Role of climate and invasive species in structuring trout distributions in the interior Columbia River Basin, USA

Seth J. Wenger, Daniel J. Isaak, Jason B. Dunham, Kurt D. Fausch, Charles H. Luce, Helen M. Neville, Bruce E. Rieman, Michael K. Young, David E. Nagel, Dona L. Horan, and Gwynne L. Chandler

Abstract: Recent and projected climate warming trends have prompted interest in impacts on coldwater fishes. We examined the role of climate (temperature and flow regime) relative to geomorphology and land use in determining the observed distributions of three trout species in the interior Columbia River Basin, USA. We considered two native species, cutthroat trout (*Oncorhynchus clarkii*) and bull trout (*Salvelinus confluentus*), as well as nonnative brook trout (*Salvelinus fontinalis*). We also examined the response of the native species to the presence of brook trout. Analyses were conducted using multi-level logistic regression applied to a geographically broad database of 4165 fish surveys. The results indicated that bull trout distributions were strongly related to climatic factors, and more weakly related to the presence of brook trout and geomorphic variables. Cutthroat trout distributions were weakly related to climate but strongly related to the presence of brook trout. Brook trout distributions were related to both climate and geomorphic variables, including proximity to unconfined valley bottoms. We conclude that brook trout and bull trout are likely to be adversely affected by climate warming, whereas cutthroat trout may be less sensitive. The results illustrate the importance of considering species interactions and flow regime alongside temperature in understanding climate effects on fish.

Résumé : Les tendances récentes et prévues de réchauffement du climat ont suscité de l'intérêt pour les impacts sur les poissons d'eau froide. Nous examinons le rôle du climat (température et régime hydraulique) en fonction de la géomorphologie et de l'utilisation des terres dans la détermination de la répartition observée chez trois espèces de « truites » dans le bassin versant intérieur du Columbia, É.-U. Nous observons deux espèces indigènes, la truite fardée (*Oncorhynchus clarkii*) et l'omble à tête plate (*Salvelinus confluentus*), ainsi que l'omble de fontaine (*Salvelinus fontinalis*) non indigène. Nous étudions aussi la réaction des espèces indigènes à la présence de l'omble de fontaine. Les analyses consistent en des régressions logistiques à niveaux multiples sur une base de données de grande envergure géographique de 4165 inventaires de poissons. Les résultats indiquent que les répartitions des ombles à tête plate sont fortement reliées aux facteurs climatiques et moins fortement corrélées à la présence d'ombles de fontaine et aux variables géomorphologiques. Les répartitions des truites fardées sont faiblement reliées au climat, mais fortement reliées à la présence de l'omble de fontaine. Les répartitions des ombles de fontaine sont reliées à la fois au climat et aux variables géomorphologiques, en particulier la proximité des fonds de vallées élargis. Nous concluons que l'omble de fontaine et l'omble à tête plate seront vraisemblablement affectés négativement par le réchauffement climatique, alors que la truite fardée sera peut-être moins sensible. Nos résultats soulignent l'importance de considérer les interactions entre les espèces et le régime hydraulique en plus de la température pour comprendre les effets du climat sur les poissons.

[Traduit par la Rédaction]

S.J. Wenger. Trout Unlimited, 322 East Front Street, Suite 401, Boise, ID 83702, USA.
D.J. Isaak, C.H. Luce, D.E. Nagel, D.L. Horan, and G.L. Chandler. US Forest Service Rocky Mountain Research Station, 322 East Front Street, Suite 401, Boise, ID 83702, USA.
J.B. Dunham. US Geological Survey Forest and Rangeland Ecosystem Science Center, 3200 SW Jefferson Way, Corvallis, OR 97331, USA.
K.D. Fausch. Colorado State University, Department of Fish, Wildlife, and Conservation Biology, Fort Collins, CO 80523-1474, USA.
H.M. Neville. Trout Unlimited, 910 Main Street, Suite 342, Boise, ID 83702, USA.
B.E. Rieman.* US Forest Service Rocky Mountain Research Station, P.O. Box 1541, Seeley Lake, MT 59868, USA.
M.K. Young. US Forest Service Rocky Mountain Research Station, 800 East Beckwith Avenue, Missoula, MT 59801, USA.

Corresponding author: Seth J. Wenger (e-mail:swenger@tu.org).

*Retired.

Introduction

Recent warming trends and projections of future climate change have prompted interest in the climate sensitivity of aquatic organisms (Parmesan 2006; Battin et al. 2007; McCullough et al. 2009). Climate sensitivity (i.e., a species' sensitivity to climate change) can differ even among closely related species (Jonsson and Jonsson 2009) and be influenced by other factors that govern species distribution and abundance. These include relatively immutable features related to basin geomorphology, as well as human activities such as land use. These variables may act independently or interact with climate impacts (e.g., the mediation of temperature and flow changes by groundwater; Power et al. 1999; Tague et al. 2008). Climate change is also expected to significantly alter invasive species distributions (Rahel and Olden 2008). Therefore, an assessment of climate sensitivity should consider both the range of direct effects on the species of concern as well as potential indirect effects resulting from changes in the distributions of invasive species (Poloczanska et al. 2008; Bradley 2009).

Trout, char, and salmon (hereinafter collectively referred to as trout) are of particular interest because of their economic importance, their need for cold water, and the imperiled status of many species. Past studies of climate influences on trout focused primarily on temperature or surrogates of temperature (Keleher and Rahel 1996; Rieman et al. 2007; Kennedy et al. 2009). This is reasonable because all climate projections agree that global temperatures will increase (IPCC 2007), potentially causing trout distributions to shift to higher latitudes and elevations (Jonsson and Jonsson 2009; Rieman and Isaak 2010). Some studies have also examined the role of climate-driven shifts of hydrologic regimes, particularly extreme flows (Jager et al. 1999; Battin et al. 2007). An example of such a hydrologic relationship is the sensitivity of trout eggs and fry to high flows. Evidence suggests that high flows in the post-spawning period can reduce recruitment (Seegrist and Gard 1972; Latterell et al. 1998; Warren et al. 2009) and limit species distributions (Fausch et al. 2001; Fausch 2008). In regions that receive precipitation mainly as snow in winter, the frequency of high winter flows is temperature-dependent and may increase in a warming climate (Hamlet and Lettenmaier 2007; Barnett et al. 2008). These changes may lead to increased bedload movement in streams, causing mortality of eggs and alevins for fall-spawning species such as brook trout (*Salvelinus fontinalis*) and bull trout (*Salvelinus confluentus*; Shellberg et al. 2010). Such changes may depend on landscape topography, since many fall-spawning species use unconfined valley bottoms (UVBs) for spawning (Baxter and Hauer 2000; Dunham et al. 2002; Benjamin et al. 2007), and these locations may provide velocity refugia at high flows (Shellberg et al. 2010). Other landscape and anthropogenic variables that may be of fundamental importance in determining trout distributions include stream size and slope (Lanka et al. 1987; Rahel and Nibbelink 1999; Isaak and Hubert 2000) and human activities such as logging and road construction (e.g., Dunham and Rieman 1999; Trombulak and Frissell 2000; Shepard et al. 2005).

Nonnative species pose another major threat to trout. In the western US, the brook trout is an invasive species that can displace native trout (Thurow et al. 1997; Dunham et al. 2002; Peterson et al. 2004a). In some locations, brook trout invasions have been so successful that native species such as cutthroat trout (*Oncorhynchus clarkii*) persist only above artificial barriers maintained to exclude invasives (Fausch et al. 2009). However, the fall-spawning brook trout may be more sensitive to a climate-associated increase in winter flooding than the spring-spawning cutthroat trout. This raises the possibility of cascading climate effects, and suggests that an analysis of the climate sensitivity of native species such as cutthroat trout should include consideration of the climate sensitivity of nonnative species such as brook trout.

In this study we assessed the relative roles of climate (temperature and flow), geomorphology (valley bottom confinement, slope, and stream size), road proximity, and species interactions in structuring the current spatial distributions of nonnative brook trout and native cutthroat and bull trout. Our study area was the US portion of the interior Columbia River Basin. Our analysis was facilitated by the recent development of a database of modeled stream flows at the reach scale (Wenger et al. 2010) and the compilation of an exceptionally large fish collection dataset.

Materials and methods

Study area and organisms

The US portion of the interior Columbia River Basin (ICRB) lies within the northern Rocky Mountains and intermountain regions of the northwestern United States (Fig. 1). The southern part of the basin is relatively dry, with most precipitation falling as snow in winter at high elevations, producing snowmelt-dominated flow regimes. The northern part of the basin is more mesic and receives a greater proportion of precipitation as rain, but still tends to be snow-dominated. Elevations range from ~500 to ~3500 m a.s.l. More detailed descriptions of climate and vegetation of the ICRB are available elsewhere (Quigley et al. 1996).

Trout that are native to at least a portion of the ICRB include bull trout, rainbow trout (*O. mykiss*), and cutthroat trout (Thurow et al. 1997). Cutthroat trout in the ICRB are separated into two subspecies: westslope (*O. c. lewisi*), and Yellowstone (*O. c. bouvieri*). The bull trout is listed as a threatened species under the US Endangered Species Act (ESA). The cutthroat trout is a species of conservation interest to state and federal management agencies, although none of the subspecies in the ICRB are currently listed under the ESA. Nonnative and potentially invasive trout introduced into the region include brook trout, brown trout (*Salmo trutta*), lake trout (*Salvelinus namaycush*), and hatchery-origin rainbow trout. All are considered threats to native trout (Thurow et al. 1997), but the ecological displacement of native species by brook trout has been a particular concern (Dunham et al. 2002; Peterson et al. 2004a; Rieman et al. 2006). In some instances, brook trout may also hybridize with bull trout, although introgression is often limited (Kanda et al. 2002; DeHaan et al. 2010).

