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The role of the geophysical template and environmental regimes in controlling stream-living trout populations

Brooke E. Penaluna, Steve F. Railsback, Jason B. Dunham, Sherri Johnson, Robert E. Bilby, and Arne E. Skaugset

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Abstract: The importance of multiple processes and instream factors to aquatic biota has been explored extensively, but questions remain about how local spatiotemporal variability of aquatic biota is tied to environmental regimes and the geophysical template of streams. We used an individual-based trout model to explore the relative role of the geophysical template versus environmental regimes on biomass of trout (*Oncorhynchus clarkii clarkii*). We parameterized the model with observed data from each of the four headwater streams (their local geophysical template and environmental regime) and then ran 12 simulations where we replaced environmental regimes (stream temperature, flow, turbidity) of a given stream with values from each neighboring stream while keeping the geophysical template fixed. We also performed single-parameter sensitivity analyses on the model results from each of the four streams. Although our modeled findings show that trout biomass is most responsive to changes in the geophysical template of streams, they also reveal that biomass is restricted by available habitat during seasonal low flow, which is a product of both the stream's geophysical template and flow regime. Our modeled results suggest that differences in the geophysical template among streams render trout more or less sensitive to environmental change, emphasizing the importance of local fish–habitat relationships in streams.

Résumé : L'importance de nombreux processus et des facteurs à l'intérieur de cours d'eau pour le biote aquatique a été examinée en détail, mais des questions demeurent concernant le lien entre la variabilité spatiotemporelle du biote aquatique et les régimes de conditions ambiantes et le gabarit géophysique des cours d'eau. Nous avons utilisé un modèle de truite basé sur l'individu pour explorer l'influence relative du gabarit géophysique et des régimes de conditions ambiantes sur la biomasse de truites (*Oncorhynchus clarkii clarkii*). Nous avons paramétrisé le modèle à partir de données d'observation pour chacun des quatre cours d'eau d'amont (leur gabarit géophysique et leur régime ambiant), puis réalisé 12 simulations dans lesquelles nous avons remplacé les régimes ambiants (température, débit, turbidité) d'un cours d'eau donnée par les valeurs de chacun des cours d'eau voisins, tout en maintenant le gabarit géophysique inchangé. Nous avons également effectué des analyses de sensibilité des résultats du modèle aux différents paramètres pour chacun des quatre cours d'eau. Bien que les résultats du modèle montrent que la biomasse de truites réagit le plus fortement à des modifications du gabarit géophysique des cours d'eau, ils révèlent également que la biomasse est limitée par l'habitat disponible durant l'étiage saisonnier, qui est un produit du gabarit géophysique du cours d'eau et du régime d'écoulement. Les résultats du modèle donnent à penser que des différences sur le plan du gabarit géophysique entre les cours d'eau rendent les truites plus ou moins sensibles aux changements des conditions ambiantes, soulignant ainsi l'importance des relations locales poissons–habitats dans les cours d'eau. [Traduit par la Rédaction]

Introduction

Our understanding that the land surrounding a stream rules the stream (Hynes 1975) is formative in stream ecology. These ideas evolved into a view of streams as a distribution of patchy and heterogeneous conditions (Vannote et al. 1980; Minshall et al. 1985; Perry and Schaeffer 1987; Townsend 1989; Thorp et al. 2006) that fluctuate across various spatiotemporal dimensions (Statzner and Higler 1985; Ward 1989; Ward and Stanford 1995) within a stream network (Benda et al. 2004). This heterogeneity in streams is influenced by spatial and temporal fluxes of resources (Elwood et al. 1983), floodplains (Junk et al. 1989), riparian zones (Gregory et al. 1991), upslope processes (Montgomery 1999), surface–groundwater interactions (Boulton et al. 1998), and low-frequency, high-magnitude events that are often regarded in the context of disturbance (Resh et al. 1988; Swanson et al. 1988; Reeves et al. 1995). Combining the understanding of the above processes with landscape ecology, ideas in stream ecology culminated with the "riverscape" concept, portraying streams as continuous and spatially heterogeneous mosaics of highly connected habitats (Fausch et al. 2002; Poole 2002; Wiens 2002). However, questions remain about the relative influence of the geophysical template and environmental regimes to aquatic biota in streams. Therefore, if we could separate the relative effect of these general classes of factors in streams, we would gain a comprehensive view of the role of each to aquatic

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biota, thereby advancing our understanding of key drivers to aquatic biota.

Environmental regimes and the geophysical template cover different spatiotemporal dimensions in streams (Arthington 2012). In the natural world, stream conditions are formed by both dynamic environmental regimes and the relatively fixed geophysical template, making it challenging to separate their effects because they are complex (Carbonneau et al. 2012) and often confounded (Wiley et al. 1997). Environmental regimes consist of stream temperature (Arismendi et al. 2013), flow (Poff et al. 1997), turbidity, chemicals, and nutrients. Although the geophysical template of a stream consists of channel form, stream bottom, instream cover, substrate types, and other forms of structure, it is also a product of not only these characteristics but also the environmental regimes that create and alter habitats along a stream. Given enough time, virtually any of these features vary, but the daily, seasonal, and annual variation in flow and likely all environmental regimes typically far exceeds that of the local geophysical template, which generally changes only in response to disturbances and infrequent high-flow events that affect the balance of sediment and water delivery to the stream (Frissell et al. 1986; Reeves et al. 1995; Benda et al. 2004). The geophysical template varies on a finer spatial scale than environmental regimes. Hence, the spatial scale at which fish experience each set of factors is also fundamentally different.

