Received: 22 November 2024 | Revised: 12 March 2025 | Accepted: 18 April 2025

DOI: 10.1002/ecs2.70299

ECOSPHERE
AN ESA OPEN ACCESS JOURNAL

ARTICLE

Freshwater Ecology

Biotic interactions and stream network position affect body size of aquatic vertebrates across watersheds

Brooke E. Penaluna[1] | **Sherri L. Johnson**[1] | **Amanda M. M. Pollock**[2] | **Ivan Arismendi**[2] | **Dana R. Warren**[3]

[1]U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Corvallis, Oregon, USA

[2]Department of Fisheries, Wildlife, and Conservation Sciences, Oregon State University, Corvallis, Oregon, USA

[3]Department of Forest Ecosystems and Society, Oregon State University, Corvallis, Oregon, USA

Correspondence
Brooke E. Penaluna
Email: brooke.penaluna@usda.gov

Funding information
National Science Foundation, Grant/Award Numbers: DEB-1440409, DEB-2025755

Handling Editor: Michael T. Bogan

Abstract

The body size of aquatic vertebrates is declining across populations and ecosystems worldwide owing to warmer water temperature and changing streamflow. In freshwaters, the effects of stream network position and density-dependent factors on body size are less understood. We used an extensive dataset spanning 41 stream sites over 7 years to evaluate how density-dependent and density-independent factors influence the size of two top predators in small watersheds, Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* and Coastal Giant Salamanders *Dicamptodon tenebrosus*. We tested three hypotheses of body-size variation for trout and salamanders, including intraspecific density dependence, interspecific density dependence, and resource availability, using empirical observations in hierarchical linear mixed models in a model-selection framework. In our best-supported models, the strongest predictors of size were conspecific negative density dependence, as expected, suggesting greater intraspecific interactions probably owing to conspecific individuals having similar requirements. We reveal a biogeographic pattern in which body size peaks in middle stream-network positions and plateaus or declines at lower and upper locations, proposing that stream network position also plays a role in determining body size in small watersheds. Salamander density also has a quadratic effect on adult trout size, with salamanders having a greater overall effect on the body size of both species than trout, suggesting that salamanders might be more dominant than trout in some interactions. Collectively, we found that biotic interactions, mainly conspecific but also interspecific, and stream-network position affect trout and salamander body sizes in small watersheds.

KEYWORDS

biotic interactions, density-dependent, density-independent, ecological modeling, freshwater vertebrates, spatial ecology

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INTRODUCTION

Aquatic vertebrate body size is influenced by numerous density-dependent (biotic) and density-independent (abiotic) factors (Gardner et al., 2011; Winemiller & Rose, 1992). The body size of an individual (measured as length) can be critical for linking individual-level processes of behavior (access to resources) and physiology of metabolism and growth to higher-level population processes that can explain broader ecological patterns. Within a species, smaller body size leads to reduced fecundity, survival, and competitive interactions (McPhee et al., 2016). Recent work has marked a resurgence in the topic of body size in the context of warming water temperature and changing streamflow (Al-Chokhachy et al., 2022; Arismendi, Gregory, et al., 2024; Solokas et al., 2023), with body size for many taxa declining owing to warming habitats (Bergmann, 1847; Daufresne et al., 2009; Gardner et al., 2011) and larger-bodied organisms showing the greatest changes (Audzijonyte et al., 2020; Solokas et al., 2023). Although variability in body size over time has been shown to change (Al-Chokhachy et al., 2022; Arismendi, Gregory, et al., 2024; Solokas et al., 2023), interestingly, some fishes have also shown increases in body size over recent decades (Audzijonyte et al., 2020; Jeffrey et al., 2017; Solokas et al., 2023). However, the effects of various density-dependent and density-independent factors on body size, especially for co-occurring species in freshwaters, are not fully understood.

Relative to marine or terrestrial ecosystems, freshwater habitats may limit body size because habitat loss and fragmentation are more common in freshwaters, and quality habitat is more variable, limiting space and the development of food webs (Clarke, 2021; Hurst, 2007). Accordingly, local stream conditions also affect the body size of freshwater vertebrates (Arismendi, Gregory, et al., 2024; Solokas et al., 2023), especially habitat size (Clarke, 2021). For example, streams with deeper pools support larger fish (Harvey & Stewart, 1991). Larger streams have been shown to have larger stream-living trout, though there is a tenfold difference in the strength of that relationship across trout taxa (Al-Chokhachy et al., 2022). Long-lived headwater salamanders *Gyrinophilus porphyriticus* are larger at metamorphosis in larger watersheds (Cochrane et al., 2024). However, the links between habitat characteristics and the body size of co-occurring species across varying densities in stream networks are not as well understood.

Stream networks expand and contract seasonally with changes in precipitation, which in turn affects stream size and stream-network connectivity (Benda et al., 2004). Although many organisms that live in or near the headwaters of stream networks are well adapted to seasonal low flows (Banks et al., 2007; Frady et al., 2007), some aquatic vertebrates experience reduced growth (Jensen, 2017) and survival (Berger & Gresswell, 2009; Sheldon & Richardson, 2022) owing to reduced habitat availability, especially in pools (Penaluna et al., 2021; Sheldon & Richardson, 2022). Seasonal low flow, which coincides with warmer stream temperatures in the Pacific Northwest, can be a period of ecological crunch (Arismendi et al., 2013). Lower water levels frequently lead to concentrated numbers of individuals in the remaining habitat of streams at or near headwaters, which in turn can lead to reductions in instream food and refugia and increased competition and predation (Sheldon & Richardson, 2022). For example, trout and salamanders might respond differently to stream drying as they have different ecological niches (e.g., constraints on habitat, feeding behaviors, and mobility), with salamanders able to inhabit areas that trout cannot, including deeper interstitial refuges in streams, smaller and/or more disconnected streams, or even leave the stream to occupy terrestrial habitats. Both salamanders and trout have been shown to differ in population responses to extreme low flows, such as during a drought, with trout declining in abundance and salamanders declining in condition (Kaylor et al., 2019). Because amphibian distributions can continue upstream of fish (Barr & Babbitt, 2007; Olson & Weaver, 2007), it is possible that amphibians might be larger in size above the upstream fish distribution boundary owing to reduced interspecific competition, including predation. Warmer temperatures and reduced precipitation may further contract summer stream networks (Olson & Burton, 2019), potentially exacerbating density-dependent and density-independent interactions among vertebrates throughout the watershed. Accordingly, evaluating the relationships between the stream network position and body size of co-occurring top vertebrate predators in freshwater offers an improved understanding of processes underlying their population dynamics.

Biotic factors influence the body size of species, mainly conspecific density (Werner, 1977), but also interspecific interactions. Conspecific negative density dependence is the main factor affecting body size across taxa and/or systems (Werner, 1977; Jenkins et al., 1999). It is suggested that density dependence operates on growth prior to survival to maintain a population at the highest possible abundance (Lobón-Cerviá, 2007). For example, trout are smaller with higher conspecific density (Al-Chokhachy et al., 2022; Jenkins et al., 1999; Lobón-Cerviá, 2007), potentially because space is progressively limited for growing individuals (Lobón-Cerviá, 2007) and/or food is reduced (Ward et al., 2006) and activity increases with an increasing number of individuals

(Guénard et al., 2012). However, variation in salmonid population size is influenced by both within- and between-species densities, such that body size may be affected by both intraspecific and interspecific interactions (Dochtermann & Peacock, 2013).