Data and hypotheses

We developed 10 hypotheses to explain the expected relationships between trout distributions and predictor variables in the ICRB (Tables 1 and 2). The hypothesized relationships

Fig. 1. Map of study area, collection sites, and validation groups in the Columbia River Basin (inset map shows location in the northwestern USA). Sites were assigned to the four validation groups based on spatial location for purposes of cross-validating model performance.
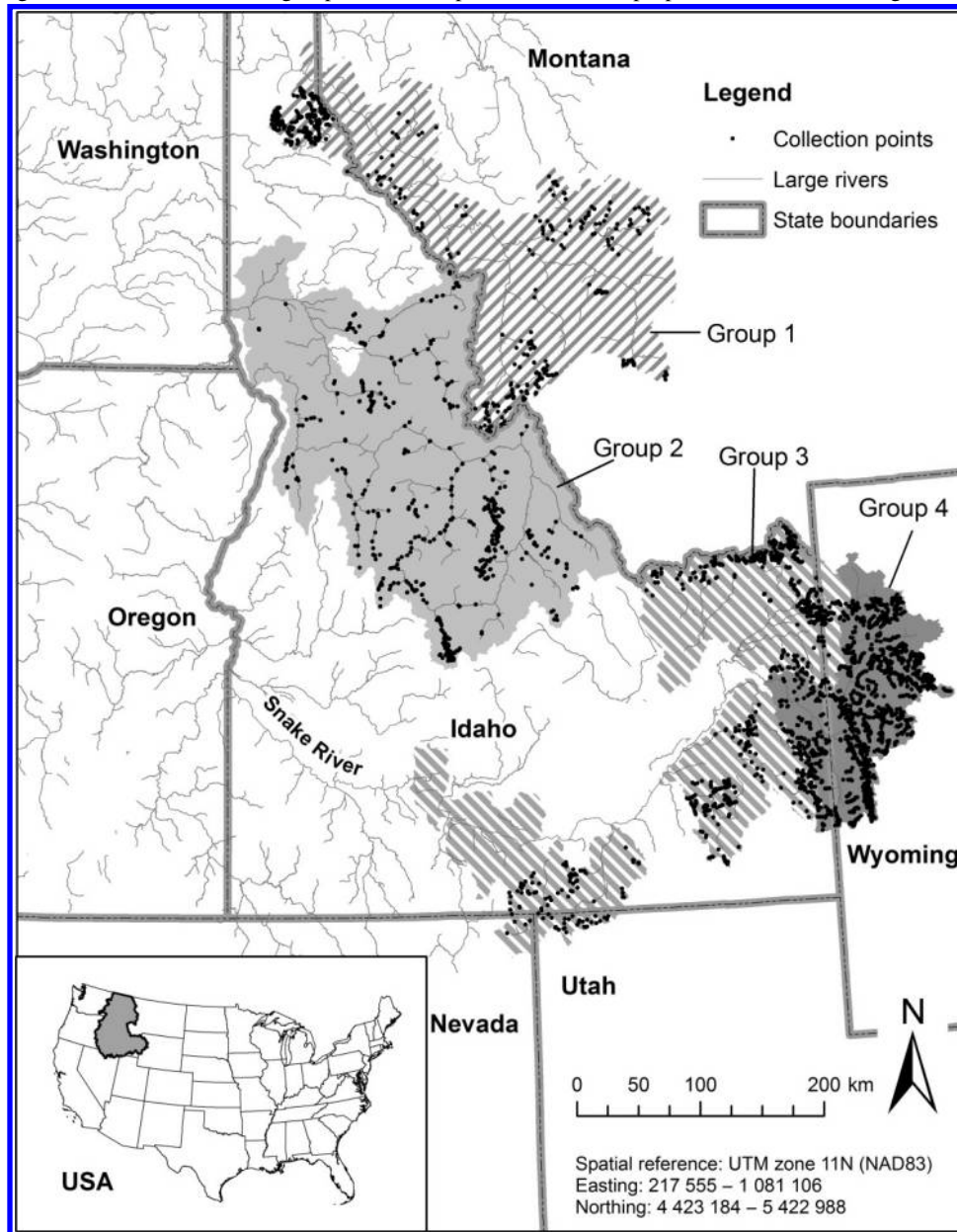
were organized into groups of climate, geomorphic, biotic, and land-use predictors, as well as two potential interactions. Below we describe the fish distribution dataset, hypotheses, and methods of quantifying the predictor variables used in hypothesis tests.

Fish occurrence database

The fish occurrence database (Fig. 1) was assembled from fish data collections made by the Idaho Fish and Game Department; Montana Fish, Wildlife and Parks; the Wyoming Game and Fish Department; and the US Forest Service. The original data collection efforts included inventories, monitoring, and research conducted from 1985 to 2004. In assembling this database, we included only sites within the historical range of cutthroat trout sampled using electrofishing or snorkeling. Because detection by snorkeling can be

less efficient than electrofishing (Thurow et al. 2006), snorkeling sites with fewer than four repeat visits were excluded from the dataset. We also excluded sites within basins with drainage areas larger than 400 km² because our method for estimating flows was not intended for large rivers (Wenger et al. 2010) and species detection probability could be lower in large streams (Thurow et al. 2006). Data from collections on the same stream within 50 m of one another were considered to be from the same location and treated as a single site. The final dataset included 4165 sites, of which only 339 were sampled by snorkeling. Cutthroat trout were detected at 2950 sites, brook trout at 1259 sites, and bull trout at 396 sites. For this analysis, samples were assumed to be contemporaneous, i.e., we coded a fish species as present at a site if at least one individual (adult or juvenile) was encountered at the site, regardless of date of collection. We restricted the analysis of

Table 1. Hypothesized responses of brook trout, bull trout, and cutthroat trout to candidate predictor variables that may explain fish distributions.

Category	Variable	Metrics	Brook trout	Bull trout	Cutthroat trout
			Hypothesized response		
Climate	Air temperature	ptemp, dtemp	+/– or –	+/– or –	+/– or –
	Winter high flow	w2, w1.5, w99, w95	–	–	0 or +
Geomorphic	Stream slope	slope	–	–	–
	Unconfined valley bottom	vbpres	+	+	+ or –
		vbdist	–	–	+ or –
	Stream size	mflow, sflow	– or +/–	0 or +/–	0 or +/–
Land use	Road presence	road	+	–	–
Invasive species	Brook trout in site	brk1, brk2	NA	–	–
	Brook trout in subwatershed	brkw	NA	–	–
Interactions	Winter high flow by valley bottom	[multiple combinations possible]	+	+	0
	Brook trout in subwatershed by valley bottom	brkw×vbdist or brkw×vbpres	NA	–	–

Note: A "+" indicates a positive relationship, a "–" indicates a negative relationships, and "+/–" means a unimodal relationship. Metrics are defined and described in Table 2.

bull trout to the subset of sites within its historical range, which excluded samples in the upper Snake River Basin above Shoshone Falls.

Climate hypotheses

We considered two hypotheses regarding the effects of climate on trout (Table 1). First, we hypothesized that each species would be less likely to occur in locations with temperatures outside its thermal optimum, which would produce a unimodal relationship between temperature and occurrence. Among the three trout species evaluated, we expected bull trout to require the coldest temperatures (Selong et al. 2001; Dunham et al. 2003). Second, we hypothesized that more frequent winter high flows would be detrimental to fall-spawning brook and bull trout, but not to spring-spawning cutthroat trout. We describe the flow data first because the temperature data were derived from the flow modeling process.

We calculated metrics representing winter high-flow frequency at each site using output from the variable infiltration capacity (VIC) macro-scale hydrologic model (Liang et al. 1994; 1996) run for the Pacific Northwest by the Climate Impacts Group at the University of Washington (Seattle, Wash.; Matheussen et al. 2000; Elsner et al. 2010). The VIC model is a distributed, largely physically based model that balances surface energy and water fluxes. It has been widely used in the western US to study past and potential future changes to water flow regimes (e.g., Hamlet et al. 2009), snowpacks (Hamlet et al. 2005), and droughts (Luo and Wood 2007). The implementation we used was run at the 1/16th degree scale (~7 km × ~5 km). We used a recently developed simplified routing method (Wenger et al. 2010) to apply VIC output to stream segments in the National Hydrography Dataset Plus (NHD Plus 2006) in US Geological Survey hydrologic region 17 (the Pacific Northwest). Previous model validations (Wenger et al. 2010) had demonstrated that metrics representing frequency of winter high flows were pre-

dicted with low bias and error. We calculated four metrics: w2, w1.5, w99, and w95. The first two measured the probability of a 2-year or 1.5-year recurrence interval flow event (respectively) during the winter. Flows of this magnitude are sufficiently large to mobilize bed material, potentially damaging redds and crushing embryos or alevins (Montgomery et al. 1996; Tonina et al. 2008). The latter two metrics, w99 and w95, were the number of days during winter that were among the highest 1% and 5% (respectively) of flows for the year. These were assumed to be flows with velocity sufficient to displace and kill newly emerged fry (Fausch et al. 2001), but not necessarily destroy embryos in redds. Winter was defined as 1 December – 28 February. The timing of emergence could vary widely within our study region, based on a variety of influences (e.g., Coleman and Fausch 2007), but we did not attempt to capture local variability in this analysis. All metrics were calculated across the 20 water-years from 1978 to 1997, which coincide with or slightly precede the fish collections, under the logic that flows during this period influenced the observed fish distributions.