Although the geophysical template and environmental regimes are important to fish (Jonsson and Jonsson 2011; Poff et al. 1997), we understand little about the relative influence of these factors in relation to one another. The geophysical template influences fish responses by setting limits on how environmental regimes play out (Elton 1966; Southwood 1977; Poff and Ward 1990), whereas environmental regimes affect fish by influencing factors that directly influence fish with most attention to streamflow (Poff et al. 1997; Power et al. 2008), but also temperature (Brett 1956) and turbidity (Harvey and White 2008). For example, flow interacts with the geophysical template, setting physical features of streams known to be important to fish, including depth and velocity distributions, which may make flow the environmental regime most likely to influence biomass. Trout survival is depressed during seasonal low flow in late summer (Berger and Gresswell 2009), leading us to expect that trout will have greater declines in biomass in summer compared with winter.

Our objective in this study was to evaluate the relative role of the geophysical template relative to environmental regimes in driving biomass of fish in streams in both summer and winter. We simulated four neighboring headwater streams from the same catchment that support coastal cutthroat trout (*Oncorhynchus clarkii clarkii*). Headwater streams are a compelling setting because they are tightly coupled with terrestrial ecosystems and may be more responsive to their location than larger channels (Vannote et al. 1980; Benda et al. 2004). In addition, cutthroat trout are widespread throughout the western United States, providing an interesting case study with the potential to generalize future hypotheses to a broader extent. We used an individual-based trout model (inSTREAM; Railsback et al. 2009) and applied a substitution–replacement approach in a manner that would be difficult or impossible to replicate in a natural setting. We parameterized the model with multiyear field data on environmental regimes, geophysical template, and trout populations for each stream. We also used sensitivity analysis to understand how trout respond to specific factors linked to the geophysical template or environmental regimes in each modeled stream. Overall, our findings will lead to a better understanding of how local spatiotemporal variability in trout populations is tied to environmental regimes or the geophysical template of stream trout, thereby advancing our understanding of key drivers to stream fish.

Methods

Study sites

Our simulations were based on measurements from four streams in the headwaters of the Trask River catchment, in the Tillamook River basin of the northern Coast Range, Oregon, USA (Table 1). Model simulations were performed for a 210 to 250 m contiguous length of stream reach, named after the streams where these reaches were located: Gus Creek, Pothole Creek, Rock Creek, and Upper Mainstem Trask (hereafter Upper Mainstem or UM). Precipitation in the headwater streams ranges from 2.25 to 2.83 m·year^{-1}, with most precipitation falling as winter rain (Daly et al. 1994). Stream temperatures are moderate (5–13 °C) year-round, and turbidity is very low (4 NTU) except during winter storm events (up to 150 NTU). Rock and Pothole creeks are located at lower elevations in the catchment (336.6 and 324.4 m, respectively), whereas Gus Creek (468.7 m) and Upper Mainstem (609.2 m) are located at higher elevations. Three streams have similar catchment areas (Gus = 302.1 ha, Upper Mainstem = 293.2 ha, Pothole = 325.4 ha), and one (Rock Creek) is twice as big (667.6 ha). Upper Mainstem (791.81 m^2) has the smallest wetted area during seasonal low flow, followed by Pothole Creek (1010.0 m^2), Rock Creek (1416.4 m^2), and Gus Creek (1500.0 m^2). Coastal cutthroat trout occur in all four headwater streams; some streams also support sculpins (*Cottus* spp.), steelhead (anadromous *Oncorhynchus mykiss*) juveniles, and coho salmon (*Oncorhynchus kisutch*) juveniles.

The trout model

As our individual-based trout population model, we used version 5.0 of inSTREAM (Lang, Railsback and Associates, Arcata, California, USA; downloaded on 30 August 2014). This model is fully described (e.g., Railsback et al. 2009, 2011) and publically available (http://www.humboldt.edu/ecomodel). InSTREAM simulates trout population dynamics in a realistic environment, and extensive model testing reproduced trout population responses typically observed in nature for both individuals (Railsback and Harvey 2002) and populations (Railsback et al. 2002; Harvey and Railsback 2014; Harvey et al. 2014). As an individual-based trout population model, inSTREAM derives population dynamics from the fate and behaviors of individual trout responses to environmental conditions that vary spatially and temporally. Our intent in applying this model was to evaluate how trout respond to environmental variability as related to influences of environmental regimes and geophysical template, and thus the model is valid for our purpose (Rykiel 1996). Here we outline how the model works and focus on features relevant to the objectives of this study. Unless noted otherwise, we used the parameter values for cutthroat trout and small streams provided by Railsback et al. (2009). We changed the latitude of model streams to 45°N, which influences photoperiod.

The model represents a simplification of many complexities of each actual stream, and each study stream is represented as one reach composed of rectangular cells. Reach variables are environmental regimes of stream temperature, flow, and turbidity, which varied daily (more details about each regime in Input section). The cells within reaches represent units of microhabitat, with typical areas of one to several square metres, and variables of depth, velocity, area of velocity shelter for drift-feeding, area of spawning gravel, and distance to hiding cover (more details in Input section). Generally, each cell is as large as the feeding territory of an adult trout and larger if the habitat is relatively homogeneous; multiple trout can occupy the same cell. Trout are represented as individuals from when they emerge from redds; trout variables include length, mass, condition (the fraction of healthy mass for their length), sex, and the cell in which they feed. The trout life cycle is completely represented in the model, beginning with redds (nest), which are represented as objects with variables for the number of live eggs they contain and the eggs' development status.