Here, we evaluate the importance of stream-network position and co-occurring population densities on the body size of Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* and Coastal Giant Salamanders *Dicamptodon tenebrosus*. Trout and salamanders are the dominant freshwater vertebrates in small streams and co-occur across many areas of North America, including in the Pacific Northwest and Appalachia regions, with the two species we studied found in the Pacific Northwest. Using empirical observations from surveys of 41 stream sites over 7 years in a model-selection framework, we evaluated three hypotheses that could account for variation in both the median and largest trout and salamander body size, including intraspecific or conspecific density dependence, interspecific density dependence, and resource availability related to stream-network position of gradient, elevation, stream order, drainage density, or upstream stream length. We expected that a combination of factors, rather than a single factor, might best explain the size distribution patterns of both species (Dochtermann & Peacock, 2013). Specifically, we assumed that population densities would drive responses to the extent that they are key to population regulation (Jenkins et al., 1999), and we aimed to understand the importance of intraspecific (Dunham & Vinyard, 1997; Lobón-Cerviá, 2007) and interspecific (Dochtermann & Peacock, 2013; Elliott, 1994; Wisz et al., 2013) densities relative to body size. Intraspecific competition has been shown to be more important for the growth of individuals of the same species and size because they share similar requirements (Werner, 1977) and, accordingly, we anticipated that conspecific densities would be most important to body size for each species. We expected that trout would be larger in larger stream reaches because productivity and food resources are typically greater (Al-Chokhachy et al., 2022; Minshall et al., 1985; Vannote et al., 1980), and that salamanders might be larger above the upstream boundary of fish distributions in the smallest streams owing to a lack of interactions with trout. Ultimately, understanding the driving factors that affect body size has been an important area of research in ecology, as body size is often a predictor of future survival and reproductive output, and variation in body size within a population can facilitate population resilience and resistance. Understanding the effect of co-occurring species and stream-network position can clarify the relative importance of density-dependent and density-independent factors underlying these processes.

MATERIALS AND METHODS

Study sites

We sampled freshwater vertebrates across small streams in the Willamette National Forest, western Cascade Range, Oregon, with most stream sites located within the H.J. Andrews Experimental Forest (Figure 1; Appendix S1: Table S1). The climate in this area has a strong contrast between cold, wet winters and warm, dry summers. Most of the 2200 mm of precipitation falls between November and April as rain (75%), with episodic snow accumulation in winter at higher elevation sites. Streamflows can be flashy during winter storms, whereas seasonal low flow occurs between July and September. Our stream sites are flanked by a mixture of riparian forest types that generally include second-growth or old-growth stands of Douglas-fir *Pseudotsuga menziesii*, western hemlock *Tsuga heterophylla*, red alder *Alnus rubra*, and vine maple *Acer circinatum*. Stream-living Coastal Cutthroat Trout and Coastal Giant Salamanders co-occur at our stream sites, except for three headwater sites that support salamanders only. Some stream sites also support Coastal Tailed Frogs *Ascaphus truei* and Paiute Sculpin *Cottus beldingii*.

We evaluated freshwater vertebrates from 41 stream reaches during the seasonal low-flow period (July to early September) from 2013 to 2019 (Figure 1; Appendix S1: Tables S2 and S3; database Johnson & Penaluna, 2020). Stream site sampling events occurred in Lookout (10), McRae (17), Mack (8), Chucksney (2), and Loon (2) Creeks, and an unnamed tributary on the east side of McRae Creek (2). Sampled stream sites ranged in elevation between 555 and 1155 m above sea level (asl), with upstream watershed areas ranging from 51 to 1552 ha (Appendix S1: Table S1). Most study stream sites were located in third- and fourth-order streams, but four sites were in fifth-order streams, one site was in a second-order stream, and one site was in a first-order stream. Stream gradients of sampled stream sites ranged from 3% to 17% and varied in geospatial position in the stream network (Figure 1; Appendix S1: Table S1).

Field methods

We used standard backpack electrofishing (Smith-Root model LR-20B) techniques to capture fishes (Bohlin et al., 1989) and stream-living amphibians (Cossel et al., 2012). Stream reaches were temporarily blocked with nets to prevent movement in and out of reaches during the sampling. Surveys occurred annually during seasonal low flow, with an average of 4 years across study

Earthstar Geographics, Airbus,USGS,NGA,NASA,CGIAR,NCEAS,NLS,OS,NMA,Geodatastyrelsen,GSA,GSI and the GIS User Community

FIGURE 1 Forty-one sites in five streams in the western Cascade Range of Oregon, including Mack Creek (dark blue), McRae Creek and tributaries (yellow), and Lookout Creek (red) in the H.J. Andrews Experimental Forest, and Loon (gray) and Chucksney (light blue) Creeks; all five streams are in the Willamette National Forest. Photo credit: Allison Swartz, Lauren Zatkos, and Lina DiGregorio.

sites, but up to 7 years at some of our sites (Appendix S1: Table S1–S3). Captured animals were anesthetized using buffered MS-222, except in Chucksney and Loon Creeks and the east tributary to McRae Creek, where we used Aqui-S. Animals were identified to species and measured to total length (in millimeters). In Mack Creek, trout total length and fork lengths (in millimeters) were measured in 2018 and 2019, and fork length was measured in all other years (note length conversion in the data analyses section). In addition to total length, trout fork length was also measured at most other sites beginning in 2017. Salamanders were measured to snout-vent length (SVL; in millimeters) at most sites, often in addition to total length measurements. We included only neotenic salamanders in our data, which we determined by the presence of gills.

Data preparation

We focused our analyses on age-1+ and older trout and used a cutoff of 70 mm total length for trout to focus on adults and to minimize handling and stress for fragile young-of-year (age-0) individuals. A cutoff of 70 mm was decided based on over 35 years of length distributions for trout (Arismendi, Gregory, et al., 2024). During some surveys, only one length measurement (fork or total) was recorded for an individual trout. We calculated relationships between total length and fork length for trout and total length and SVL for salamanders using individuals that had both measurements recorded. These linear regressions for length had an R^2 value of 0.99 for trout and 0.95 for salamanders (Appendix S1: Figure S1), so we used values predicted by the linear model to fill in missing length values when needed. For salamanders, we used SVL measurements and did not establish a size cutoff because there was no distinct size class for young-of-year, as was also done in Arismendi, Gregory, et al. (2024). Salamander and trout densities were calculated as the total number of captured individuals per species at a site divided by the number of electrofishing passes performed, divided by survey stream reach length (in meters). The stream reach length is a standardized way to measure relative abundance for electrofishing (Hubert & Fabrizio, 2007; Reynolds, 1996), allowing us to account for slight differences in sampling effort.

We measured various aspects of stream-network characteristics to evaluate different characteristics of stream size, including more commonly used metrics of elevation, Strahler stream order (Strahler, 1957), and drainage density (Appendix S1: Table S2). Gradient (slope) is an important predictor of fish distributions (Fransen et al., 2006; Penaluna et al., 2022), along with upstream stream length, the sum of the channel length upstream from a site, which captures aspects of the spatial layout of a stream network, stream size, and proximity to headwaters (Penaluna et al., 2022). For all streams, we used light detection and ranging (LiDAR) data (1-m) to calculate elevation. We used LiDAR-derived National Hydrologic Data (NHD) for Lookout, McRae, and Mack Creeks to calculate percent gradient, Strahler stream order, drainage density (in kilometers per square kilometer), and upstream stream length (in kilometers, wetted) in ArcGIS. For Chucksney and Loon Creeks, we did not have LiDAR-derived NHD layers and used high-resolution NHD.

Data analyses

We used two analytical methods to evaluate the spatial structure of our data. First, to compare the size of salamanders that were collected upstream of the upper extent of fish distributions (three salamander-only sites) with those that co-occurred with fish immediately downstream, we performed two-sample *t*-tests (significance level $\alpha = 0.05$) on salamander SVL in Lookout, Mack, and McRae Creeks. Second, we modeled trout and salamander body size using hierarchical linear mixed models implemented in the package "lme4" using R statistical software, version 4.2.0 (Bates et al., 2014; R Core Team, 2022). Stream-living salamanders and trout may have distinct populations owing to limited dispersal distances (Berger & Gresswell, 2009; Blaustein et al., 1994). To account for potential population differences and the structure of our data, we delineated sites by stream and used the multi-level capabilities of hierarchical linear mixed models to nest sampling sites within streams. We examined the proportion of variation in body size attributable to sites and streams to assess possible population-level effects.

We constructed four separate model sets to evaluate (1) trout 95th-percentile total length, (2) trout 50th-percentile total length, (3) salamander 95th-percentile SVL, and (4) salamander 50th-percentile SVL. We used both the 95th-percentile and 50th-percentile lengths for each species to assess factors influencing the largest and median-sized animals, including determining whether large individuals had different relationships with stream-network characteristics compared to moderate-sized individuals. We selected these metrics because the median is not skewed by outliers, unlike the mean, and the 95th-percentile can provide a reasonable measurement for large individuals while being less variable than the maximum.