Because stream temperature data were not available for many fish sample sites, we used air temperature as a surrogate (Keleher and Rahel 1996; Rieman et al. 2007; Williams et al. 2009), even though correlations between air temperature and water temperature are variable and sometimes weak (Isaak et al. 2010). We calculated three air temperature metrics: mean summer temperature, maximum summer temperature, and maximum weekly maximum temperature, all based on the 48-day period between 15 July and 31 August, and averaged across the 20-year period used to calculate the flow metrics described above. The three air temperature metrics were highly correlated ($r > 0.98$), so we selected mean summer temperature as a representative air temperature metric. We selected the mean because previous analyses showed a stronger air–water temperature correlation for this metric than for metrics related to maxima (Isaak et al. 2010).

For consistency we based mean summer air temperatures on the same gridded temperature values used to force the VIC hydrologic model; these in turn were derived from weather station data using empirical statistical relationships (Hamlet and Lettenmaier 2005). Air temperature data were available as a single value for the centroid of each 1/16th degree grid cell across the ICRB. Because of large elevation variability within cells, owing to complex mountain topography, we derived site-specific temperature values based on the difference in elevation between individual sites and the mean elevation of their corresponding cells, calculated from 30-m digital elevation models (DEMs; distributed as part of the NHD-plus dataset). We used an elevation adjustment value or "lapse rate" of –6.0 °C·km^{-1} derived for the ICRB by Rieman et al. (2007); this value is roughly similar to those derived for the entire Columbia River Basin (Dodson and Marks 1997) and the Alps (Rolland 2003). For each site we calculated mean summer temperature at the collection site (ptemp, for point temperature) and mean summer temperature averaged across the watershed that drains to the stream segment in which the site was located (dtemp, for drainage temperature). We assumed that this latter measurement would be better correlated with the stream temperature at each site, which is influenced by upstream temperatures (Isaak and Hubert 2001; Isaak et al. 2010).

Geomorphic hypotheses

We developed hypotheses about three predictor variables related to the geomorphic context of the stream (Table 1). First, we hypothesized that brook trout and bull trout would be more likely to occur in or near UVBs (Cavallo 1997; Baxter and Hauer 2000; Benjamin et al. 2007). We hypothesized that cutthroat trout relationships with UVBs could either be positive, if these contain favored habitats, or negative, if brook trout displace cutthroat trout from such locations (Cavallo 1997). We included an interaction term in our models to test this (see below). Second, high stream slopes could be associated with the upstream distribution limits of trout, owing to an increasing prevalence of dispersal barriers in steep channels (e.g., Fausch 1989; Dunham et al. 1999; Dunham et al. 2002). Accordingly we predicted that all three species would respond negatively to increasing stream slopes. Third, we hypothesized that brook trout, which tend to use smaller streams over large rivers (Rahel and Nibbelink 1999; Dunham et al. 2002; Öhlund et al. 2008), would show a negative or unimodal relationship with stream size. We hypothesized that bull and cutthroat trout would either show little association with stream size or a unimodal relationship driven by lower probability of their being present in the smallest and largest streams (Thurow et al. 1997).

We used an empirically derived algorithm implemented in a geographic information system (GIS), based on 30-m DEMs, to identify UVBs as relatively flat, wide valleys along streams (Nagel 2009). Valley bottoms were delineated using ground slope and convolution filtering methods. The algorithm was field validated and found to distinguish unconfined and confined valleys successfully; the former had field-measured widths of 60–500 m and a mean valley-width/channel-width ratio of 17.09, whereas the latter had widths of 5–30 m and a mean valley-width/channel-width ratio of 2.11 ($n = 60$; see RMRS 2010). We calculated two metrics from the valley

confinement results: a binary classification of whether or not a site was in a UVB (vbpres), and distance to the nearest UVB in kilometres (vbdist).

For stream slope, we used values included in the NHD-plus dataset, which were derived for stream segments from 30-m DEMs. For stream size we used mean annual flow (mflow) and mean summer flow (sflow; summer period defined as above) from the VIC-modeled flow dataset described previously. We used flow rather than drainage area because of considerable spatial variation in precipitation across the study area. Because of this, it would have been reasonable to place this variable in the climate category rather than the geomorphic category; we chose the latter because most of the site-to-site variability in mean flow was due to watershed contributing area.

Land use hypothesis

We hypothesized that native trout species were less likely to occur in regions where there are roads near the streams (road; Table 1) because roads may reduce habitat quality and connectivity and facilitate introductions of nonnative species (Trombulak and Frissell 2000). In contrast, we hypothesized that nonnative brook trout would show a positive relationship with roads, owing to the greater probability of introductions (legal or illegal) of this species in locations accessible by road (Paul and Post 2001). The road variable was calculated as a value of 1 if the 2000 TIGER/Line road database (US Census Bureau 2002) indicated a road within 1 km of the stream segment on which the site was located, and 0 otherwise. We used this indicator of road influence, rather than road density (Rieman et al. 1997; Thurow et al. 1997; Dunham and Rieman 1999) because we were more interested in exploring site-specific impacts of roads (species introductions, angling) as opposed to impacts of roads on more diffuse watershed processes (e.g., geomorphic and hydrological impacts; Trombulak and Frissell 2000).

Invasive species hypotheses

We hypothesized that bull trout and cutthroat trout would show a negative relationship with brook trout occurrence at the scales of the site and subwatershed (40–160 km^2 based on the 12-digit NRCS hydrologic unit code; NRCS 2009). We used two candidate metrics for brook trout occurrence at the site scale: (i) all sites with any brook trout records (brk1, 1259 occurrences), and (ii) a subset of brk1 that excluded sites in which brook trout were present in <50% of samples, for those sites with multiple samples (brk2, 1143 occurrences). We calculated one subwatershed-scale metric (brkw), in which all subwatersheds with at least one brook trout occurrence were assigned the value of 1, and all other subwatersheds were assigned a value of 0.

Interactions

We considered two interactions (Table 1). First, we tested the hypothesis that UVBs provided high-flow refugia (Shellberg et al. 2010) by adding an interaction between UVBs and winter high flows, hypothesizing that response to winter high flows would be less strong within a UVB than outside of a UVB. Second, we tested the hypothesis that when brook trout were present in a watershed, they would exclude cutthroat trout and bull trout from UVBs (Cavallo 1997). We

Table 2. Descriptive statistics of metrics used as predictor variables in analyses of cutthroat trout, bull trout, and brook trout distribution in the Interior Columbia River Basin.

Metric	Abbrev.	Category	Description	Units	Range	Mean
Mean summer air temp. at point	ptemp	Climate	Mean summer temperature (15 July – 31 August) at the collection point	C	10.76–23.21	16.13
Mean summer air temp. in drainage	dtemp	Climate	Mean summer temperature (15 July – 31 August) averaged across the upstream subwatershed	C	11.15–21.63	15.96
Winter high flow 2y	w2	Climate	Probability of a 2-year recurrence interval flow in winter	Prob.	0–0.60	0.094
Winter high flow 1.5y	w1.5	Climate	Probability of a 1.5-year recurrence interval flow in winter	Prob.	0–2.00	0.166
Winter high flow 99%	w99	Climate	Number of high-flow days (top 1% of annual flows) in winter	Freq.	0–2.50	0.254
Winter high flow 95%	w95	Climate	Number of high-flow days (top 5% of annual flows) in winter	Freq.	0–8.40	0.884
Stream slope	slope	Geomorphic	Slope/gradient of the stream segment, from NHD-plus	Elev. · dist^{-1}	0–0.261	0.045
UVB (binary)	vbpres	Geomorphic	Within or outside of an unconfined valley bottom	—	0–1	0.247
UVB distance	vbdist	Geomorphic	Kilometres from the nearest unconfined valley bottom (UVB)	km	0–31	4.78
Mean summer flow	sflow	Geomorphic	Mean daily flow, calculated during summer months	$\text{ft}^3 \cdot \text{s}^{-1}$	0–544	12.33
Mean annual flow	mflow	Geomorphic	Mean daily flow, calculated for all months	$\text{ft}^3 \cdot \text{s}^{-1}$	0–1716	26.88
Road presence (binary)	road	Land Use	Presence/absence of a road within 1km of the site	—	0–1	0.697
Brook trout pres. (binary)	brk1	Invasive species	Presence of brook trout in one or more sample at the site.	—	0–1	0.302
Brook trout pres., v.2 (binary)	brk2	Invasive species	Presence of brook trout in a majority of samples at the site.	—	0–1	0.274
Brook trout pres. in subwatershed (binary)	brkw	Invasive species	Presence of brook trout in one or more samples in the subwatershed	—	0–1	0.44

Note: Prob., probability; Freq., frequency; Elev., elevation; dist, distance. 1 ft = 0.30 m.

represented this with a negative interaction between brook trout presence at the subwatershed scale and UVB distance/presence, such that within subwatersheds with brook trout, the other species would be less likely to occur in UVBs than they would be in subwatersheds without brook trout.