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Table 1. Description of environmental (ENVR) regimes, geophysical template, and calibration values for Gus Creek, Pothole Creek, Rock Creek, and Upper Mainstem Trask (UM) in Trask River catchment, Oregon.

		Headwater stream			
Model input	Factor	Gus	Pothole	Rock	UM
ENVR regimes	Winter stream temp. (°C)	4.8±1.4	6.4±0.9	5.8±1.2	4.7±1.1
	Winter stream flow ($m^3 \cdot s^{-1}$)	0.51±1.22	0.37±0.48	0.73±0.74	0.26±0.24
	Winter turbidity (NTU)	11.6±39.6	17.6±52.1	7.7±18.6	11.8±17.3
	Summer stream temp. (°C)	11.1±1.3	10.9±0.7	11.3±1.0	10.5±1.1
	Summer stream flow ($m^3 \cdot s^{-1}$)	0.03±0.02	0.03±0.00	0.03±4.10	0.04±0.02
	Summer turbidity (NTU)	9.9±8.1	3.6±2.1	4.9±0.0	10.5±8.9
Geophysical template	Catchment area (ha)	302.1	325.4	667.6	293.2
	Wetted area in summer (ha)	0.15	0.101	0.142	0.079
	Elevation (m)	469	324	337	609
	Distance to hiding cover (m)	2.40	2.30	1.75	1.06
	Velocity shelter	0.40	0.36	0.88	0.32
	Spawning gravel	0.14	0.06	0.10	0.17
	Velocity ($m \cdot s^{-1}$)	0.18 (0.42)	0.16 (0.32)	0.19 (0.40)	0.09 (0.20)
	Depth (m)	0.205 (0.239)	0.18 (0.202)	0.285 (0.359)	0.287 (0.218)
	Max. depth (m)	0.9 (1.15)	0.665 (0.845)	0.625 (0.69)	0.97 (0.54)
	Wetted width (m)	5.01 (5.369)	4.969 (4.973)	6.634 (6.634)	4.089 (4.896)
	Max. wetted width (m)	10.55 (11.14)	11.48 (11.48)	10.43 (10.57)	8.725 (8.725)
	Width to depth ratio	5.567 (4.668)	7.472 (5.885)	10.615 (9.615)	4.215 (9.067)
	Froude number	0.328 (0.81)	0.717 (0.83)	0.746 (0.724)	0.65 (0.587)
	Reynolds number (×1000)	11.398 (36.311)	21.05 (28.944)	43.621 (59.884)	38.282 (22.971)
	Cells (no. per stream)	35	35	31	32
Calibration	Drift food (g)	1.5×10^{-9}	1.5×10^{-9}	1.5×10^{-9}	6×10^{-10}
	Benthic food (g)	5×10^{-7}	5×10^{-7}	5×10^{-7}	8×10^{-7}
	Aquatic predation	0.900	0.900	0.900	0.960
	Terrestrial predation	0.990	0.990	0.990	0.985

Note: Winter is January and February and summer is July and August. Distance to hiding cover, availability of velocity shelter, spawning gravel, velocity by season, and depth by season are averaged values (total/no. of cells in stream). Higher distance to hiding cover values represent less overall hiding cover availability. Velocity shelter and spawning gravel are each estimated as a percentage of cell area with that characteristic. Values for the geophysical template denote mean summer conditions (unless noted), while parenthetical data represent mean winter. ENVR regimes display mean values ± standard deviation for data collected from March 2007 to September 2011.

InSTREAM uses a daily time step for six consecutive actions. (1) Daily values of stream temperature, flow, and turbidity are taken from files of actual field observations (Fig. 1). The depth and velocity of each cell is then calculated from streamflow to allow for changing environmental conditions. (2) The first trout action is spawning; female trout age 1 or older with fork length >10 cm spawn within specific dates if environmental thresholds are met. When they spawn, female trout move to cells with spawning gravel and construct a redd. The number of eggs deposited in a redd increases with female fork length. The representation of spawning and redds is simplified in the model, but it enables the model to simulate the full life cycle and long-term population dynamics (Railsback et al. 2009). (3) All trout select a cell for feeding or hiding by making a trade-off between energy intake and mortality risk (Railsback et al. 1999; Railsback and Harvey 2002). Trout select a habitat cell, in order of trout size, with the largest trout selecting cells first leading to a length-based hierarchy (see ideal despotic distribution; Fretwell 1972). Generally, this habitat selection method causes individuals to choose available habitat cells not already occupied by a larger trout, which minimizes risk while avoiding mass loss (Railsback and Harvey 2002). Then, in this same step, trout decide the best activity: feed or hide. Trout that hide have zero food intake and swimming speed leading to slight mass loss. Alternatively, trout can choose to feed during daylight hours. Food intake consists of two sources: drift (food items entrained in the flow) and benthic (food that trout must actively seek from the benthos). Benthic food, however, is a small portion of the total food supply for adults (10%–20%), whereas young-of-year depend on it completely. Each time a trout feeds in a habitat cell, its food consumption is subtracted from that remaining for smaller trout. Food availability depends on how much food was in each cell and the trout's ability to capture food. Food capture depends on trout size (with increasing length because larger trout see and swim better) and food availability. (4) Daily growth is calculated as a function of trout size and habitat conditions in the selected cell, especially depth and velocity. It is the difference between energy intake from food and metabolic costs. Metabolic costs increase with trout length, swimming speed, and temperature. As a consequence, growth peaks at an optimal velocity that delivers sufficient food while not requiring excessive energy for swimming. However, trout can also lose energy during spawning season (if mature and if spawn). (5) Mortality is modelled by calculating the daily probability of each trout's survival, then stochastically determining if it dies. The daily probability that trout will survive depends on individual attributes (length, mass), variables of its cell, and vulnerability to stochastic events. Trout can die from predation by terrestrial animals, predation by larger trout, and starvation. Trout are assumed to have accurate knowledge of predation risks and how they vary among habitat cells. (6) Redd actions include updating its developmental stage (a function of temperature), subtracting egg mortality due to temperature stress, disease, scouring, or desiccation. When a redd is fully developed, recruitment of new trout is a function of surviving eggs.