We included density-dependent and density-independent factors as fixed effects to understand relationships with trout or salamander body size within each model set. The density-dependent fixed effects were trout catch-per-unit-effort (CPUE) density and salamander CPUE density, and the density-independent fixed effects consisted of percent gradient, Strahler stream order, drainage density, and upstream stream length. We standardized these predictor variables (mean = 0, SD = 1) to allow for comparisons of effect size among them. Then, we constructed hierarchical linear mixed models with predictors as linear or quadratic terms, or a combination of both. We explored models with additive components or two-way interactions between density-independent and density-dependent variables but did not allow three-way interactions. To account for sample size, we used the number of trout or salamanders captured as an offset term. Linear mixed models were fit using maximum likelihood, which allowed us to compare models that differed in fixed effects. We included site and stream as random intercepts, with site nested within stream.

We compared models with different predictors using corrected Akaike's information criterion with the small sample adjustment (AIC_c; Hurvich & Tsai, 1989) so models could represent competing hypotheses (Burnham et al., 2011) regarding which predictors were most likely to influence trout or salamander length. We tested for multicollinearity among predictor variables by using Pearson's correlation coefficient and only included uncorrelated variables ($|r| < 0.6$) within the same model (Dormann et al., 2013). To evaluate the relative plausibility of correlated variables, we compared separate models. For example, Strahler stream order and elevation exhibit strong negative correlations because larger Strahler-order streams are typically associated with lower elevations. Therefore, in our model sets we did not include Strahler stream order and elevation in the same model, but instead we created separate models, one containing Strahler stream order and another containing elevation as a fixed effect. We could then compare AIC_c scores and effect sizes between these competing models.

For each model set, we used the "AICcmodavg" package (Mazerolle, 2023) to construct a model selection table that included all models within the set. We identified the model with the smallest AIC_c score as the top-supported model in each set and examined the fixed-effect estimates. Additionally, we reviewed estimates from models within 2 AIC_c of this top-supported model. We compared fixed-effect estimates, or effect sizes, between models to evaluate the relative strength of relationships for describing trout or salamander length. To assess precision, we created 90% and 95% CIs for each fixed-effect estimate. We then determined the significance of a predictor variable by whether the 95% CI contained 0, comparable with a 0.05 alpha value. To graphically visualize the top-supported model results, we estimated fixed effects by allowing one predictor to vary while using mean values for the remaining predictors. We created 95% CIs around these visualized estimates through bootstrapping, with 999 simulations run for each top model. We used the "MuMIn" package (Bartoń, 2023) to calculate marginal and conditional coefficients, or R^2 values, for the top models in each model set. The marginal R^2 represents variance explained by fixed effects, whereas the conditional R^2 value represents variance explained by the entire model.

RESULTS

In evaluating pairwise correlations among the density-independent predictors, elevation was negatively associated with both Strahler stream order and upstream stream length. Upstream stream length was negatively associated with gradient and positively associated with Strahler stream order (Appendix S1: Figure S2). Consequently, we created separate models for upstream stream length, gradient, and Strahler stream order to evaluate the relative plausibility of these predictors. Density-dependent predictors did not display strong associations with any other predictor ($|r| < 0.6$), and accordingly, these predictors were included in models with density-independent predictors.

Across streams, the longest observed adult trout (age-1^+) were found in McRae Creek, followed by Mack, Lookout, Chucksney, and Loon Creeks, respectively (Appendix S1: Figure S3). Similarly, the longest observed neotenic salamander (SVL) was also found in McRae Creek, followed by Mack, Chucksney, Lookout, and Loon Creeks, respectively (Appendix S1: Figure S3). Observed trout ranged in total length from 70 to 249 mm, whereas salamanders ranged in SVL from 11 to 177 mm. Both species occupied all stream sites, except for three sites with only salamanders. Trout upstream presence was limited in Mack and Lookout Creeks by physical barriers or obstacles of cascade falls, but McRae Creek did not have an apparent physical barrier to trout dispersal. There was no evidence for observed differences in salamander length (p-values >0.05) between stream sites immediately upstream of the upper extent of fish distributions versus at downstream sites co-occupied by both species (Appendix S1: Figure S4).

The top-supported model for the largest adult trout (95th-percentile) showed trout density as a strongly negative linear fixed effect ($\beta = -21.90$), though the second and third models in this set included additional predictors and had similar AIC_c scores (<1 ΔAIC_c; Table 1, Figures 2 and 3; Appendix S1: Figure S4 and S5, Table S4). For example, the second best-supported model included a marginal positive linear fixed effect for elevation ($\beta = 3.10$); however, both the 95% and 90% CIs for this estimate contained 0, suggesting uncertainty in the direction of this effect and reduced precision in the estimate (Table 1). The other models <2 ΔAIC_c contained additional terms with smaller effect sizes than trout CPUE and quadratic terms (CT CPUE^2 or upstream stream length^2) that also included 0 in their 95% CIs. Strahler stream order was an uninformative parameter because it contained 0 in its 95% CI, and this model was only slightly less than 2 ΔAIC_c from the top model, meaning the additional parameter contributed nothing to the model to overcome the 2 AIC_c penalty (Arnold, 2010). The top-supported model for median-sized trout was driven by a strongly negative effect of conspecific density ($\beta = -31.43$); although a positive quadratic term was also included ($\beta = 4.44$), creating a predominately decreasing relationship with slight curvature (Figures 2 and 3; Appendix S1: Table S5). Quadratic effects were also present for upstream stream length and salamander

TABLE 1 Model selection results for models within two AIC_c units of the top linear mixed model for each model set.

Model and fixed effects in model	*K*	AIC_c	ΔAIC_c	AIC_c weight	LL
Coastal Cutthroat Trout 95th percentile total length					
CT CPUE	5	1262.685	0.000	0.109	−626.14
CT CPUE + elevation	6	1263.103	0.418	0.089	−625.27
CT CPUE + CT CPUE^2 + upstream stream length + upstream stream length^2	8	1263.405	0.720	0.076	−623.21
CT CPUE + upstream stream length + upstream stream length^2	7	1263.813	1.128	0.062	−624.53
CT CPUE + CT CPUE^2	6	1263.877	1.192	0.060	−625.66
CT CPUE + upstream stream length^2	6	1264.169	1.484	0.052	−625.80
CT CPUE + Strahler	6	1264.667	1.982	0.041	−626.05
Coastal Cutthroat Trout median total length					
CT CPUE + CT CPUE^2 + GS CPUE + GS CPUE^2 + upstream stream length + upstream stream length^2	10	1239.777	0.000	0.457	−609.13
CT CPUE + CT CPUE^2 + GS CPUE + upstream stream length + upstream stream length^2	9	1240.450	0.673	0.326	−610.61
Coastal Giant Salamander 95th percentile snout-vent length					
GS CPUE + GS CPUE^2 + upstream stream length + upstream stream length^2	8	1394.558	0.000	0.834	−688.81
Coastal Giant Salamander median snout-vent length					
GS CPUE + GS CPUE^2 + upstream stream length + upstream stream length^2	8	1292.686	0.000	0.956	−637.88

Note: The model name lists fixed variables used in the model, although all models also included an intercept, an offset term for the number of individuals captured, and a nested random intercept consisting of site nested within stream. CT is Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* and GS is Coastal Giant Salamander *Dicamptodon tenebrosus* density measured as catch per unit effort (CPUE). *K* is the number of parameters, AIC_c is the Akaike information criterion with small sample size adjustment, ΔAIC_c is the difference between the selected model and the best model in the set, the AIC_c weight is the Akaike model weight, and LL is the log-likelihood of the model. We tested for potential multicollinearity and removed factors with strong correlations in each model using Pearson's correlation analyses (see *Materials and methods* for more details).

density in the best-fitting model for median trout length. Upstream stream length was the second strongest predictor in the top-supported model explaining median trout length, with a positive linear component ($\beta = 10.51$) and a negative quadratic term ($\beta = -6.35$) producing a concave downward curve. Accordingly, median trout length increased initially as upstream stream length increased, reached an apex at 37.7 upstream stream km, then decreased as upstream stream length continued increasing, analogous to moving further downstream in the stream network. Median trout length initially increased with increasing salamander density, then plateaued near 2 salamander CPUE (2 salamanders per pass per meter) and began decreasing slightly. The quadratic effect for salamander density was weaker, and the 95% CI contained 0, although the 90% CI did not (Appendix S1: Table S6), which reflects that AIC model selection is similar to a more liberal threshold of $\alpha = 0.157$ (Sutherland et al., 2023). The second best-supported model predicting median trout length reflected this uncertainty in the salamander relationship shape because it contained the same structure as the top model but excluded the quadratic term for salamander density (Table 1). When combined, the top two models for median trout length garnered most of the AIC_c weight with a total of 0.783, providing strong evidence for the effects of trout density, salamander density, and upstream stream length (Appendix S1: Table S5).