Analyses

We conducted our analyses in several stages. In the first stage we screened each of the hypotheses individually using multilevel logistic regression (a form of generalized linear modeling or GLM), comparing each predictor variable with an intercept-only model using Akaike's information criterion (AIC; Burnham and Anderson 2002). We employed a multi-level modeling approach because our fish collection sites were nonrandom and often strongly clustered (Fig. 1), and likely to violate the parametric assumption of spatial independence of errors. Failing to account for spatial autocorrelation can lead to biases in both the means and standard errors of parameter estimates (Snijders and Bosker 1999; Raudenbush and Bryk 2002; Isaak et al. 2010). Multilevel or hierarchical modeling addresses this problem by modeling errors at more than one level of organization: in addition to the data-level error term, an error term (i.e., a random effect) is included for groups, clusters, or (in our case) subwatersheds (Snijders and Bosker 1999; Raudenbush and Bryk 2002; Gel-

man and Hill 2007). Multilevel modeling is widely used in the social sciences but has seen fewer applications in ecology (McMahon and Diez 2007), even though it is well suited to modeling naturally hierarchical systems such as streams within subwatersheds (Wagner et al. 2006). We specified a multilevel model with clusters at the subwatershed level, which meant that sites within a subwatershed were assumed to be similar to one another. We verified that the multilevel approach was justified by testing the significance of the random effects using a bootstrapping approach (5000 replicates) implemented in the glmmML package (Broström 2009) in R (R Development Core Team 2009). The test was also repeated with the final fitted models.

We tested for relationships between species occurrence and each of the individual predictors (Table 2), except that brook trout metrics were not tested in brook trout models. We also tested a quadratic form of each of the continuous predictor variables; for example, slope was tested by itself and as slope + slope^2. Quadratic forms were necessary to capture the unimodal relationships hypothesized for some variables, but they were also included for their ability to capture threshold responses better than simple linear predictors. Each model was fit using the glmer function in the lme4 package (Bates and Maechler 2009) using R 2.11 software (R Development Core Team 2009). Predictor variables were standar-

Table 3. Pearson correlations among continuous predictor variables used in analyses of cutthroat trout, bull trout, and brook trout distribution in the Interior Columbia River Basin.

	w2	w1.5	w99	w95	mflow	sflow	vbdist	ptemp	dtemp
w1.5	0.84								
w99	0.75	0.81							
w95	0.72	0.75	0.93						
mflow	−0.09	−0.07	−0.10	−0.14					
sflow	−0.08	−0.06	−0.09	−0.12	0.96				
vbdist	0.04	0.05	0.07	0.09	−0.03	−0.04			
ptemp	0.47	0.42	0.40	0.42	0.09	0.10	0.13		
dtemp	0.56	0.49	0.49	0.52	−0.11	−0.11	0.09	0.91	
slope	0.13	0.10	0.17	0.19	−0.28	−0.30	0.15	0.02	0.14

dized by subtracting the mean and dividing by 2× the standard deviation, which improves both model convergence and interpretation of coefficients (Gelman and Hill 2007). Models were ranked by AIC score.

For several groups of predictors we had correlated candidate metrics (Table 3). There were four metrics of winter high flows, two metrics of baseflow, two metrics of temperature, two metrics related to UVB, and two metrics of brook trout occurrence at the site scale. Correlations among predictors in different groups were generally low, with the exception of correlations between air temperature and winter high flow metrics ($r = 0.40$–0.56; Table 3). For the screening stage, we wanted to identify the best-supported metric in each group in either its simple or quadratic form, based on AIC score. If no metric in a group had an AIC score better than the intercept-only model we considered the corresponding hypothesis to be unsupported. Once variables were tested individually, we used the best-supported metrics to construct the hypothesized interactions, which we also tested. For example, for a species with vbdist as the best UVB predictor and w95 as the best winter high flow predictor, we evaluated the model vbdist + w95 + vbdist × w95 to test the hypothesized interaction of winter high flows and valley bottom proximity. To be supported, the interaction model needed an AIC score that was better (lower) than the model without the interaction included.

In the second stage of the analysis, we constructed a global model for each species. The global model included the best-supported metric in each group (for hypotheses that were supported), plus all supported interactions. We allowed models to include both a predictor of brook trout at the site and at the subwatershed level because exploratory analyses showed that parameter estimates of the two variables changed little whether they were included separately or together, suggesting that confounding effects of correlation were small. We fit the global model and all possible subsets using the multilevel logistic regression approach described above. We ranked the resulting models by AIC score and retained all models within 6 points of the best overall model as a confidence set of models (Burnham and Anderson 2002), excluding models that were the same as a better-ranked model except for the addition of an uninformative parameter (i.e., one that improved the likelihood by <2; Burnham and Anderson 2002; Arnold 2010). To evaluate the importance of climate in determining the distributions of each species, we compared the best-overall models with reduced models that excluded climate variables. We evaluated the relative importance of geo-

morphic variables and brook trout the same way. We calculated Akaike model weights (Burnham and Anderson 2002) for the best-overall and the best reduced models (i.e., the no climate, no geomorphic, and no brook trout models). This was a post-hoc analysis that compared only those best models for the sake of illustrating the gain of adding or subtracting climate variables vs. other variables. In addition, for the best overall model we plotted species response curves for each predictor variable by holding all other variables to their mean values and varying the predictor of interest across its full range of values in the dataset.

We conducted a second ranking of all models according to their predictive performance in a form of fourfold cross validation. This involved first dividing the dataset into four geographic regions (Fig. 1). We withheld data from each of the regions in turn, fit the models using data from the other three regions, and predicted presence and absence at sites in the withheld regions (for bull trout, which only occurs in regions 1 and 4, we conducted twofold cross-validation). This form of cross validation provides an indication of model transferability i.e., how well the model would perform in a new region (Fielding and Haworth 1995; Randin et al. 2006). We assessed model performance by constructing 2 × 2 confusion matrices showing correctly and incorrectly predicted presences and absences. In constructing a confusion matrix it is necessary to specify a threshold or cutoff for predicted presence (i.e., the level of predicted probability of occurrence at which a species is assumed to be present) and there are various methods for making this choice (Freeman and Moisen 2008). We determined the optimal cutoff separately for each model as the value between 0.01 and 0.99 (in 0.01 increments) that maximized the true skill statistic (TSS; Allouche et al. 2006), which is defined as sensitivity + specificity − 1. Sensitivity is the proportion of observed presences correctly predicted, and specificity is the proportion of observed absences correctly predicted. The maximum TSS is closely related to the commonly used performance metric AUC, which is the area under the curve of the receiver–operator characteristic plot, and like AUC it has the advantage of being unbiased by prevalence (Manel et al. 2001; Allouche et al. 2006). We used cross-validation maximum TSS (hereinafter, CVTSS) as our measure of cross-validated model performance. We retained a set of best models that included all those with scores within 0.03 points of the best overall. TSS scores potentially range from 0–1 (unless the model is worse than random, in which case it is negative), and this was an arbitrary threshold that retained 3–8 models per species. We evaluated the rela-

Table 4. Support for hypotheses in the first stage of the data analysis, with best-supported metrics for each variable.

Category	Variable	Hypothesis supported? (metric)		
		Brook trout	Bull trout	Cutthroat trout
Climate	Air temperature	**Y** ($-$ dtemp $-$ dtemp^2)	**Y** ($-$ dtemp)	**Y** ($-$ dtemp)
	Winter high flow	**Y** ($-$ w95 $+$ w95^2)	**Y** ($-$ w95)	**Y** (none)
Geomorphic	Stream slope	**Y** ($-$ slope)	**Y** ($-$ slope)	**Y** ($-$ slope $-$ slope^2)
	Unconfined valley bottom	**Y** ($-$ vbdist $+$ vbdist^2)	**N** ($+$ vbdist)	**Y/N** ($+$ vbdist $-$ vbdist^2)
	Stream size	**Y** (mflow $-$ mflow^2)	**Y** ($+$ sflow $-$ sflow^2)	**N** ($+$ mflow)
Land use	Road presence	**Y** ($+$ road)	**N** (none)	**N** (none)
Invasive species	Brook trout in site	NA	**N** (none)	**Y** ($-$ brk2)
	Brook trout in subwatershed	NA	**N** (none)*	**Y** ($-$ brkw)
Interactions	Winter high flow x valley bottom	**N** ($-$ w95 $\times$ vbdist)	**N** ($-$ w95 $\times$ vbdist)	**Y** (none)
	Brook trout in subwatershed x valley bottom	NA	**N** ($-$ brkw $\times$ vbdist)	**Y** ($+$ brkw $\times$ vbdist)

Note: "Y" means the hypothesis was supported; "N" means it was not. Best-supported metrics are indicated in parentheses; "none" means that no metric was better than an intercept-only model. If a metric is listed for an unsupported hypothesis, it means that the direction of the effect was opposite what was predicted. "NA" means the variable does not apply for that species. "Y (none)" means that no response was predicted and none was observed.

*, The metric brkw was not supported as a simple predictor for bull trout, but was included in models because the interaction brkw×vbdist was supported.

tive importance of climate variables, geomorphic variables, and brook trout variables by removing all variables in each class, one class at a time, and comparing the CVTSS score of the resulting model to that of the best overall model. We also plotted response curves for the predictor variables in the best overall model.