Input

Measurements of the geophysical template were collected to parameterize the model for each stream. During seasonal low flow in 2009, measurements of channel shape were made and used to delineate cells. For each cell, we measured availability of velocity shelters, spawning gravel, and distance to hiding cover. Depth, velocity, and water surface elevation of each cell were measured over a range of low, medium, and high flows from 2009 to 2010. Depth is the distance from the water surface to the stream bed, and water surface elevation is the elevation of the water surface relative to a known elevation. We computed daily mean

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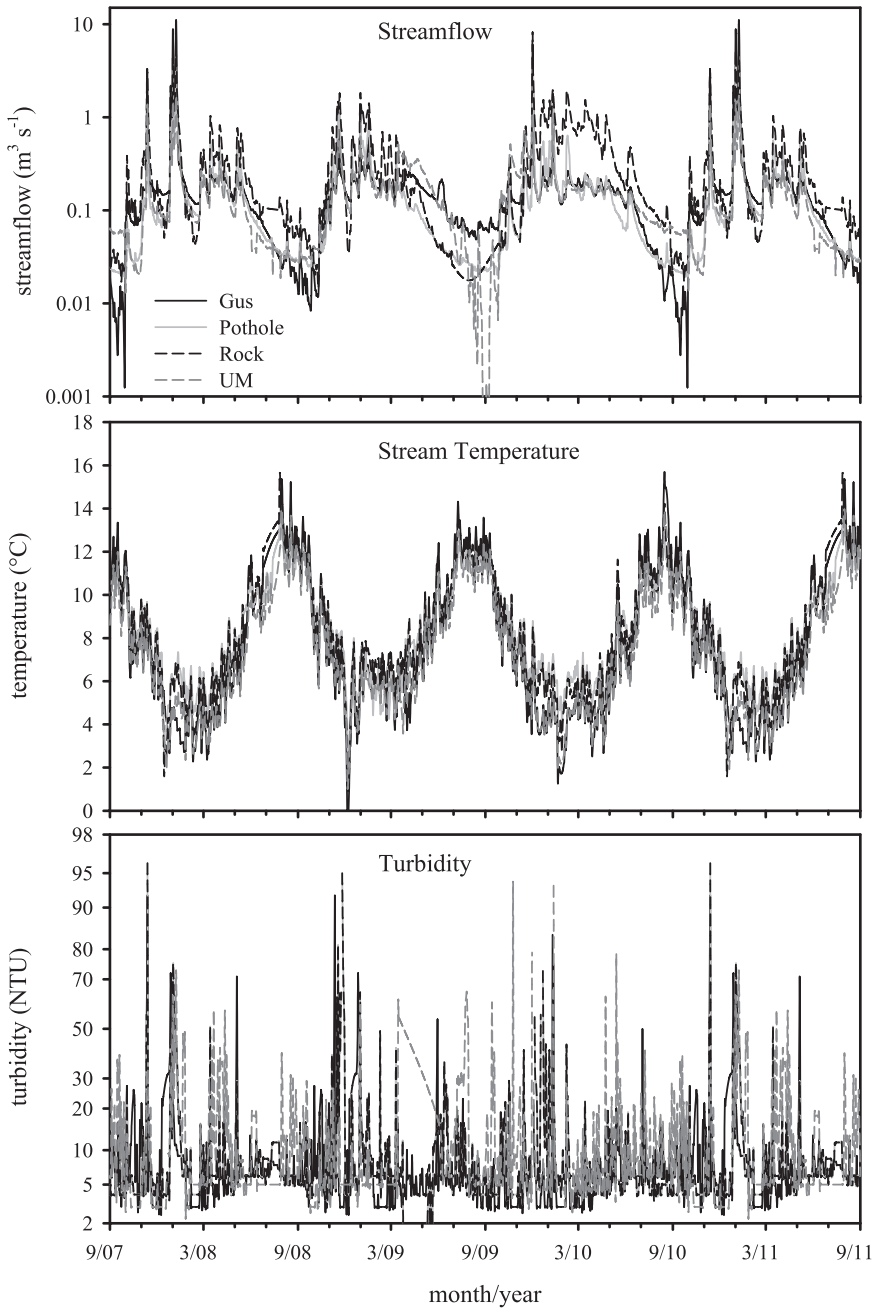
Fig. 1. Environmental regimes of streamflow, stream temperature, and turbidity capturing the natural variability observed in Gus Creek, Pothole Creek, Rock Creek, and Upper Mainstem Trask (UM) from 2007 to 2011.



streamflow, stream temperature, and turbidity from field measurements recorded every 10 min from March 2007 to September 2011. Mean streamflow and temperature were measured using a Montana-style Parshall flume with a water temperature sensor. Mean daily streamflow was calculated as the total 24 h flow volume divided by the number of measurements in 24 h. Mean daily temperature was the sum of all the values in 24 h divided by the number of measurements in that same time period. Mean turbidity was measured using an instream nephelometer, which measures the scatter of a focused light beam by suspended solids. Following standard procedure to minimize initialization effects (Railsback et al. 2009, 2011), we simulated 8 years by repeating the 4 years of data for environmental regimes and analyzed results from the last 4 years.