Top-supported models for salamanders, both the largest (95th-percentile) and median salamander size, consisted of quadratic effects for both salamander density and upstream stream length (Table 1, Figure 2; Appendix S1: Tables S7 and S8). In each model set, the density-dependent variable of salamander CPUE was the strongest predictor, with a predominantly negative linear term (95th-percentile $\beta = -42.17$, median $\beta = -41.76$) and a smaller positive quadratic term (95th-percentile $\beta = 3.42$, median $\beta = 3.09$). This resulted in a strong negative relationship between salamander length and conspecific density (Figures 2 and 3). Upstream stream length had a curved relationship with salamander length, with salamander length positively increasing with upstream stream length and then plateauing near 62.1 km for larger salamanders (95th-percentile) or reaching an apex at 45.5 km and then declining for median salamanders

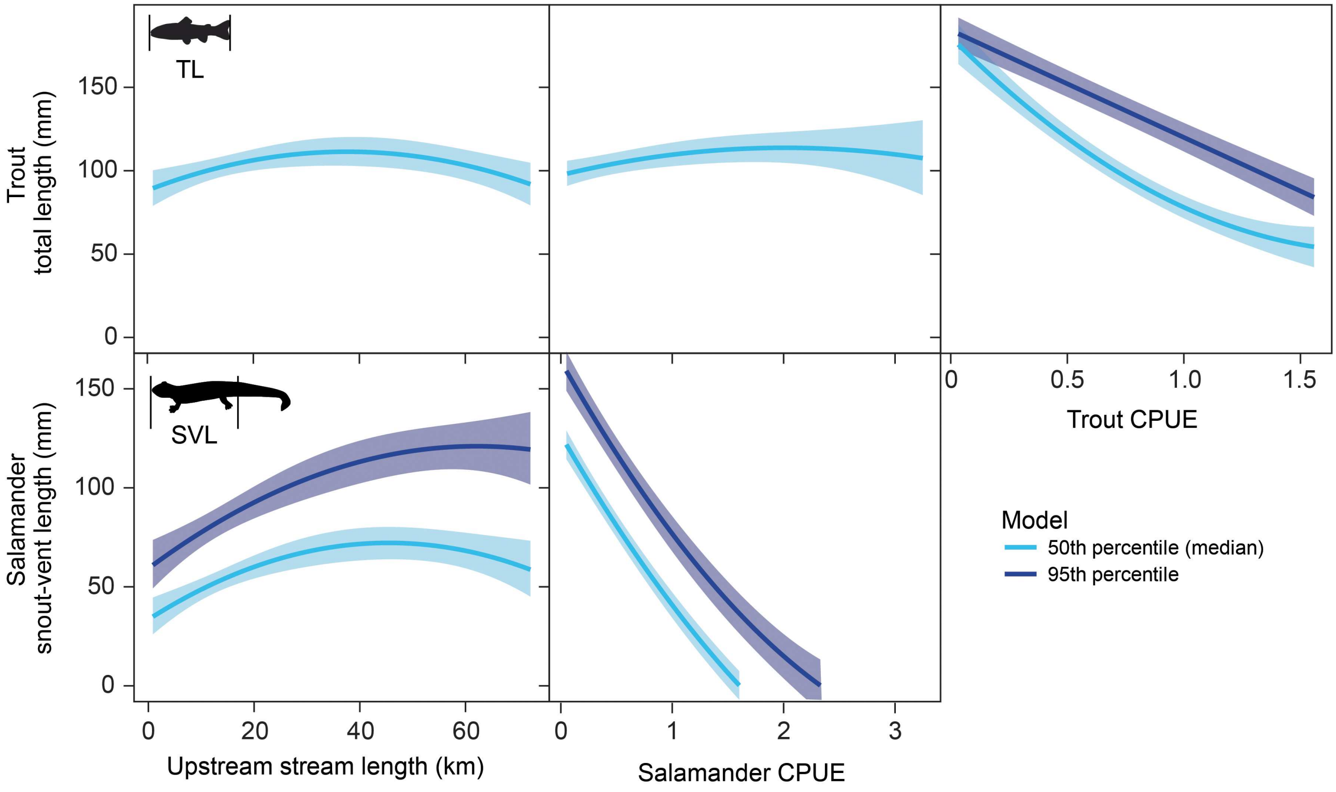

FIGURE 2 Fixed-effect predictors in the top-performing models for body size of Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* and Coastal Giant Salamanders *Dicamptodon tenebrosus* Solid lines represent fixed effects from the top-supported model, calculated by allowing a predictor to vary while using mean values for the other predictors. The shaded ribbons represent 95% CIs created through bootstrapping. CPUE is catch-per-unit effort, or the number of individuals captured per pass per meter. Trout and salamander silhouettes credit: Kathryn Ronnenberg. TL, total length and SVL, snout-vent length.

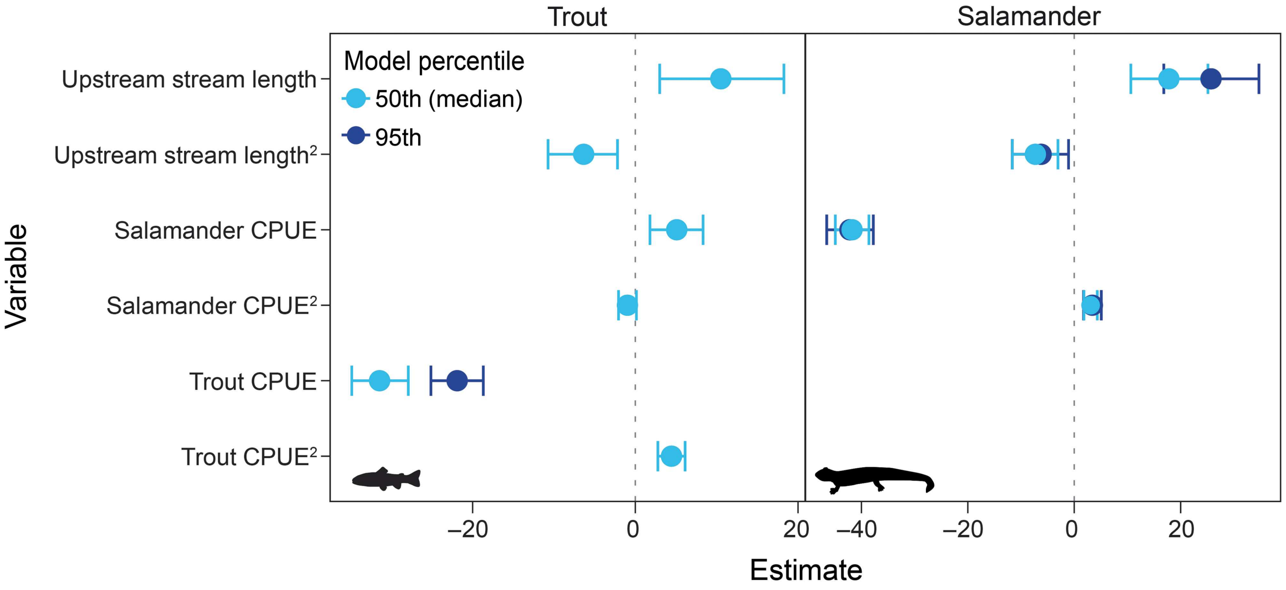

FIGURE 3 Modeled estimates for upstream stream length (in kilometers), catch-per-unit effort (CPUE; number of individuals per pass per meter) of Coastal Giant Salamanders *Dicamptodon tenebrosus*, and catch-per-unit effort (CPUE; number of individuals per pass per meter) of Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* predictors in the top-supported linear mixed models (Table 1; Appendix S1: Table S2) for size of trout and salamanders. The whiskers represent 95% CIs. Trout and salamander silhouettes credit: Kathryn Ronnenberg.