Results

Tests of individual metrics in the first stage showed support for all climate hypotheses, whereas the invasive species hypotheses were better supported for cutthroat trout than bull trout (Table 4; full results are in Appendix A, Tables A1–A3). Support for geomorphic, land use, and interaction hypotheses were mixed. Notably, hypotheses regarding UVBs, road presence, and interactions were not supported for bull trout, and hypotheses regarding stream size and road presence were not supported for cutthroat trout (Table 4). The random effect for subwatershed was supported for all species for all models ($p \approx 0$).

Brook trout

Brook trout showed a unimodal relationship with dtemp in all of the best-supported models (Tables 5 and 6; Fig. 2*a*). Winter high flow (w95) was also supported in all of the top models based on AIC score and nearly all of the top models based on CVTSS. The relationship was predominantly negative in both cases (Fig. 2*d*). The best nonclimate model had an AIC score nearly 34 points worse, while the best nongeomorphic model had an AIC score over 77 points worse (Tables 5 and 7), indicating that both climate and geomorphic variables were important in describing brook trout distributions. Negative responses to slope, vbdist, and mflow were included in most models in the AIC confidence set, and the top model based on CVTSS (Table 5; Figs. 2*f*, 2*i*, and 2*l*).

However, based on CVTSS, the best nongeomorphic model provided nearly as good a fit as the best-overall model CVTSS (Table 5), indicating that climate alone provided good predictions of brook trout occurrence. Although road and the w95 $\times$ vbdist interaction were supported in the first stage of analysis and included in the global model, these variables dropped out of all of the top-supported models. Model selection by CVTSS consistently yielded models that were simpler than those selected by AIC, particularly in having fewer second-order terms (Table 5). The highest CVTSS score was 0.366, indicating a 68% overall correct classification rate (classification rate $= 0.5$(CVTSS $+ 1$)).

Bull trout

Bull trout displayed a strong negative relationship with dtemp in the best-supported models (Tables 6 and 8; Fig. 2*b*). All of the models in the AIC confidence set also included a negative response to w95, but the top model based on CVTSS did not (Tables 6 and 8; Fig. 2*e*). The bull trout response to w95 in the best model by AIC was complicated by the inclusion of an interaction between w95 and vbdist that had a sign opposite the expected direction; that is, bull trout showed a stronger negative response to winter high flows in or near valley bottoms than away from valley bottoms (Fig. 2*e*). However, the uncertainty on the parameter estimate for the interaction term was large (Table 6). The best nonclimate models by both AIC and CVTSS scored much worse than the best-overall models (Tables 7 and 8), indicating that climate variables were critical in describing bull trout distributions. The best nongeomorphic model also had low support, partly because a negative response to slope appeared in all of the models in the AIC confidence set and the top three models based on CVTSS. A positive response to vbdist appeared in some of the models in the AIC confidence set but none of the top models based on CVTSS; conversely, a

Table 5. Brook trout: global model and best-supported models ranked by Akaike's information criterion (AIC) and cross-validated predictive performance (CVTSS).

Model	Delta AIC	AIC weight	CVTSS
Global model			
$+ dtemp - dtemp^2 - w95 + w95^2 - slope - vbdist - vbdist^2 + mflow - mflow^2 + road - w95 \times vbdist$	0.70		
Best models by AIC (AIC confidence set)			
$+ dtemp - dtemp^2 - w95 + w95^2 - slope - vbdist - vbdist^2 + mflow - mflow^2$	0	25.8%	
$+ dtemp - dtemp^2 - w95 + w95^2 - slope - vbdist - vbdist^2 - mflow$	0.02	25.6%	
$+ dtemp - dtemp^2 - w95 + w95^2 - slope - vbdist + mflow - mflow^2$	0.33	21.9%	
$+ dtemp - dtemp^2 - w95 + w95^2 - slope - vbdist - mflow$	0.34	21.8%	
$+ dtemp - dtemp^2 - w95 + w95^2 - slope - vbdist - vbdist^2$	4.45	2.8%	
$+ dtemp - dtemp^2 - w95 + w95^2 - slope - vbdist$	5.01	2.1%	
Best model by AIC, no climate variables			
$- slope - vbdist - vbdist^2 + mflow - mflow^2$	33.98		
Best model by AIC, no geomorphic variables			
$+ dtemp - dtemp^2 - w95 + w95^2 + road$	77.15		
Best models by CVTSS			
$+ dtemp - dtemp^2 - w95 - slope - vbdist - mflow$			0.366
$+ dtemp - dtemp^2 - w95 + w95^2$			0.364
$+ dtemp - dtemp^2 - w95 - slope - vbdist$			0.356
$+ dtemp - dtemp^2 - w95 - vbdist - slope + mflow - mflow^2$			0.352
$+ dtemp - dtemp^2 - slope - mflow$			0.350
Best model by CVTSS, no climate variables			
$- slope - mflow$			0.293
Best model by CVTSS, no geomorphic variables			
$+ dtemp - dtemp^2 - w95 + w95^2$			0.364

Note: Leading symbols (+ or –) indicate direction of effect for each predictor variable. Delta AIC gives the difference in AIC score from the best-overall model. Model weights are calculated only for the best models by AIC (the AIC confidence set).

positive or unimodal response to sflow was included in some of the best models by CVTSS but none of the models in the AIC confidence set. The best model by AIC included a negative response to brkw, though the best nonbrook trout model was also in the confidence set and none of the top models based on CVTSS included brook trout as a predictor variable. The highest CVTSS score was 0.488, indicating a 74% overall correct classification rate.

Cutthroat trout

Cutthroat trout had a weak negative relationship with dtemp in some of the best-supported models (Tables 6 and 9; Fig. 2c), and no relationship with winter high flow variables (consistent with our hypothesis). A model without climate variables had strong support by AIC (Tables 7 and 9), and was the best model overall based on CVTSS (Table 9). A negative response to slope and a positive response to mflow appeared in many of the highly ranked models (Table 9; Figs. 2h and 2m). A response to vbdist was in most of the models, and the best models overall also included the brkw × vbdist interaction. This meant that the cutthroat trout relationship with vbdist depended on whether brook trout were present in the subwatershed: when brook trout were present, cutthroat trout showed a generally negative response, but when brook trout were absent, cutthroat trout showed a neutral to positive response, consistent with our hypothesis (Fig. 2k). Cutthroat trout showed a strong response to brook trout presence either at the site or the subwatershed scale (Tables 6 and 9; Fig. 2o). This was reflected in the low AIC

and CVTSS scores of the best non-brook-trout models (Tables 7 and 9), which were much worse than those of the best-overall models. The highest CVTSS score was 0.426, indicating a 71% overall correct classification rate.

Discussion

Our results suggest considerable variation in the relative importance of factors regulating trout distributions in the ICRB, which has important implications for the species considered. Bull trout distributions were primarily related to climatic variables, with geomorphic variables playing a lesser but still substantial role. Brook trout distributions were influenced strongly by both climatic and geomorphic variables; removing either of these classes of predictors resulted in much weaker models. In contrast, cutthroat trout distributions were weakly associated with climate variables across the range of conditions evaluated in the ICRB, suggesting less sensitivity to climatic trends. Cutthroat trout did, however, display a strong negative response to the presence of nonnative brook trout, which were affected by climatic variables, thereby opening the possibility of an indirect positive response to climate change if brook trout distributions were significantly altered in the future.

Our finding that bull trout was the most temperature-sensitive species is consistent with past work showing that bull trout have lower thermal optima and tolerances than most other salmonids (Selong et al. 2001) and that temperature is an important determinant of the species' distribution (Dunham et al. 2003; Rieman et al. 2007; Isaak et al. 2010). We found

Table 6. Parameter estimates for best-supported models based on Akaike's information criterion (AIC) and cross-validated predictive performance (CVTSS) for brook trout, bull trout and cutthroat trout distributions in the interior Columbia River Basin.

Model	Temperature		Winter high flow		Slope	UVB	
	dtemp	dtemp²	w95	w95²	slope	vbdist	vbdist²
Brook trout (AIC)	+0.27±0.28	−1.33±0.33	−1.35±0.31	+0.80±0.20	−0.47±0.15	−1.51±0.24	−0.31±0.20
Brook trout (CVTSS)	+0.08±0.28	−1.31±0.33	−0.50±0.21		−0.54±0.14	−1.31±0.19	
Bull trout (AIC)	−2.38±0.44		−1.52±0.29		−0.80±0.25	+0.55±0.21	
Bull trout (CVTSS)	−3.25±0.44				−0.79±0.25		
Cutthroat trout (AIC)	−0.28±0.23				−0.46±0.13	+0.56±0.36	−0.52±0.19
Cutthroat trout (CVTSS)						−0.15±0.29	

Model	Size (meanflow)		Brook trout		Interactions	
	mflow	mflow²	brk2	brkw	w95×vbdist	vbdist×brkw
Brook trout (AIC)	+0.07±0.35	−0.14±0.11				
Brook trout (CVTSS)	−0.33±0.15					
Bull trout (AIC)				−1.13±0.39	+0.63±0.37	
Bull trout (CVTSS)						
Cutthroat trout (AIC)	+0.62±0.25		−0.85±0.14	−1.21±0.32		+0.72±0.37
Cutthroat trout (CVTSS)				−1.63±0.31		+1.17±0.37

Note: Values are Mean ± SE. Predictor variables have been standardized by subtracting the mean and dividing by 2×SD, so the relative magnitudes of the parameter estimates indicate the importance of the variables.

no lower thermal limit for bull trout; the coldest sites in our dataset were the most likely to be occupied. Brook trout in the ICRB had a unimodal thermal response with a peak in predicted presence at 16 °C air temperature. Unlike the other two species, cutthroat trout in our dataset showed only a slight negative response to temperature. However, this should not be taken as evidence that cutthroat trout are not sensitive to temperature, which has been clearly demonstrated (Bear et al. 2007; Dunham et al. 1999). The muted response may have been because the dataset was confined to the historical range of cutthroat trout, and therefore included few sites that were too warm. Further, detailed post-hoc examination of our results revealed that the relationship between cutthroat trout presence and temperature was complex and did include thresholds at low and high temperatures (~13 °C and ~21 °C). Nevertheless, relative to the other two species cutthroat trout appeared to be less sensitive to thermal variability, at least within the ICRB. Finally, it is important to acknowledge that part of the uncertainty in relationships with temperature is related to using air temperature as a surrogate for water temperatures. Future work to model and predict water temperature is needed to improve predictions of thermal impacts (Isaak et al. 2010).