Calibration

Model calibration allows the model to match empirical observations and estimates the values of parameters that we cannot evaluate directly (Railsback and Grimm 2012). Although inSTREAM is composed of multiple equations and parameters, it is less reliant on calibration than simple models (Railsback and Grimm 2012). Following Railsback et al. (2009), we found a combination of parameter values for each modeled stream that best matched the field data for that stream (estimated trout densities and length by age class in September from 2007 to 2009). We varied four parameters in inSTREAM that have different effects on trout populations: concentration of drift food, concentration of benthic food that trout search for, risk of terrestrial predation, and risk of trout predation. We explored multiple parameter combinations to iden-

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tify our best match parameter set. We compared length and abundance of simulated trout from the model by minimizing sum of squared deviations for all age classes to actual trout data estimated from mark and recapture at the corresponding field stream (J. Dunham, unpublished data). We classified cutthroat trout into four age classes: age 0, age 1, age 2, and age ≥3.

Scenarios

We modeled trout biomass in relation to conditions within each stream (the local geophysical template and environmental regime) and then conducted a substitution of condition among streams, replacing the dynamic environmental regimes (streamflow, stream temperature, turbidity) of a given stream with values from each of the three neighboring streams while keeping the geophysical template (channel shape, instream cover, spawning gravel) fixed. This resulted in 16 scenarios for both summer and winter over a 4-year period. This substitution and replacement process was continued until all possible combinations of environmental regimes and geophysical templates were examined. During the substitutions, we did not adjust the environmental regimes for proportional differences in catchment area or other features (Table 1) because the complex links among streamflow, temperature, and turbidity would be lost with such changes.

Sensitivity analysis

We evaluated sensitivity of simulated trout biomass to single factors important to adult stream-living trout populations: base flow, drift food, hiding cover, piscivory risk, redd scour, spawning gravel, summer temperature, velocity shelter, and winter temperature (Railsback et al. 2011). To this end, we performed a sensitivity analysis for each of the four headwater streams with their own environmental regimes using inSTREAM's "limiting factors tool" (Railsback et al. 2011), which automates the generation of input files for sensitivity scenarios. The sensitivity analysis assesses the relative effect of the key factors by running the model multiple times using a wide range of values for one factor, reflecting the range of conditions found in our study streams. We added a range of values for each key factor bounded by a highest and lowest value to the actual value. Flows varied from 0 to 4 $m^3 \cdot s^{-1}$, temperatures varied from –4 to 4 °C, food varied from 0.5 to 2 g, gravel availability varied from 0.25 to 1.5, velocity shelter varied from 0.25 to 1.5, hiding cover varied from 0.25 to 1.5 m, piscivory risk was a fraction of the standard value ranging from 0.9 to 1.0, and redd scour ratio varied from 0.5 to 1.5. After scaling the factor scenarios from 0 to 1, results were analyzed via linear regression of simulated trout biomass versus factor value. High sensitivity to a factor is indicated by larger slopes and R^2 values. We also examined results for strong but nonlinear responses. Only older (≥age 1) trout were considered for the sensitivity analysis because simulated age 0 trout biomass is more variable and less important to long-term populations.

Distance to hiding cover and availability of velocity shelter and spawning gravel are averaged values (total/no. of cells in stream). Higher distance to hiding cover values represents less overall hiding cover availability. Velocity shelter and spawning gravel are each estimated as a percentage of cell area having that characteristic. Aquatic and terrestrial predation are each estimated as probability of occurrence ranging from 0 to 1.

Population-level responses, hydraulic dimensions, and data analysis

We analyzed biomass output every 10 days during the 4-year study from five replicate model runs. We averaged biomass for each of the four age classes for both summer (July and August) and winter (January and February) for the 16 scenarios each year based on the five replicate model runs.

We calculated various hydraulic dimensions from our field measurements to more deeply characterize each stream in both summer and winter. Depth measures the distance from the water surface to the stream bed, where mean depth comprises every cell value and max. depth is the highest value in the reach. Wetted width represents the distance between the left wetted edge to the right wetted edge, where mean wetted width consists of all transect measurements and max. wetted width is the highest width in the reach. Width to depth ratios of the mean values reflects the shape of the wetted cross-sections. Froude number is a ratio between kinetic and gravitation forces. It is very sensitive to the proportion of riffles versus pools in reaches, because it has very different values for these habitat types (it is <0.2 in pools and >0.4 in riffles; Jowett 1993; Lamouroux and Capra 2002). The Reynolds number is multiplied by 1000 throughout this paper, and it represents discharge per unit width. Hence, it is sensitive to flow rate and quantifies the level of turbulence in each stream (Lamouroux and Capra 2002).

We captured the complexities within a population among four age classes of trout from all modeled scenarios using nonmetric multidimensional scaling (NMDS), a nonparametric ordination technique (Kruskal 1964; Mather 1976). NMDS is an iterative process that seeks to minimize the "stress" of a *k*-dimensional configuration. To calculate the similarity matrix, we used the square root transformation of the Euclidean distance among biomass values for each age class to reduce the influence of highly influential age classes (Clarke 1993; McCune and Grace 2002). The resulting matrix was 128 rows (16 scenarios for both summer and winter during a 4-year period) × 4 trout age classes, for a total of 512 values. To understand which age class was driving the ordination on each NMDS axis, we correlated the ranks of the ordination axis scores of biomass by age class with Kendall's τ. We used multiresponse permutation procedures (MRPP) of Euclidean distances ($\alpha = 0.05$; Mielke and Berry 2001) to examine the hypothesis of no difference among stream or environmental regime between pairs of modeled streams (Gus versus Pothole, Gus versus Rock, Gus versus UM, Pothole versus Rock, Pothole versus UM, Rock versus UM) and between seasons (winter versus summer). MRPP is a nonparametric procedure for testing the hypothesis of no difference among pairs or groups (McCune and Grace 2002). To further describe patterns, we examined dispersion, defined as the spread in multivariate space among streams for trout biomass, measured as the area of a convex hull. We analyzed all data using PC-ORD software (MjM Software Design, Gleneden Beach, Oregon), except for dispersion, for which we used software R version 2.11.1 (R Development Core Team 2012) with the siar package.