(Figure 2). Variability in body size was also reduced upstream; the median and largest salamanders were more similar in size near headwaters compared to downstream (Figure 2). The top-supported models for the largest (95th-percentile) and median salamanders received the majority of the AIC$_c$ model weight, with values of 0.834 and 0.956, respectively (Table 1; Appendix S1: Tables S7 and S8). The top-supported model for the largest salamander was 5.2 times more likely than the next best model, whereas the median salamander top-supported model was 33 times more likely than the second-best model in that set, providing substantial evidence for relationships between salamander body size and both upstream stream length and salamander density. We found little to no support for two-way interactions between density-dependent and density-independent factors across all model sets.

Fixed effects explained the majority of variance in all top models (range = 0.645–0.872; Appendix S1: Figure S9), highlighting the importance of trout CPUE, salamander CPUE, and upstream stream length on stream vertebrate body size. The conditional variance values were also high ($R^2 > 0.8$), particularly for salamander top models (Appendix S1: Table S9). These values represent variance explained by the entire model (both fixed and random effects), which supports top models as being effective in explaining most of the variability observed in our data. Stream and site also had notable effects on trout and salamander length, accounting for 52.8% of the random effect variance on average (range = 49.8%–58.1%) in the top-supported models (Figure 4; Appendix S1: Table S10). Stream had a greater influence on the random-effect variation in 95th-percentile lengths for both trout (19.2%) and salamanders (5.2%) compared with median lengths for each species (7.8% and 2.1%, respectively).

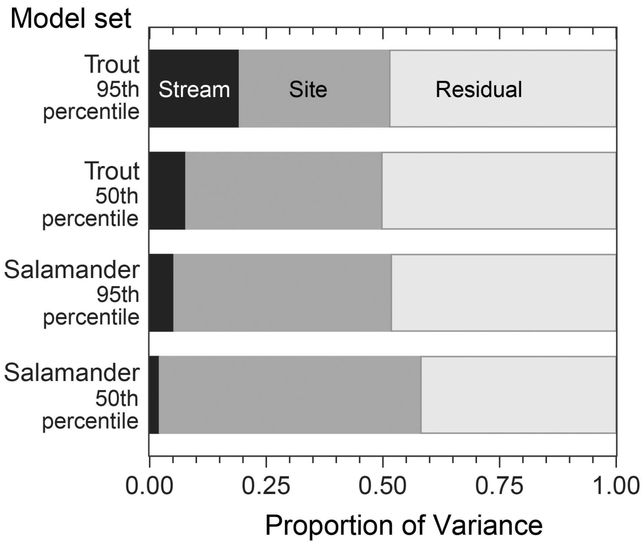

FIGURE 4 Proportion of variation in body size of Coastal Cutthroat Trout *Oncorhynchus clarkii clarkii* and Coastal Giant Salamanders *Dicamptodon tenebrosus* explained by stream and site.

DISCUSSION

We evaluated hypotheses related to intraspecific density dependence, interspecific density dependence, and resource availability in explaining the median and largest sizes of two sympatric freshwater vertebrates in small, forested watersheds using empirical observations in a model-selection framework. The best-supported models for body size consistently included density of the same species (conspecific negative density dependence) followed by a metric that collectively captures stream network position incorporating the spatial layout of a stream, stream size, and proximity to headwaters (upstream stream length) as main predictors. Trout were not largest in the biggest streams as expected; rather, median trout body size peaked in middle stream-network positions and declined at lower and upper locations. Upstream stream length was not included in the top model for 95th-percentile trout, suggesting little effect of network position on the largest trout sizes. Conversely, upstream stream length was included in top models for both the largest (95th-percentile) and median salamanders, suggesting a more consistent influence of stream-network position on salamander body size. Salamander density also affected median trout size, though trout did not have the same effect on salamanders, suggesting salamanders might be more dominant than trout in some interactions, but this effect could also result from co-occurring in high quality habitats. Collectively, we demonstrated the complex interplay of dynamic and interdependent drivers of intraspecific density dependence, interspecific density dependence, and resource availability for the body size of both taxa in small watersheds.

The combination of factors affecting the body size of aquatic taxa supports the intricate roles of biotic interactions and stream-network position. In addition, we present evidence for non-linear relationships between top aquatic predator body size and both density-dependent and density-independent predictors. This highlights the need to take multiple factors into account and consider complex relationships to understand trout and salamander body sizes. A combination of density-dependent and density-independent factors affecting body size has been observed in long-term studies of trout and salamanders from Mack Creek (Arismendi, Gregory, et al., 2024; Arismendi, Penaluna, & Gregory, 2024), in other trout populations (Al-Chokhachy et al., 2022), and in salmon returning from the ocean in western North America

(Helle et al., 2007; Jeffrey et al., 2017; Ohlberger et al., 2023).

Density-dependent effects on size

Conspecific negative density dependence is the most important predictor of body size for both trout and salamanders, whereby body size declines owing to biotic feedbacks from individuals of the same species, probably because they have similar requirements (Arismendi, Gregory, et al., 2024; Arismendi, Penaluna, & Gregory, 2024; Bohlin et al., 1994; Chapman, 1966; Zaradic, 2003). Larger trout and salamanders are found where conspecifics are fewer, so individuals are likely released from intraspecific interactions, such as competition and predation, allowing them the opportunity to grow larger. This circumstance can lead to population self-thinning, as larger individuals require greater amounts of space or food, leading to lower population densities (Dunham & Vinyard, 1997). Populations that frequently display negative density dependence typically are considered to be at or near carrying capacity, with increased growth or survivorship proposed to occur in response to environmental disturbances (Grossman & Simon, 2020). Our results suggest that intraspecific interactions have the greatest influence on body size in these mostly second- to fourth-order streams.

Salamander density appears to influence median trout size, but trout density does not appear to influence salamander size, collective evidence for an overall greater relative effect of salamanders on both species than trout. Our findings suggest that salamanders might be more dominant than trout in some interactions; however, the literature recognizes very little competition owing to diet differences and/or diurnal habitat partitioning (Li et al., 2016; Parker, 1994). Accordingly, if there is dominance by salamanders over trout in some interactions, it is likely small, which is reflected by the smaller effect sizes for salamander CPUE in the top model for trout median total length. In an experimental study, larval salamanders increased their use of refuge in response to trout chemical cues (Rundio & Olson, 2003), which is a behavior that would likely further reduce the probability of encounters between species. Alternatively, these species could be co-occurring in high-quality habitat patches, which inherently allows both taxa to increase in numbers and/or size. In addition, we only consider age 1+ trout in this study, so it is possible that young-of-year trout could affect the body size of salamanders, given that salamanders occasionally consume young trout as prey (Parker, 1994). However, we did not find evidence for salamander size differences in sites upstream of trout distribution, and previous studies did not find associations between young-of-year trout abundance and salamander body size (Arismendi, Gregory, et al., 2024). Although we expected to see larger salamander sizes where trout are not present in uppermost reaches owing to concepts of ecological release, we did not find evidence that trout presence affects salamander body size, and no relationships were revealed in our modeling results.

Density-independent effects on size

Density-independent factors can be important in accounting for variation in the size of trout and salamanders across stream networks, and we found that upstream stream length is a key predictor of size for these top aquatic predators. Greater upstream stream length corresponds with stream network position and captures the spatial structure of the stream network, stream size, and proximity to headwaters, which aligns with major ecosystem changes including energy sources, ecosystem metabolism, habitat characteristics, and biodiversity (Minshall et al., 1985; Vannote et al., 1980). Headwaters are areas from which water originates in a stream network, characterized by hydrologic, geomorphic, and biological processes (Gomi et al., 2002), and though the conditions can be harsh, individuals in these habitats are likely to experience fewer interactions with other biota. Sites furthest away from headwaters (with greater upstream stream length) would be expected to have the largest salamanders; however, the median sizes of trout and salamanders are the largest in mid-stream sites of stream networks. Larger streams offer greater opportunities for some taxa to grow, providing more space and greater diversity of habitats, but that relationship seems to dissipate when streams become too big, at least for the stream-living trout considered here and likely also eventually for salamanders. In larger rivers, trout sizes are larger than for stream-living trout in smaller streams (Al-Chokhachy et al., 2022). Larger trout are frequently associated with larger, deeper pools or more refuges in streams (Bisson et al., 1988; Heggenes & Metcalfe, 1991; Latterell et al., 2003; Penaluna et al., 2021), and larger salamanders are found in pools compared to other habitat types (Roni, 2002). The median and largest salamanders are more similar in size near headwaters compared to downstream sites, likely because larger and more diverse habitat patches downstream lead to a greater range of body sizes as seen for mammals (Brown & Nicoletto, 1991). Unfortunately, we do not have the fine-scale habitat data to evaluate habitat differences among streams and sites, such as the size of pools and available food resources, that would have the potential to further account for differences across sites. In another study of 110 stream reaches in temperate systems in New Zealand, stream-network spatial factors explained the majority of the variance in trophic position across fish species (Fraley et al., 2020).