Our modeling results were generally consistent with the hypothesis that high flows in the post-spawning period restrict fall-spawning trout distributions. We found support for this hypothesis with both model selection methods we employed, although our cross-validation suggested that observed distributions of bull trout could also be explained very well by temperature alone. Two mechanisms have been proposed for this high-flow response. The first is that large floods may cause bed scour sufficient to destroy salmonid redds, embryos, and alevins prior to emergence (Seegrist and Gard 1972; Montgomery et al. 1996; Tonina et al. 2008). The second is that trout are vulnerable to displacement during the first month after emergence from the substrate (Nehring and Anderson 1993; Fausch et al. 2001) because they cannot yet hold position in high-velocity water (Heggenes and Traaen 1988; Crisp and Hurley 1991). The first mechanism involves large events (as measured by our metrics w1.5 or w2) while the second can be caused by smaller events (such as correspond to the w95 and w99 metrics). We found that for brook and bull trout, the best-supported predictor was w95, which is consistent with the second mechanism. This is not strong evidence, however, and additional research would be needed to disentangle these two hypotheses.

All three species were less likely to occur as stream slope increased. This contrasts with previous studies (Fausch 1989; Hilderbrand 1998; Dunham et al. 1999) that found that cutthroat trout occurred more frequently in higher gradient reaches, whereas brook trout occurred in lower gradient reaches. However, previous studies (Fausch 1989) also noted that such a pattern could have resulted from brook trout excluding cutthroat trout rather than a habitat preference per se. Our analysis was less confounded because our broad coverage allowed us to model cutthroat trout response to slope in both sympatry and allopatry with brook trout, better separating the slope effect from the brook trout effect. Another geomorphic variable, stream size, was supported as a predictor variable for all species in the screening stage, but dropped out of later models for bull trout and some models for cut-

Fig. 2. Species response to continuous predictor variables for the best overall models by Akaike information criterion (AIC, grey line) and cross validated predictive performance (CVTSS, black line). For parameters with interactions (panels e, j and k), broken lines indicate responses at alternative levels of the interacting variable, as noted.
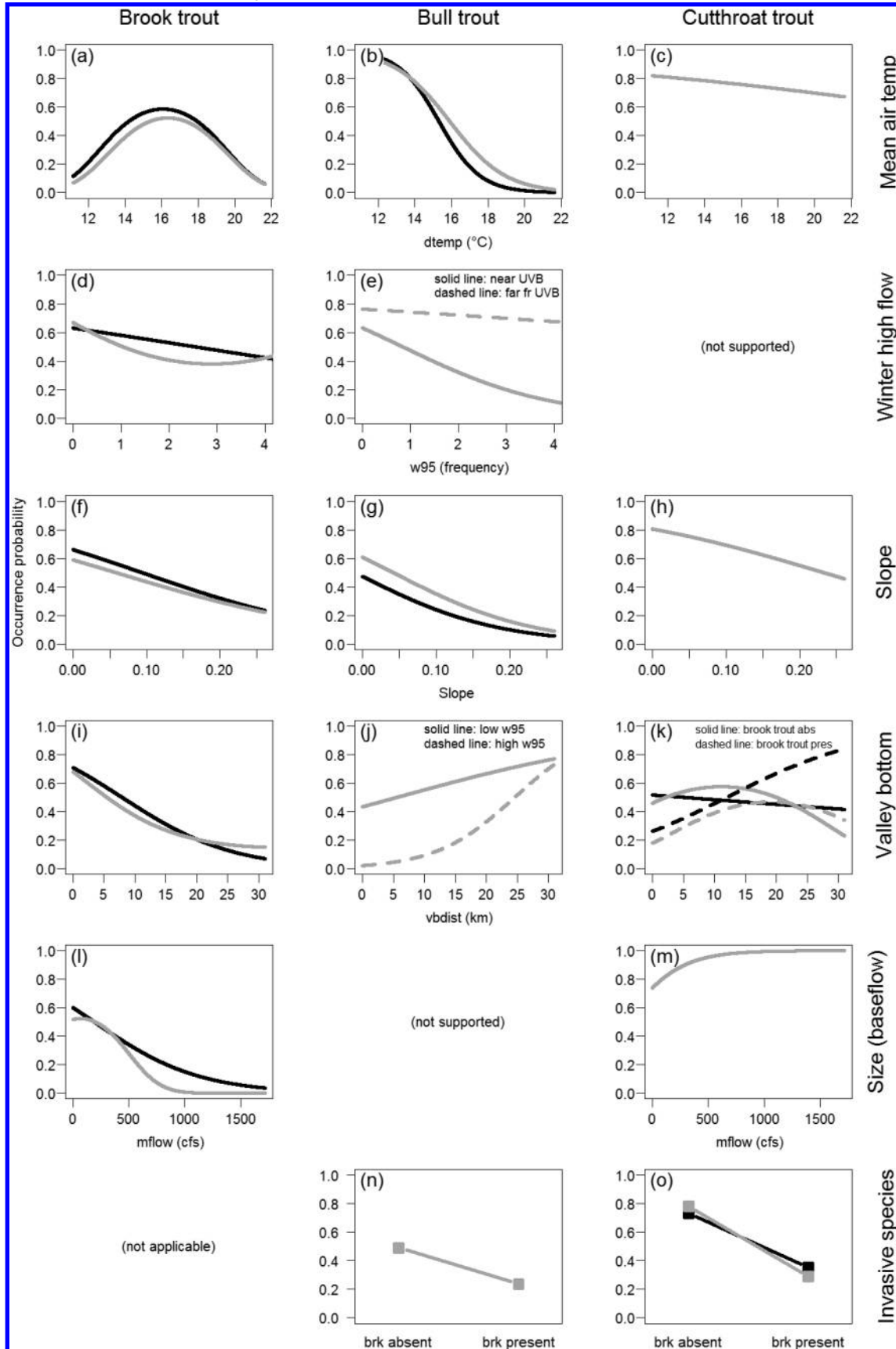
Table 7. Best models for brook trout, bull trout, and cutthroat trout with and without variables for climate, geomorphic, and invasive species, ranked by Akaike's information criterion (AIC).

Model	Delta AIC	Model weight
Brook trout		
Best overall	0	100%
Best no climate	34.0	0%
Best no geomorphic	77.2	0%
Bull trout		
Best overall	0	95%
Best no climate	91.2	0%
Best no geomorphic	16.5	0%
Best no invasives	6	5%
Best overall		
Best overall	0	61%
Best no climate	0.9	39%
Best no geomorphic	33.0	0%
Best no invasives	58.4	0%

Note: Model weights are calculated as if the models listed (the best-supported in each category) were the only candidate models.

throat trout, indicating that apparent associations with stream size were better explained by other variables. All brook trout models showed that occurrence probability declined as stream size increased, consistent with hypotheses and previous observations (Rahel and Nibbelink 1999; Dunham et al. 2002; Öhlund et al. 2008).

Brook trout had a positive association with UVBs, which is consistent with past observations (Collen and Gibson 2001; Dunham et al. 2002; Benjamin et al. 2007). However, contrary to our hypotheses and past research (Baxter and Hauer 2000), we found a negative association of bull trout with UVBs. We had hypothesized that this negative relationship was an indirect response to brook trout occupying UVBs and excluding bull trout, and tested for this by modeling an interaction between brook trout presence and UVB distance. This interaction was not supported by AIC or CVTSS. At present we have no alternative hypotheses to explain the observed bull trout – UVB relationship. In contrast, cutthroat trout displayed a negative relationship with UVBs only in subwatersheds with brook trout present, supporting the hypothesis that brook trout excluded cutthroat trout from these otherwise favorable habitats. The reason that brook trout use and appear to dominate UVBs is not completely clear. It has long been known that brook trout favor sites with groundwater upwelling for spawning (Benson 1953; Witzel and MacCrimmon 1983), probably because the warmer groundwater provides favorable conditions for egg incubation (Curry et al. 1995). Therefore, the high degree of hyporheic exchange typical of channels in UVBs (Baxter and Hauer 2000) may explain the higher probability of occurrence of brook trout. In addition, the lack of confinement of UVBs results in high sinuosity and abundant low-gradient, off-channel water storage, particularly when beavers are present (Johnston and Naiman 1987). We hypothesized that these areas would provide a velocity refuge for redds and juvenile trout during periods of high flow (Shellberg et al. 2010). We tested for this by modeling an interaction between valley bot-

toms and high flows; results showed that for both brook trout and bull trout the interaction was supported but the sign was opposite the expected direction. This result is confusing, but at a minimum indicates that there is no support for the velocity-refuge hypothesis in this dataset.