Results

To determine the relative role of the geophysical template versus environmental regimes on trout biomass, we first considered the conditions for each factor that corresponded to each stream with its own local regime in its observed state. Simulations of these conditions revealed that biomass increased with increasing values of ages 2 and 3+ trout on axis 1 from the highest overall biomass in Gus Creek to next highest biomass in Rock Creek, Upper Mainstem, and Pothole Creek, in that order (Fig. 2*a*; Table 2). In addition, as biomass increased by stream there was a general increase in the variability of biomass within each stream, as measured by the convex hull area (Pothole Creek = 0.09; Upper Mainstem = 0.50; Rock Creek = 0.60; Gus Creek = 0.62). Although there was a lot of overlap in the ordination among modeled streams, trout from different streams displayed unique characteristics. For example, we found more ages 2 and 3+ trout in Gus Creek, more ages 0 and 1 trout in summer in Rock Creek, and less trout of all ages in winter in Upper Mainstem compared with other study streams. Although total trout biomass in summer followed a similar pattern in the ordering of streams as trout biomass by age in the NMDS ordinations, total trout biomass showed that the year-to-year variability within a stream was greater than the differences

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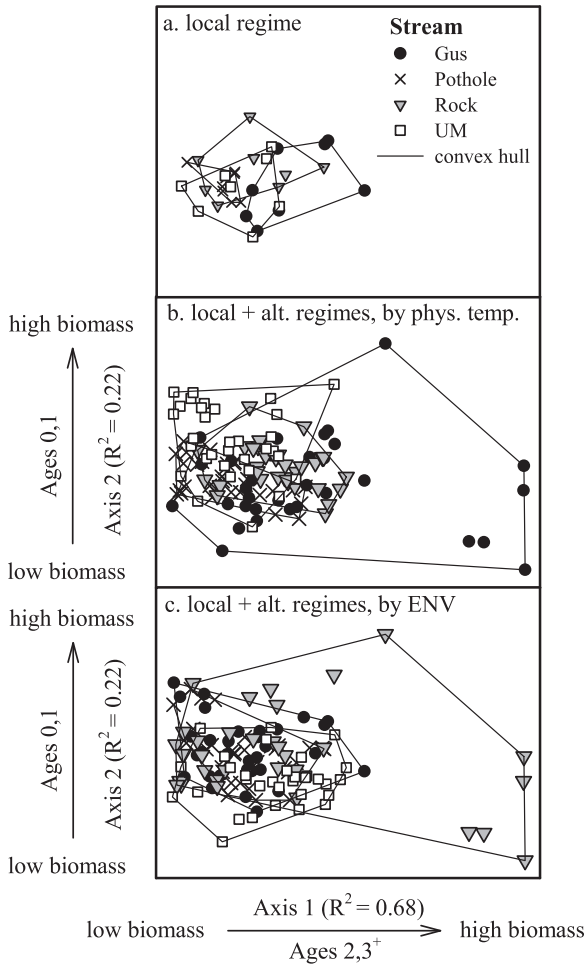
Fig. 2. Nonmetric multidimensional scaling ordination of mean biomass of coastal cutthroat trout from five replicated simulations (*a*) in four modeled streams (stress = 2.20) observed in Gus Creek, Pothole Creek, Rock Creek, and Upper Mainstem Trask (UM). The solid line represents convex hull area for each stream. The four modeled streams are again plotted in panels (*b*) and (*c*), in addition to the 12 stream combinations where we replaced the environmental regime (flow, temperature, turbidity) of a given stream with those from each of the three neighboring streams (stress = 5.90). The ordination in panel (*b*) is coded by geophysical template of the stream used, with the solid line indicating the convex hull area. The ordination in panel (*c*) has the same points as in panel (*b*), but this time we have coded for environmental regime of stream. Influential age classes for panels (*b*) and (*c*) are indicated for biomass, with arrows indicating positive or negative correlations for each axis.



in trout biomass among three of the four streams, except Gus Creek (Fig. 3).