Stream and site were also important to the body size of trout and salamanders, with the site having a greater influence than stream for top models in each set, suggesting local conditions such as pools, food resources, and stream-network position were more influential than stream-scale differences. Across model sets, stream differences had a greater influence on larger individuals than median-sized ones, for both trout and salamanders. Stream differences also had a more pronounced effect on trout compared to salamanders, possibly because Coastal Giant Salamanders can transition to the terrestrial environment if conditions make that strategy more favorable. Local environmental conditions at each stream comprise a unique combination of biotic and abiotic characteristics, even though there are general patterns across streams for the responses.

There was no distinct size class for young-of-year salamanders, and accordingly, we included small salamanders in our analyses. However, this may have influenced results by altering relationships between body size and predictor variables, particularly density-dependent factors. Including small salamanders would increase estimates of salamander density at sites, whereas excluding small trout would decrease estimates of trout density. As a result, the effect of salamander density on trout may have been altered, or the effect of trout density on trout body size could be stronger than we report here. However, the overall conspecific density relationships we observed were negative as we expected and as reported elsewhere (Arismendi, Gregory, et al., 2024; Jenkins et al., 1999). In addition, the effect of upstream stream length on salamander body size seems unlikely to be substantially altered by including small salamanders in the analyses because we found upstream stream length to be consistently important for both median and large salamanders, and it has also been found to be important to the upstream distribution of fish (Penaluna et al., 2022).

Longer-term studies might discover patterns related to multi-year temperature and precipitation cycles and periodic disturbance events, such as wildfire, that might not be captured in a span of less than a decade. We encourage further annual sampling to compare responses across a range of climatic conditions and to determine the influence of other key factors, including temperature and flow, on modifying biotic interactions. Controlled experiments using varying animal densities and density-independent factors may improve our understanding of interactions and cause-and-effect. Although we find compelling relationships with stream-network position, more work is needed to test mechanisms underlying these patterns to understand which component is limiting the body size of top predators, including the spatial structure of streams, stream size, or proximity to headwaters. Salamanders affected both species, and more work needs to be done to understand whether salamanders have a dominant role in survival and population dynamics for both species.

CONCLUSIONS

Our study enhances the biogeographic understanding of the size of trout and salamanders in forested watersheds, providing evidence to support the hypothesis that size is linked to a combination of density-dependent and density-independent factors. Managers may consider both types of factors as affecting populations in these mostly second- to fourth-order streams, with intraspecific interactions being stronger influences than interspecific. Given our results, it is plausible that intraspecific competition may be stronger downstream and that space or food may be limiting upstream, but this hypothesis remains to be tested.

AUTHOR CONTRIBUTIONS

Brooke E. Penaluna, Ivan Arismendi, Dana R. Warren, and Sherri L. Johnson had the original idea for the manuscript, and each led field crews collecting biological data. Amanda M. M. Pollock analyzed the data. Brooke E. Penaluna drafted the original manuscript. All co-authors contributed to revisions of the original draft.

ACKNOWLEDGMENTS

Thanks to field crew members for over 7 years of help in the field. Kelly Christiansen developed the Figure 1 map. Kathryn Ronnenberg drew the animal silhouettes used in figures and beautified figures. Fish collections were authorized by Oregon Department of Fish and Wildlife scientific take permits 18085, 18804, 19490, 20428, 21310, 22210, 23089, 23880, and 24058. Animal collections were done in compliance with Animal Care and Use Committee guidelines from Oregon State University 3720, 4076, 4379, 4796, 4439, 4816, and 5029. Funding for this work is from the PNW Research Station, USDA Forest Service and is also supported by the H.J. Andrews Experimental Forest and Long-Term Ecological Research (LTER) program under the NSF grants DEB-1440409 and DEB-2025755.

FUNDING INFORMATION

Funding came from the Pacific Northwest Research Station and the Andrews Long-Term Ecological

Research (LTER) program under the NSF grants DEB-1440409 and DEB-2025755.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Trout and salamander biomass from sites L755, L769, L894, L906, R620, and R631 are also reported in Kaylor et al. (2017; database Kaylor, 2019); trout and salamander abundances for Mack Creek sites are reported in Arismendi, Gregory, et al. (2024; database Gregory & Arismendi, 2023); and trout and salamander data from sites in Chucksney and Loon Creeks and the east tributary to McRae Creek are reported in Swartz and Warren (2022), except that we excluded data from manipulated sites on this stream in the post-manipulation surveys of 2018 and 2019. Data generated and analyzed during this study (Gregory & Arismendi, 2023; Johnson & Penaluna, 2020; Kaylor, 2019) are available from the Environmental Data Initiative (EDI) Data Portal: https://doi.org/10.6073/pasta/753b1ca1837049bc7c3e77e784408a1e, https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-and.5330.3, and https://portal.edirepository.org/nis/mapbrowse?packageid=knb-lter-and.5484.3.

ORCID

Brooke E. Penaluna https://orcid.org/0000-0001-7215-770X
Sherri L. Johnson https://orcid.org/0000-0002-4223-3465
Amanda M. M. Pollock https://orcid.org/0000-0002-9658-2716
Ivan Arismendi https://orcid.org/0000-0002-8774-9350
Dana R. Warren https://orcid.org/0000-0001-5282-7972

REFERENCES

Al-Chokhachy, R., B. H. Letcher, C. C. Muhlfeld, J. B. Dunham, T. Cline, N. P. Hitt, J. J. Roberts, and D. Schmetterling. 2022. "Stream Size, Temperature, and Density Explain Body Sizes of Freshwater Salmonids Across a Range of Climate Conditions." *Canadian Journal of Fisheries and Aquatic Sciences* 79(10): 1729–44.

Arismendi, I., B. E. Penaluna, and S. V. Gregory. 2024. "Trout under Drought: A Long-Term Study of Annual Growth and Condition of Stream-Living Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*)." In *Advances in the Ecology of Stream-Dwelling Salmonids. Fish and Fisheries Series*, Vol. 44, edited by J. Lobón-Cerviá, P. Budy, and R. Gresswell. Cham: Springer.

Arismendi, I., M. Safeeq, S. L. Johnson, J. B. Dunham, and R. Haggerty. 2013. "Increasing Synchrony of High Temperature and Low Flow in Western North American Streams: Double Trouble for Coldwater Biota?" *Hydrobiologia* 712: 61–70.

Arismendi, I., S. V. Gregory, D. S. Bateman, and B. E. Penaluna. 2024. "Shrinking Sizes of Trout and Salamanders Are Unexplained by Warming Alone." *Scientific Reports* 14: 13614. https://doi.org/10.1038/s41598-024-64145-x.

Arnold, T. W. 2010. "Uninformative Parameters and Model Selection Using Akaike's Information Criterion." *Journal of Wildlife Management* 74(6): 1175–78. https://doi.org/10.2193/2009-367.

Audzijonyte, A., S. A. Richards, R. D. Stuart-Smith, G. Pecl, G. J. Edgar, N. S. Barrett, N. Payne, and J. L. Blanchard. 2020. "Fish Body Sizes Change with Temperature but Not All Species Shrink with Warming." *Nature Ecology & Evolution* 4(6): 809–814.

Banks, J. L., J. Li, and A. T. Herlihy. 2007. "Influence of Clearcut Logging, Flow Duration, and Season on Emergent Aquatic Insects in Headwater Streams of the Central Oregon Coast Range." *Journal of the North American Benthological Society* 26(4): 620–632.

Barr, G. E., and K. J. Babbitt. 2007. "Trout Affect the Density, Activity and Feeding of a Larval Plethodontid Salamander." *Freshwater Biology* 52(7): 1239–48.