We found strong support for the hypothesis that cutthroat trout were less likely to occur when brook trout were present at the site or within the subwatershed (Gresswell 1988; Dunham et al. 2002; Peterson et al. 2004a). We found weaker evidence for a negative response of bull trout to brook trout presence at the subwatershed scale. Previous studies also reported mixed results on brook trout/bull trout co-occurrence and suggested spatial variability in the nature of the interactions (Dunham and Rieman 1999; Rich et al. 2003; Rieman et al. 2006). An exploration of spatial variability in biotic interactions was beyond the scope of our study, but this would be a promising avenue for future analyses using this dataset.

Roads were predictive of the presence of nonnative brook trout in the first stage of our data analysis, but did not explain presence of native trout. This stands in contrast to past work on native trout in the region (Rieman et al. 1997; Thurow et al. 1997), and the diverse range of negative impacts that roads can have on aquatic ecosystems and species (Trombulak and Frissell 2000). The lack of land use effects may reflect that most study sites were in relatively pristine areas, since the sampling design of many of the original datasets was intended to detect native cutthroat and bull trout. Alternatively, our predictor variable may simply have been too crude an indicator of human land use alteration. Accordingly, results of this work should not be construed to suggest that roads do not pose threats to native trout.

Modeling issues and limitations

We used multiple techniques to attempt to identify which predictor variables had support across the geographic range of the dataset and therefore represented general, consistent relationships. We found that models selected by CVTSS had fewer predictors and second-order terms than those selected by AIC. This suggests that in terms of model transferability (Fielding and Haworth 1995; Randin et al. 2006), selection by AIC resulted in models that were somewhat overfit; the simpler models are probably more appropriate for predictions in new locations and under new climatic conditions. Nevertheless, there is value in examining the models selected by AIC, because these describe species responses to predictors across the full dataset and the entire region and therefore incorporate all available information. Variables supported by AIC but not CVTSS merit further study and perhaps regional-scale analysis. Many variables were supported by both methods, though, providing strong evidence in favor of the associated hypotheses.

Cross validation indicated that the best GLM models had classification success rates of 66%–74%. This suggests that even with the best models there is a significant amount of unexplained variability in species distributions. We suspect a major reason is the lack of information on local factors that play a role in determining species presence, including movement barriers (Fausch et al. 2009) and stocking histories (Paul and Post 2001). Other potential influences could include uncertainty contributed by lumping together data represented by different life stages (e.g., juveniles versus adults)

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Table 8. Bull trout: global model and best-supported models by Akaike's information criterion (AIC) and cross-validated predictive performance (CVTSS).

Model	Delta AIC	Model weight	CVTSS
Global model			
– dtemp – w95 – slope + vbdist + sflow – sflow^2 – brkw + w95×vbdist – brkw×vbdist	7.59		
Best models by AIC (AIC confidence set)			
– dtemp – w95 – slope + vbdist – brkw + w95×vbdist	0	43.7%	
– dtemp – w95 – slope + vbdist – brkw	0.87	28.3%	
– dtemp – w95 – slope + vbdist + sflow – brkw + w95×vbdist	1.23	23.7%	
– dtemp – w95 – slope – brkw	6.02	2.2%	
– dtemp – w95 – slope + vbdist + w95×vbdist	6.05	2.1%	
Best model by AIC, no climate variables			
vbdist – slope – brkw – brkw×vbdist	91.22		
Best model by AIC, no geomorphic variables			
– dtemp – w95	16.49		
Best model by AIC, no brook trout variables			
– dtemp – w95 – slope + vbdist – w95×vbdist	6.05		
Best models by CVTSS			
– dtemp – slope			0.488
– dtemp – w95 – slope			0.479
– dtemp – slope + sflow – sflow^2			0.477
– dtemp + sflow – sflow^2			0.476
– dtemp – w95 + vbdist – slope + sflow – sflow^2			0.473
– dtemp + sflow			0.472
– dtemp			0.472
– dtemp – slope + sflow			0.470
Best model by CVTSS, no climate variables			
+ vbdist + sflow			0.344
Best model by CVTSS, no geomorphic variables			
– dtemp			0.472
Best model by CVTSS, no brook trout variables			
– dtemp – slope			0.488

Note: Leading symbols (+ or –) indicate direction of effect for each predictor variable. Delta AIC gives the difference in AIC score from the best-overall model. Model weights are calculated only for the best models by AIC (the AIC confidence set).

and the timing of sample collection within the summer – early fall low-flow season. For cutthroat trout and bull trout, there was a great deal of model uncertainty in the results based on cross validation; models with very different sets of variables had almost equal support. For cutthroat trout it was clear that the presence of brook trout was critically important, but the role of other variables was less certain. Similarly, for bull trout, only temperature was an essential predictor variable; a number of other variables had varying levels of support. These issues do not alter the main conclusions of this study (a strong role of climate in determining brook trout and bull trout distributions, and a strong effect of brook trout on cutthroat distributions), but we would caution against making predictions based on any single model or at fine spatial scales (e.g., individual stream reaches or subwatersheds).

A final concern is that our methods did not explicitly address imperfect detection. Although methods exist to incorporate imperfect detection in occupancy modeling (MacKenzie et al. 2002), doing so in a multilevel modeling framework is complex (Wenger et al. 2008), and we judged it to be of limited benefit. Our dataset consisted of samples collected using multipass electrofishing (one or more surveys) and snorkeling

(four or more surveys). Past studies have shown that multi-pass electrofishing capture efficiency (i.e., chance of detecting a single individual) of the species considered here is approximately 40%–60% (Peterson et al. 2004b). Even assuming the low end of this range, this implies that if there were 5 individual fish at a site, the chances of detecting at least one was >92%; if there were 10 fish, the chance of detecting one or more was >99%. Therefore, in our dataset only sites with very low abundances of fish were likely to be incorrectly labeled as absences, which we contend is reasonable, since sites with very few individuals are not likely to represent optimal habitat or persistent populations for that species. In any case, assuming that there is no large bias to patterns of capture efficiency, the principal consequence of ignoring incomplete detection is to underestimate the magnitude of covariates (Tyre et al. 2003), which implies that our hypothesis tests are somewhat conservative.

Conservation and management implications

Our results indicate a high climate sensitivity for brook trout and bull trout, consistent with previous studies (Flebbe et al. 2006; Rieman et al. 2007; Isaak et al. 2010), but poten-

Table 9. Cutthroat trout: global model and best-supported models by Akaike's information criterion (AIC) and cross-validated predictive performance (CVTSS).

Model	Delta AIC	Model weight	CVTSS
Global model			
$- dtemp - brk2 - brkw + vbdist - vbdist^2 + brkw \times vbdist + mflow - slope - slope^2$	1.89		
Best models by AIC (AIC confidence set)			
$- dtemp - brk2 - brkw + vbdist - vbdist^2 + brkw \times vbdist + mflow - slope$	0	28.2%	
$- dtemp - brk2 - brkw + vbdist - vbdist^2 + mflow - slope + slope^2$	0.27	24.7%	
$- brk2 - brkw + vbdist - vbdist^2 + brkw \times vbdist + mflow - slope$	0.93	17.7%	
$- brk2 - brkw + vbdist - vbdist^2 + mflow - slope - slope^2$	1.99	10.4%	
$- dtemp - brk2 - brkw - vbdist + brkw \times vbdist + mflow - slope + slope^2$	2.60	7.7%	
$- brk2 - brkw + vbdist - vbdist^2 + mflow - slope$	3.38	5.2%	
$- brk2 - brkw - vbdist + brkw \times vbdist + mflow - slope + slope^2$	4.07	3.7%	
$- dtemp - brk2 - brkw - vbdist + brkw \times vbdist + mflow - slope$	4.98	2.3%	
Best model by AIC, no climate variables			
$- brk2 - brkw + vbdist - vbdist^2 + brkw \times vbdist + mflow - slope$	0.93		
Best model by AIC, no geomorphic variables			
$- dtemp - brk2 - brkw$	32.97		
Best model by AIC, no brook trout variables			
$+ vbdist - vbdist^2 + mflow - slope + slope^2$	58.40		
Best models by CVTSS			
$- brkw - vbdist + brkw \times vbdist$			0.426
$- dtemp - brk2 + vbdist - vbdist^2 - slope + mflow$			0.426
$- dtemp - brkw - vbdist + brkw \times vbdist$			0.423
$- brk2$			0.422
$- brkw - slope + vbdist + mflow$			0.421
$- brkw + vbdist$			0.416
$- brkw - slope + mflow$			0.415
$- brkw - dtemp - slope + mflow$			0.414
$- brkw + mflow$			0.413
Best model by CVTSS, no climate variables			
$- brkw - vbdist + brkw \times vbdist$			0.426
Best model by CVTSS, no geomorphic variables			
$- brk2$			0.422
Best model by CVTSS, no brook trout variables			
$- dtemp + mflow - slope - slope^2$			0.388

Notes: Leading symbols (+ or –) indicate direction of effect for each predictor variable. Delta AIC gives the difference in AIC score from the best-overall model. Model weights are calculated only for the best models by AIC (the AIC confidence set).