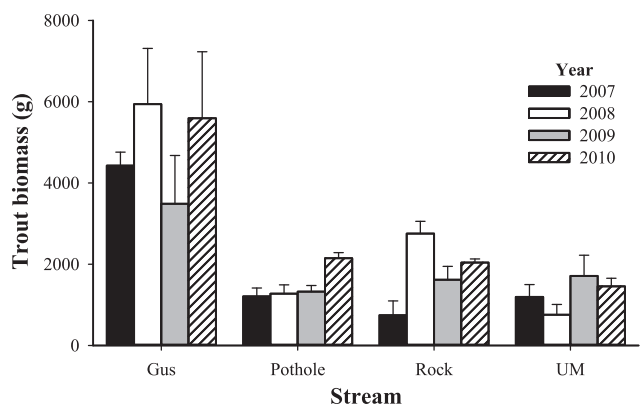
When we replaced the local environmental regimes for each stream with alternative regimes from neighboring streams, a similar pattern of differences in trout biomass among streams was observed (Fig. 2*b*; Table 2). Although trout biomass for each stream maintained the same relative order in trout biomass (Gus Creek highest, next highest in Rock Creek, Upper Mainstem, and Pothole Creek, in that order), alternative environmental regimes expand the boundaries of biomass for each stream (Figs. 2*a* versus 2*b*). Convex hull area also increased for trout biomass under scenarios of alternative environmental regimes when compared with streams modeled with their own environmental regimes (Pothole Creek = 0.09 to 0.56; Upper Mainstem = 0.50 to 1.54; Rock Creek = 0.60 to 1.02; Gus Creek = 0.62 to 5.32). For all study streams, application of the environmental regime from Rock Creek led to projected biomass values higher than those generated by the application of regimes from other streams (Fig. 2*c*; Table 2). We observed significant seasonal differences in the NMDS ordination along axis 2, with summer displaying higher biomass of ages 0 and 1 trout (Fig. 4).

Table 2. Multiresponse permutation procedure results for coastal cutthroat trout populations at four headwater streams in the Trask River Catchment, Oregon, where alternative environmental (ENVR) regimes were substituted among local regimes while geophysical template from a stream remained fixed.

Scenarios grouped by:	Pairwise comparison	*A*	*P*
Stream	Gus versus Pothole	0.22	**<0.001**
	Gus versus Rock	0.31	**<0.001**
	Gus versus UM	0.12	**<0.001**
	Pothole versus Rock	0.09	**<0.001**
	Pothole versus UM	0.15	**<0.001**
	Rock versus UM	0.19	**<0.001**
ENVR regime	Gus versus Pothole	0.00	0.96
	Gus versus Rock	0.00	0.25
	Gus versus UM	0.06	**<0.001**
	Pothole versus Rock	0.01	**0.05**
	Pothole versus UM	0.05	**<0.001**
	Rock versus UM	0.07	**<0.001**
Season	Winter versus summer	0.08	**<0.001**

Note: We examined the hypothesis of no difference among stream or environmental regime between pairs of modeled streams and between seasons. Streams are Gus Creek, Pothole Creek, Rock Creek, and Upper Mainstem Trask (UM). Significant *p* values indicate differences within the pair in question and are indicated in bold (α = 0.05). "*A*" is chance-corrected within group agreement, and it is a measure of effect size (*A* = 1 – (observed delta/expected delta)).

Fig. 3. Example mean biomass (+1 SD) of coastal cutthroat trout during summer (July and August) in Gus Creek, Pothole Creek, Rock Creek, and Upper Mainstem Trask (UM). Standard deviations represent variability among five replicated simulations. All age classes are combined.



Biomass was consistently sensitive to base flow; in all modeled streams, higher base flows resulted in greater biomass of adult trout (Table 3). Trout biomass was also sensitive to food in three streams (except in Pothole Creek). For the three streams where food was influential in the model, greater food availability led to higher biomass of adult trout. Elevated summer temperatures and increased hiding cover led to increased biomass of adult trout in Rock Creek.

Discussion

Our modeling approach separates the relative effects of the geophysical template from environmental regimes and provides a sensitivity analysis to provide a detailed picture of how processes affect trout biomass in headwater streams. Because trout biomass

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Fig. 4. Nonmetric multidimensional scaling ordination of mean biomass of coastal cutthroat trout from five replicated simulations in the four modeled streams (Gus Creek, Pothole Creek, Rock Creek, and Upper Mainstem River Trask (UM)) and the 12 stream combinations where we replaced the environmental regime (flow, temperature, turbidity) of a given stream with those from each of the three neighboring streams (stress = 5.90). The ordination has the same points as in Figs. 1*b* and 1*c*, but here we have coded by season to explain the variability along axis 2. Winter is January and February and summer is July and August. Influential age classes are shown for biomass, with arrows indicating positive or negative correlations for each axis.

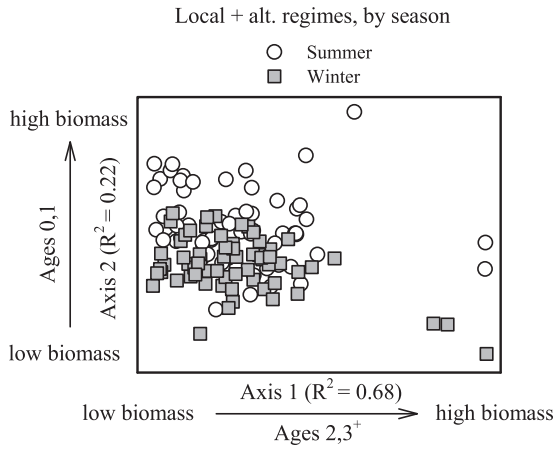

Table 3. Sensitivity analysis of key factors that may affect age 1+ coastal cutthroat trout population biomass (g) in four headwater streams in Trask River Catchement, including Gus Creek, Pothole Creek, and Rock Creek, and Upper Mainstem Trask River (UM).