Bartoń, K. 2023. "MuMIn: Multi-Model Inference." R Package Version 1.47.5. https://CRAN.R-project.org/package=MuMIn.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2014. "Fitting Linear Mixed-Effects Models Using lme4." *Journal of Statistical Software* 67(1): 1–48.

Benda, L., N. L. Poff, D. Miller, T. Dunne, G. Reeves, G. Pess, and M. Pollock. 2004. "The Network Dynamics Hypothesis: How Channel Networks Structure Riverine Habitats." *Bioscience* 54(5): 413–427.

Berger, A. M., and R. E. Gresswell. 2009. "Factors Influencing Coastal Cutthroat Trout (*Oncorhynchus clarkii clarkii*) Seasonal Survival Rates: A Spatially Continuous Approach within Stream Networks." *Canadian Journal of Fisheries and Aquatic Sciences* 66(4): 613–632.

Bergmann, C. 1847. "Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse." *Göttinger Studien*: 1595–1708.

Bisson, P. A., K. Sullivan, and J. L. Nielsen. 1988. "Channel Hydraulics, Habitat Use, and Body Form of Juvenile Coho Salmon, Steelhead, and Cutthroat Trout in Streams." *Transactions of the American Fisheries Society* 117(3): 262–273.

Blaustein, A. R., D. B. Wake, and W. P. Sousa. 1994. "Amphibian Declines: Judging Stability, Persistence, and Susceptibility of Populations to Local and Global Extinctions." *Conservation Biology* 8(1): 60–71.

Bohlin, T., C. Dellefors, U. Faremo, and A. Johlander. 1994. "The Energetic Equivalence Hypothesis and the Relation between Population Density and Body Size in Stream-Living Salmonids." *The American Naturalist* 143(3): 478–493.

Bohlin, T., S. Hamrin, T. G. Heggberget, G. Rasmussen, and S. J. Saltveit. 1989. "Electrofishing—Theory and Practice with Special Emphasis on Salmonids." *Hydrobiologia* 173: 9–43.

Brown, J. H., and P. F. Nicoletto. 1991. "Spatial Scaling of Species Composition: Body Masses of North American Land Mammals." *The American Naturalist* 138(6): 1478–1512.

Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. "AIC Model Selection and Multimodel Inference in Behavioral Ecology: Some Background, Observations, and Comparisons." *Behavioral Ecology and Sociobiology* 65: 23–35.

Chapman, D. W. 1966. "Food and Space as Regulators of Salmonid Populations in Streams." *The American Naturalist* 100(913): 345–357.

Clarke, J. T. 2021. "Evidence for General Size-by-Habitat Rules in Actinopterygian Fishes Across Nine Scales of Observation." *Ecology Letters* 24(8): 1569–81.

Cochrane, M. M., B. R. Addis, L. K. Swartz, and W. H. Lowe. 2024. "Individual Growth Rates and Size at Metamorphosis Increase with Watershed Area in a Stream Salamander." *Ecology* 105(2): e4217. https://doi.org/10.1002/ecy.4217.

Cossel, J. O., Jr., M. G. Gaige, and J. D. Sauder. 2012. "Electroshocking as a Survey Technique for Stream-Dwelling Amphibians." *Wildlife Society Bulletin* 36(2): 358–364.

Daufresne, M., K. Lengfellner, and U. Sommer. 2009. "Global Warming Benefits the Small in Aquatic Ecosystems." *Proceedings of the National Academy of Sciences of the United States of America* 106(31): 12788–93.

Dochtermann, N. A., and M. M. Peacock. 2013. "Inter-and Intra-Specific Patterns of Density Dependence and Population Size Variability in Salmoniformes." *Oecologia* 171: 153–162.

Dormann, C. F., J. Elith, S. Bacher, C. Buchmann, G. Carl, G. Carré, J. R. G. Marquéz, et al. 2013. "Collinearity: A Review of Methods to Deal with It and a Simulation Study Evaluating their Performance." *Ecography* 36(1): 27–46.

Dunham, J. B., and G. L. Vinyard. 1997. "Relationships between Body Mass, Population Density, and the Self-Thinning Rule in Stream-Living Salmonids." *Canadian Journal of Fisheries and Aquatic Sciences* 54(5): 1025–30.

Elliott, J. M. 1994. *Quantitative Ecology and the Brown Trout*. Oxford: Oxford University Press.

Frady, C., S. Johnson, and J. Li. 2007. "Stream Macroinvertebrate Community Responses as Legacies of Forest Harvest at the HJ Andrews Experimental Forest, Oregon." *Forest Science* 53(2): 281–293.

Fraley, K. M., H. J. Warburton, P. G. Jellyman, D. Kelly, and A. R. McIntosh. 2020. "Do Body Mass and Habitat Factors Predict Trophic Position in Temperate Stream Fishes?" *Freshwater Science* 39(3): 405–414.

Fransen, B. R., S. D. Duke, L. G. McWethy, J. K. Walter, and R. E. Bilby. 2006. "A Logistic Regression Model for Predicting the Upstream Extent of Fish Occurrence Based on Geographical Information Systems Data." *North American Journal of Fisheries Management* 26(4): 960–975.

Gardner, J. L., A. Peters, M. R. Kearney, L. Joseph, and R. Heinsohn. 2011. "Declining Body Size: A Third Universal Response to Warming?" *Trends in Ecology & Evolution* 26(6): 285–291.

Gomi, T., R. C. Sidle, and J. S. Richardson. 2002. "Understanding Processes and Downstream Linkages of Headwater Systems: Headwaters Differ from Downstream Reaches by Their Close Coupling to Hillslope Processes, More Temporal and Spatial Variation, and Their Need for Different Means of Protection from Land Use." *Bioscience* 52(10): 905–916.

Gregory, S. V., and I. Arismendi. 2023. "Aquatic Vertebrate Population study in Mack Creek, Andrews Experimental Forest, 1987 to Present." Environmental Data Initiative. https://doi.org/10.6073/pasta/753b1ca1837049bc7c3e77e784408a1e

Grossman, G. D., and T. N. Simon. 2020. "Density-Dependent Effects on Salmonid Populations: A Review." *Ecology of Freshwater Fish* 29(3): 400–418.

Guénard, G., D. Boisclair, O. Ugedal, T. Forseth, I. A. Fleming, and B. Jonsson. 2012. "The Bioenergetics of Density-Dependent Growth in Arctic Char (*Salvelinus alpinus*)." *Canadian Journal of Fisheries and Aquatic Sciences* 69(10): 1651–62.

Harvey, B. C., and A. J. Stewart. 1991. "Fish Size and Habitat Depth Relationships in Headwater Streams." *Oecologia* 87: 336–342.

Heggenes, J., and N. B. Metcalfe. 1991. "Bimodal Size Distributions in Wild Juvenile Atlantic Salmon Populations and Their Relationship with Age at Smolt Migration." *Journal of Fish Biology* 39(6): 905–7.

Helle, J. H., E. C. Martinson, D. M. Eggers, and O. Gritsenko. 2007. "Influence of Salmon Abundance and Ocean Conditions on Body Size of Pacific Salmon." *North Pacific Anadromous Fish Commission Bulletin* 4: 289–298.

Hubert, W. A., and M. C. Fabrizio. 2007. "Relative Abundance and Catch per Unit Effort." In *Analysis and Interpretation of Freshwater Fisheries Data* 279–325. Bethesda, MD: American Fisheries Society.

Hurst, T. P. 2007. "Causes and Consequences of Winter Mortality in Fishes." *Journal of Fish Biology* 71(2): 315–345.

Hurvich, C. M., and C. L. Tsai. 1989. "Regression and Time Series Model Selection in Small Samples." *Biometrika* 76(2): 297–307.

Jeffrey, K. M., I. M. Côté, J. R. Irvine, and J. D. Reynolds. 2017. "Changes in Body Size of Canadian Pacific Salmon Over Six Decades." *Canadian Journal of Fisheries and Aquatic Sciences* 74(2): 191–201.

Jenkins, T. M., Jr., S. Diehl, K. W. Kratz, and S. D. Cooper. 1999. "Effects of Population Density on Individual Growth of Brown Trout in Streams." *Ecology* 80(3): 941–956.

Jensen, L. R. 2017. "Factors Influencing Growth and Bioenergetics of Fish in Forested Headwater Streams Downstream of Forest Harvest." Master's thesis, Oregon State University. https://ir.library.oregonstate.edu/concern/graduate_thesis_or_dissertations/1544bv18p.