tially low climate sensitivity for cutthroat trout, in contrast to earlier work (Dunham et al. 1999; Bear et al. 2007; Williams et al. 2009). Our results also suggest that the presence of brook trout is the single largest influence on cutthroat trout distribution in the ICRB, implying that future climate changes may alter cutthroat trout distributions indirectly via changes to brook trout distributions. If brook trout respond more negatively to warming temperatures than do cutthroat trout, as suggested by our results, then the net outcome of a warming climate could be favorable to cutthroat trout. An increase in frequency of winter high flow events (as would be expected with warming; Elsner et al. 2010) could further stress brook trout populations. Ours is not the first study to suggest that climate change could provide some benefit to cutthroat trout. Cooney et al. (2005) speculated that because cutthroat trout in the central and southern Rocky Mountains are often confined to headwater refugia in which cold temperatures limit productivity and recruitment (Isaak and Hubert 2004; Young and Guenther-Gloss 2004; Coleman and Fausch 2007), warming could increase population sizes (as-

suming that base flows remain adequate to support upstream expansion). Such an outcome is far from certain, however. Isaak et al. (2010) recently projected that warming of some Rocky Mountain streams could cause an upward shift in elevation of rainbow trout populations with little net change in habitat area. The same could occur with brook trout. There may be additional small, high-elevation streams that could become more suitable for brook trout in the future, enabling an upward shift in elevation with no net loss in habitat. Further research is needed to determine the likely trajectories of brook trout and cutthroat trout under different climatic and landscape conditions. Our scenario for cutthroat trout also ignores the potential range expansion of other native or introduced species with even higher temperature tolerances, such as brown trout and smallmouth bass (*Micropterus dolomieu*), which could prove to have strong negative interactions with cutthroat trout.

Bull trout is the most climate sensitive of the trout species considered here. Its strong temperature sensitivity, coupled with a likely sensitivity to an increase in winter high flow

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frequency, mean that a warming climate in the ICRB will likely lead to losses of suitable habitat. Our analysis indicates that the species already inhabits the coldest available streams, so unlike brook trout, it does not have the potential to shift to higher elevation habitats.

Our results have several implications for management. The first is that in locations that (*i*) support both cutthroat trout and brook trout but (*ii*) are warmer than optimal for brook trout and (*iii*) have high flows in the winter, brook trout control efforts may be highly feasible and provide significant benefits to cutthroat trout. Second, preventing brook trout from accessing uninvaded UVBs may be important for protecting habitat for native trout, as removal of established populations of brook trout from UVBs is unlikely to be effective (e.g., Meyer et al. 2006). Third, areas where brook trout currently dominate over cutthroat trout still have conservation value, because these locations may become less hospitable to brook trout and more so to cutthroat trout in the future. An important intermediate management step in these locations may be to guard against the invasion of warm-water species, perhaps using barriers to upstream migration (Fausch et al. 2009) and through the application of distributional monitoring protocols (Isaak et al. 2009) that facilitate the early detection of invasions and increase the chances of population eradication. Finally, our results reinforce those of other researchers (e.g., Rieman et al. 2007; Isaak et al. 2010) that suggest effective long-term management for bull trout in the face of climate change will require prioritization to ensure that resources are allocated to those locations with the coldest temperatures that offer the greatest long-term potential to sustain the species.

Acknowledgments

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Table A1. Brook trout results from screening stage.

Model	AIC	Predictor 1	Predictor 2	Predictor 3
w95 + vbdist + w95×vbdist	**3435**	**−0.65±0.18**	**−1.32±0.18**	**0.56±0.32**
w95 + vbdist	3436	−0.64±0.18	−1.39±0.18	
vbdist + vbdist^2	**3442**	**−1.79±0.23**	**-0.50±0.19**	
vbdist	3448	−1.26±0.18		
slope	**3480**	**−0.75±0.13**		
slope + slope^2	3482	−0.80±0.17	0.07±0.16	
w95 + w95^2	**3488**	**−1.49±0.28**	**0.77±0.20**	
dtemp + dtemp^2	**3490**	**−0.08±0.26**	**−1.47±0.34**	
ptemp + ptemp^2	3490	0.36±0.25	−1.30±0.28	
mflow + mflow^2	**3498**	**1.00±0.31**	**−0.38±0.11**	
w95	3500	−0.66±0.18		
sflow + sflow^2	3501	0.95±0.32	−0.41±0.12	
vbpres	3501	−0.44±0.12		
road	**3505**	**0.41±0.14**		
w1.5 + w1.5^2	3505	−0.60±0.25	0.39±0.12	
w99	3507	−0.52±0.20		
w99 + w99^2	3508	−0.78±0.31	0.20±0.18	
w2 + w2^2	3508	−0.58±0.23	0.41±0.17	
dtemp	3508	−0.50±0.23		
(intercept only)	3511			
w2	3512	−0.20±0.17		
ptemp	3512	−0.25±0.21		
mflow	3512	−0.14±0.12		
sflow + sflow^2	3512	−0.12±0.12		
w1.5	3513	−0.02±0.17		

Note: Akaike information criterion (AIC) scores and parameter estimates (mean ± SE) are given for each model. Text in bold indicates a supported metric that was included in the global model.

Table A2. Bull trout results from screening stage.

Model	AIC	Predictor 1	Predictor 2	Predictor 3
w95 + vbdist + w95×vbdist	**984**	**−2.20±0.27**	**0.36±0.19**	**−0.64±0.35**
w95 + vbdist	985	−2.08±0.26	0.37±0.19	
w95	**987**	**−2.14±0.26**		
w99	988	−2.47±0.32		
w95 + w95^2	989	−2.04±0.46	−0.12±0.44	
w99 + w99^2	989	−2.22±0.51	−0.30±0.54	
dtemp	**994**	**−3.48±0.43**		
dtemp + dtemp^2	996	−3.41±0.52	−0.19±0.89	
w2	1017	−1.84±0.28		
w2 + w2^2	1018	−1.65±0.36	−0.33±0.42	
w1.5	1026	−1.75±0.30		
w1.5 + w1.5^2	1027	−2.01±0.38	0.24±0.24	
slope	**1044**	**−1.24±0.25**		
slope + slope^2	1046	−1.23±0.34	−0.02±0.25	
sflow + sflow^2	**1061**	**0.91±0.29**	**−0.11±0.05**	
mflow + mflow^2	1062	0.77±0.27	−0.06±0.03	
mflow	1062	0.45±0.18		
sflow	1062	0.46±0.18		
vbdist	**1063**	**0.54±0.20**		
brkw + vbdist + brkw×vbdist	**1063**	**−0.23±0.45**	**1.02±0.36**	**−0.75±0.43**
brkw + vbdist	1064	−0.41±0.43	0.51±0.20	
vbdist + vbdist^2	**1065**	**0.47±0.36**	**−0.05±0.23**	
ptemp	1065	−0.55±0.27		
ptemp + ptemp^2	1067	−0.84±0.42	0.32±0.36	
(intercept only)	1067			
brkw	1068	−0.60±0.44		
brk1	1069	0.19±0.23		
brk2	1069	−0.02±0.26		
road	1069	−0.01±0.27		
vbpres	1069	0.01±0.28		

Note: Akaike information criterion (AIC) scores and parameter estimates (mean±SE) are given for each model. Text in bold indicates a supported metric that was included in the global model.

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Table A3. Cutthroat trout results from screening stage.

Model	AIC	Predictor 1	Predictor 2	Predictor 3
brk2	**3327**	**−1.08±0.14**		
brkw + vbdist + brkw×vbdist	**3341**	**−1.63±0.31**	**−0.15±0.29**	**1.17±0.37**
brk1	3343	−0.91±0.13		
brkw + vbdist	3350	−1.40±0.30	0.59±0.17	
brkw	3358	−1.75±0.31		
mflow	**3363**	**0.91±0.25**		
mflow + mflow^2	3364	0.66±0.44	0.15±0.29	
sflow	3365	0.80±0.21		
sflow + sflow^2	3367	0.97±0.33	−0.07±0.11	
vbdist + vbdist^2	**3368**	**1.05±0.23**	**−0.48±0.18**	
vbdist	3372	0.68±0.18		
w99 + vbdist	3374	0.00±0.20	0.70±0.18	
w99×vbdist	3374	0.15±0.20	0.69±0.18	−0.40±0.38
slope + slope^2	**3377**	**−0.18±0.17**	**−0.26±0.15**	
slope	3378	−0.38±0.12		
dtemp	**3383**	**-0.48±0.22**		
dtemp + dtemp^2	3384	−0.32±0.26	−0.34±0.28	
vbpres	3384	0.24±0.13		
(intercept only)	3385			
road	3385	−0.21±0.14		
w99 + w99^2	3385	−0.39±0.33	0.44±0.23	
w2	3386	−0.17±0.16		
w99	3387	0.11±0.20		
w1.5	3387	−0.06±0.18		
w95	3387	−0.03±0.18		
ptemp	3387	0.01±0.21		
w95 + w95^2	3388	−0.32±0.29	0.27±0.23	
w2 + w2^2	3388	−0.03±0.24	−0.15±0.20	
ptemp + ptemp^2	3388	−0.13±0.25	0.25±0.25	
w1.5 + w1.5^2	3389	−0.09±0.26	0.03±0.15	

Note: Akaike information criterion (AIC) scores and parameter estimates (mean ± SE) are given for each model. Text in bold indicates a supported metric that was included in the global model.