		Headwater stream			
		Gus	UM	Rock	Pothole
Base flow ($m^3 \cdot s^{-1}$)	Slope	138 150	29 820	54 553	48 208
	R^2	0.63*	0.53*	0.58*	0.60*
Benthic and drift food (g)	Slope	7 794	4 370	2 078	1 607
	R^2	0.18*	0.49*	0.20*	0.03
Summer temperature (°C)	Slope	3 900	150	1 370	1 356
	R^2	0.04	<0.001	0.14*	0.03
Hiding cover (m)	Slope	1 335	275	1 138	1 064
	R^2	<0.001	0.01	0.10*	0.02
Piscivory risk	Slope	4 950	37	25	119
	R^2	0.03	<0.001	<0.001	<0.001
Redd scour	Slope	0	0	0	0
	R^2	<0.001	<0.001	<0.001	<0.001
Spawning gravel	Slope	566	60	42	30
	R^2	<0.001	<0.001	<0.001	<0.001
Velocity shelter	Slope	82	79	330	101
	R^2	<0.001	<0.001	<0.001	<0.001
Winter temperature (°C)	Slope	1 144	109	53	64
	R^2	0.04	<0.001	<0.001	<0.001

Note: Population data were analyzed using linear regression analyses against factor values scaled 0–1, with positive or negative slope values indicated. Factors are more important when they have higher slope magnitude and R^2.

*Factor–stream combinations that have $R^2 > 0.05$.

remains in the same relative order when alternative environmental regimes are applied, we demonstrated that the geophysical template is a dominant influence on trout biomass compared with environmental regimes. Based on the sensitivity analysis, we also showed that trout biomass is influenced by the interactions of the geophysical template and environmental regimes. In particular, seasonal low flow interacts with the geophysical template to minimize available habitat, thereby restricting biomass. Our modeled findings are supported by Hynes (1975), who argues that the land surrounding a stream rules the stream, because we show that the layout under the stream rules the stream. Below, we explain how the geophysical template alone and by interactions with environmental regimes influence trout biomass in neighboring headwater streams.

Biomass of trout is locally responsive to the geophysical template because even when alternative environmental regimes are applied, they remain in the same relative order. The dominance of the geophysical template to fish has also been suggested by other authors (Southwood 1977, 1988) where the geophysical template influences fish life histories, behavior, and physiology. Here, the geophysical template describes the structural environment of a stream, including channel form, instream cover (hiding cover and velocity shelter for drift feeding), and spawning gravel. For example, sensitivity analysis demonstrates that hiding cover influences biomass in Rock Creek, whereas in other streams hiding cover is considerably less important. In our model, environmental regimes consist of stream temperature, streamflow, and turbidity, which are highly dynamic in nature and are attributed to the reach scale. In our modeled streams, the magnitude of turbidity (Harvey and White 2008), temperature (Meeuwig et al. 2004; Bear et al. 2007), and flow (Poff et al. 1997) are likely not extreme enough to produce strong responses in trout biomass, with the exception of the flow regime in Rock Creek. When the Rock Creek environmental regime is applied to any stream, the highest biomass for each trout population occurs, because its flow is the highest of all the local regimes, allowing trout more available habitat and deeper pools during seasonal low flow (when flow and, therefore, available habitat can be limiting).

As in real streams, interactions among key factors and processes in the model likely play a stronger role than single influences. Local environmental conditions created by stream hydraulics represent an interaction between the geophysical template and streamflow, creating unique microhabitats where individual trout experience change. Accordingly, the same flows in streams with a different geophysical template can produce radically different microhabitat conditions and thus the varied, localized responses of trout that we observed (Statzner et al. 1988). Local hydraulics affect four main factors in the model that influence trout: food availability, depth, velocity, and available habitat. Food can be particularly important to stream-living fish (Chapman 1966); however, food is not contributing to the differences in biomasses among streams because three of the four streams were assigned the same food concentration values in model calibration. Fine-scale differences in food availability, stream depth, and velocity can strongly influence positions selected by trout in streams (Fausch 1984). Habitat selection rules in the model are designed to reflect the interplay among these factors (Railsback et al. 2011), but the sensitivity analyses suggested that none of these factors are limiting. Available habitat, however, plays an important role in influencing trout biomass, as seen in the sensitivity analysis. The amount of available habitat appears to be the factor that restricts biomass during seasonal low flow, a biological crunch time identified in empirical work (Berger and Gresswell 2009). In support of our findings, other studies have shown that streamflow influences available habitat area and volume, affecting the number of fish present and the body size of individuals (Chapman 1966; Bohlin et al. 1994; Dunham and Vinyard 1997; Dodds et al. 2012).

Our modeled results have valuable implications for management because trout populations in neighboring headwater streams have different biomasses due to the geophysical template of streams, rendering some populations more or less sensitive to environmental change. Our findings suggest that trout populations from nearby streams, where the environmental conditions are relatively similar, are differentially sensitive to environmental change because of the geophysical template alone (e.g., Jeffress

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et al. 2013). Hence, we need to consider key features that contribute to local variability, which have a long and ongoing history in applied ecology. By incorporating fish–habitat relationships into our thinking about broad-scale change, we infer that generalizing responses of stream fish to projected broad-scale change across a landscape may mask important factors of the geophysical template occurring at the local scale. In addition, providing uniform standards, as is currently done to manage species, runs the risk of ignoring the importance of natural spatiotemporal variability to trout populations (Bisson et al. 2009). If we can better understand the drivers of natural variability of stream populations, we may better manage both streams and stream-living trout. We show that the geophysical template plays a key role in headwater streams; however, in rivers or larger streams, biological interactions and environmental factors, including water chemistry, may play a larger role. Although the geophysical template has the greatest influence on trout biomass in the short term, over the longer term alterations to environmental regimes may be large enough to overwhelm the effects of the geophysical template, but also alter the geophysical template itself. The importance of the geophysical template is likely dependent on both variability of environmental regimes and the time scale over which the physical dynamics of streams are considered; nonetheless, our work shows that the geophysical template can be a dominant factor influencing fish in headwater streams.

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