Johnson, S. L., and B. E. Penaluna. 2020. "Aquatic Vertebrate Populations in Streams Throughout the H.J. Andrews Experimental Forest, 2013 to Present Ver 3." Environmental Data Initiative. https://doi.org/10.6073/pasta/26d9b20ccc07dd4446bf582db426f32a.

Kaylor, M. J. 2019. "Riparian Controls on Light Availability, Primary Producers, Invertebrates, Fish and Salamanders in Streams in and Near the Andrews Experimental Forest, 2014–2018 Ver 3." Environmental Data Initiative. https://doi.org/10.6073/pasta/4159cb86beb23c683b59b329601f1861.

Kaylor, M. J., B. J. VerWey, A. Cortes, and D. R. Warren. 2019. "Drought Impacts to Trout and Salamanders in Cool, Forested Headwater Ecosystems in the Western Cascade Mountains, OR." *Hydrobiologia* 833: 65–80.

Kaylor, M. J., D. R. Warren, and P. M. Kiffney. 2017. "Long-Term Effects of Riparian Forest Harvest on Light in Pacific Northwest (USA) Streams." *Freshwater Science* 36(1): 1–13.

Latterell, J. J., R. J. Naiman, B. R. Fransen, and P. A. Bisson. 2003. "Physical Constraints on Trout (*Oncorhynchus* spp.) Distribution in the Cascade Mountains: A Comparison of Logged and Unlogged Streams." *Canadian Journal of Fisheries and Aquatic Sciences* 60(8): 1007–17.

Li, J. L., W. J. Gerth, R. P. Van Driesche, D. S. Bateman, and A. T. Herlihy. 2016. "Seasonal and Spatial Fluctuations in Oncorhynchus Trout Diet in a Temperate Mixed-Forest Watershed." *Canadian Journal of Fisheries and Aquatic Sciences* 73(11): 1642–49. https://doi.org/10.1139/cjfas-2015-0520.

Lobón-Cerviá, J. 2007. “Density-Dependent Growth in Stream-Living Brown Trout *Salmo trutta* L.” *Functional Ecology* 21(1): 117–124. https://doi.org/10.1111/j.1365-2435.2006.01204.x.

Mazerolle, M. J. 2023. “AICcmodavg: Model Selection and Multimodel Inference Based on (Q)AIC(c).” R Package Version 2.3.3. https://cran.rproject.org/package=AICcmodavg.

McPhee, M. V., J. M. Leon, L. I. Wilson, J. E. Siegel, and B. A. Agler. 2016. “Changing Growth and Maturity in Western Alaskan Chinook Salmon *Oncorhynchus tshawytscha*, Brood Years 1975–2005.” *North Pacific Anadromous Fish Commission Bulletin* 6(1): 307–327.

Minshall, G. W., R. C. Petersen, Jr., and C. F. Nimz. 1985. “Species Richness in Streams of Different Size from the Same Drainage Basin.” *The American Naturalist* 125(1): 16–38. https://doi.org/10.1086/284326.

Ohlberger, J., T. J. Cline, D. E. Schindler, and B. Lewis. 2023. “Declines in Body Size of Sockeye Salmon Associated with Increased Competition in the Ocean.” *Proceedings of the Royal Society B: Biological Sciences* 290(1992): 20222248.

Olson, D. H., and G. Weaver. 2007. “Vertebrate Assemblages Associated with Headwater Hydrology in Western Oregon Managed Forests.” *Forest Science* 53(2): 343–355.

Olson, D. H., and J. I. Burton. 2019. “Climate Associations with Headwater Streamflow in Managed Forests over 16 Years and Projections of Future Dry Headwater Stream Channels.” *Forests* 10(11): 968.

Parker, M. S. 1994. “Feeding Ecology of Stream-Dwelling Pacific Giant Salamander Larvae (*Dicamptodon tenebrosus*).” *Copeia* 1994(3): 705–718.

Penaluna, B. E., J. B. Dunham, and H. V. Andersen. 2021. “Nowhere to Hide: The Importance of Instream Cover for Stream-Living Coastal Cutthroat Trout During Seasonal Low Flow.” *Ecology of Freshwater Fish* 30(2): 256–269.

Penaluna, B. E., J. D. Burnett, K. Christiansen, I. Arismendi, S. L. Johnson, K. Griswold, B. Holycross, and S. H. Kolstoe. 2022. “UPRLIMET: UPstream Regional LiDAR Model for Extent of Trout in Stream Networks.” *Scientific Reports* 12(1): 20266.

R Core Team. 2022. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. https://www.R-project.org.

Reynolds, J. B. 1996. In *Fisheries techniques*, 2nd ed., edited by B. R. Murphy and D. W. Willis, 221–254. Bethesda, MD: American Fisheries Society.

Roni, P. 2002. “Habitat Use by Fishes and Pacific Giant Salamanders in Small Western Oregon and Washington Streams.” *Transactions of the American Fisheries Society* 131(4): 743–761.

Rundio, D. E., and D. H. Olson. 2003. “Antipredator Defenses of Larval Pacific Giant Salamanders (*Dicamptodon tenebrosus*) against Cutthroat Trout (*Oncorhynchus clarki*).” *Copeia* 2003(2): 402–7.

Sheldon, K. A., and J. S. Richardson. 2022. “Season-Specific Survival Rates and Densities of Coastal Cutthroat Trout across Stream Sizes in Southwestern British Columbia.” *Ecology of Freshwater Fish* 31(1): 102–117.

Solokas, M. A., Z. S. Feiner, R. Al-Chokachy, P. Budy, J. T. DeWeber, J. Sarvala, G. G. Sass, S. A. Tolentino, T. E. Walsworth, and O. P. Jensen. 2023. “Shrinking Body Size and Climate Warming: Many Freshwater Salmonids Do Not Follow the Rule.” *Global Change Biology* 29(9): 2478–92.

Strahler, A. N. 1957. “Quantitative Analysis of Watershed Geomorphology.” *American Geophysical Union, Transactions* 38, no 6: 913–920.

Sutherland, C., D. Hare, P. J. Johnson, D. W. Linden, R. A. Montgomery, and E. Droge. 2023. “Practical Advice on Variable Selection and Reporting Using Akaike Information Criterion.” *Procedings of the Royal Society B* 290(2007): 2023126. https://doi.org/10.1098/rspb.2023.1261.

Swartz, A., and D. Warren. 2022. “Wildfire in Western Oregon Increases Stream Temperatures, Benthic Biofilms, and Juvenile Coastal Cutthroat Trout Size and Densities with Mixed Effects on Adult Trout and Coastal Giant Salamanders.” *Canadian Journal of Fisheries and Aquatic Sciences* 80(3): 503–516.

Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing. 1980. “The River Continuum Concept.” *Canadian Journal of Fisheries and Aquatic Sciences* 37(1): 130–37.

Ward, A. J., M. M. Webster, and P. J. Hart. 2006. “Intraspecific Food Competition in Fishes.” *Fish and Fisheries* 7(4): 231–261.

Werner, E. E. 1977. “Species Packing and Niche Complementarity in Three Sunfishes.” *The American Naturalist* 111(979): 553–578.

Winemiller, K. O., and K. A. Rose. 1992. “Patterns of Life-History Diversification in North American Fishes: Implications for Population Regulation.” *Canadian Journal of Fisheries and Aquatic Sciences* 49(10): 2196–2218.

Wisz, M. S., J. Pottier, W. D. Kissling, L. Pellissier, J. Lenoir, C. F. Damgaard, C. F. Dormann, et al. 2013. “The Role of Biotic Interactions in Shaping Distributions and Realised Assemblages of Species: Implications for Species Distribution Modelling.” *Biological Reviews* 88(1): 15–30.

Zaradic, P. A. 2003. “Food Limited to Habitat Limited: Predator Prey Uncoupled.” Ph.D. dissertation, Philadelphia, PA: University of Pennsylvania. 150 p.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Penaluna, Brooke E., Sherri L. Johnson, Amanda M. M. Pollock, Ivan Arismendi, and Dana R. Warren. 2025. “Biotic Interactions and Stream Network Position Affect Body Size of Aquatic Vertebrates across Watersheds.” *Ecosphere* 16(6): e70299. https://doi.org/10.1002/ecs2.70299