine-scale variables responsible for controlling coastal giant salamander populations in this region.

Substrate size and pool area, the two most important predictors explaining coastal giant salamander population and biomass densities in our study, are often cited as important parameters for the preferred habitat of this species (Murphy and Hall 1981, Corn and Bury 1989, Wilkins and Peterson 2000, Roni 2002, Welsh and Lind 2002, Leuthold et al. 2012). Across flow regimes spanning non-perennial to perennial, Olson and Ares (2022) reported coastal giant salamanders, sculpins, and coastal cutthroat trout were associated with perennial streams characterized by greater substrate size with less fines. By restricting our analysis to perennial streams, we found an opposite response, with coastal giant salamander biomass and population densities increasing with decreasing pool area and substrate size. Importantly, across our sites it was the combined effects of substrate size and pool area rather than substrate size or pool area alone that explained variation in these populations. Clear characterization of these ecological associations in perennial and non-perennial reaches are important to predict salamander populations, but the directionality of these responses appear to differ when examined across flow classifications.

In our study, the negative relationships between substrate size and both biomass density and population density contradict our prediction of coastal giant salamander preference for greater pool area and coarse substrate; however, these findings are consistent with studies on other species within the *Dicamptodon* genus. Sepulveda and Lowe (2009) found that Idaho giant salamanders (*D. atterimus*) prefer smaller substrate sizes due to local adaptations to silt mobilization following fires and anthropogenic development near the Lochsa River, Idaho. In addition to potential increases in sediment from timber harvest and road building (Karwan et al. 2007, Bywater-Reyes et al. 2017), local populations of coastal giant salamanders in this region must contend with silt. Several factors in the Oregon Coast Range may contribute sources of fine sediment across our study streams including historic fires or debris flow history, forest management activities, and underlying substrate comprised of sandstone (Tyee formation) (May and Gresswell 2003). Another study in the Oregon Coast Range focused on the movement of coastal giant salamanders around culverts found a strong association between larger substrates and larvae density, but also noted that the ability to evade detection increased with body size (Sagar et al. 2007). Most individuals in our study streams were young, small larvae (< 50 mm SVT), which is common in small headwaters (Hunter 1998); therefore, the trends we observed may represent primarily the preference of this portion of the demographic.

Pool area was also negatively related with coastal giant salamander biomass and population densities, a finding contrary to our expectations and previous findings (Wilkins and Peterson 2000). However, we may also have observed this relationship because we sampled relatively small streams containing smaller-bodied individuals. One previous study found that *Dicamptodon* spp. salamanders in pools had a larger mean length compared to those in other stream habitats (Roni 2002), while another study observed that smaller individuals prefer shallow riffle-like habitats (Kelsey 1995). We may have captured size class separation between meso-habitats. The preference of small coastal giant salamanders for non-pool habitats may be related to predator avoidance. Although we did not observe a strong influence of fish (sculpin or salmonid) on salamander densities at the reach scale, within pools there could be exclusion of salamanders by larger salmonids that often dominate these habitats. Most pools were small, had high visibility, and were relatively easy to access with nets and hands, but there is a potential collection bias in pools where smaller salamanders were more difficult to capture compared to larger ones.

We expected sculpin biomass density to explain variation in coastal giant salamanders because they occupy a similar benthic predator niche (Bond 1963, Daniels and Moyle 1978, Wells 2007, Cudmore and Bury 2014, Falke et al. 2020). One study that investigated the inter- and intraspecific diet variation in coastal giant salamanders, sculpins, and trout found substantial overlap in diet content between salamanders and sculpins (Falke et al. 2020). However, we did not find significant evidence for any competitive exclusion between these species in our study streams. We expected other biotic variables such as periphyton ash-free dry mass and total macroinvertebrate population density to explain much more variation in coastal giant salamander biomass and population densities. Other studies have found that vertebrate population density is closely linked to basal resource productivity (Kiffney and Roni 2007, Kaylor et al. 2017). The lack of a clear relationship between salamanders and basal resource productivity found in our study could be due to limited influences of these basal resources over our assessment time scales. These coastal giant salamanders can be long-lived (Sagar et al. 2007) while the biotic metrics we evaluated are highly seasonal and spatially heterogeneous.

Throughout the study, the coastal giant salamander condition factor was not explained by any of the predictor variables incorporated in our models. AICc model selection placed the null model as the best, with no strong relationships found in the correlation matrix either. Study site selection for perennial fish-bearing streams in second-growth forests limited observed variation in canopy cover and temperature. Other implementations of a similar condition factor formula, however, found significant changes in condition over a yearly basis (Kaylor et al. 2019). The condition factor may better represent large temporal changes over regional variation among streams of similar fish presence, classification, and ecosystem type.

While reach-scale stream assessments are common in evaluating a range of biota and ecosystem processes in streams and are generally accepted units of assessment, these surveys have important limitations. By focusing on reach-scale processes, we cannot make explicit conclusions about more localized habitat unit conditions or responses, and more broadly, they do not encompass the larger riverscape (Fausch et al. 2002). Aquatic biota move through river networks with varying degrees of residency in different sections (Gowan et al. 1994, Rodríguez 2002, Chelgren and Adams 2017), and in any reach-scale study without explicit telemetry we are necessarily making assumptions that the densities of salamanders, macroinvertebrates, fishes, and benthic primary producers, etc., in each study reach are representative of the abundances of these organisms more broadly in the system. This assumption is likely to be reasonable within the fish-bearing sections of Coast Range headwater streams, but results should not be extrapolated to the smaller non-fish-bearing headwaters or to larger river systems.

Conclusion

This study assessed the predictive value of 12 variables with the goal of better understanding ecosystem preferences of coastal giant salamanders in the Oregon Coast Range. Broadly, the AIC analysis indicated that in these systems, abiotic metrics consistently outperformed biotic metrics in explaining variation in salamander population density across our 24 study sites. Yet, in the best model, fixed and random effects only explained about 49% of coastal giant salamander variability and fixed effects alone accounted for 32% of variability, even as the study included habitat variables generally recognized as important in streams. Two abiotic factors in particular, pool depth and substrate composition, were identified as the best factors explaining variation in coastal giant salamander population density and biomass density, however, these relationships were not always consistent with earlier studies from this region. For example, within perennial fish-bearing streams we found negative relationships between substrate size and coastal giant salamander population density and biomass density, which contrasts with prior studies in Oregon headwaters that found positive relationships (Hawkins et al. 1983, Rundio and Olson 2003). However, our finding is not unprecedented, as Sepulveda and Lowe (2009) found a similar relationship for a related giant salamander species in forested streams in Idaho. More work into the mechanisms behind these relationships is needed as well as exploration of other factors that may account for variability missed in this study. Metrics that warrant future consideration include population movement, salamander life span, and landscape legacies, as none of these are captured in this assessment.

The separation in predictive value between abiotic and biotic metrics placed emphasis on the importance of habitat over competition or nutrient availability. Particularly in terms of a lack of competitive exclusion, the study hints at the generalist history of coastal giant salamanders. Their ability to rely on the most abundant prey in any stream likely allows populations to remain less affected by competition (relative to habitat factors). Further exploration of the exact mechanisms behind coastal giant salamander preference may require broader variability in predictive metrics and a wider geographic range. Although on a limited scale, this study provided insight into the explanatory value of abiotic metrics and the surprisingly muted link to biotic variables in accounting for salamander abundance differences across forested headwater streams in western Oregon.

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