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Factors related to the distribution and abundance of westslope cutthroat trout in central Idaho

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ABSTRACT.—Native resident salmonids throughout North America have experienced population declines, and understanding factors that influence their contemporary distribution and abundance may help conserve and manage such species. We examined the influence of several environmental factors on the current distribution and abundance of westslope cutthroat trout *Oncorhynchus clarkii lewisi* in central Idaho, based on snorkel survey data collected from 2010 to 2019. In total, 2758 snorkel surveys were conducted at 1000 sites; cutthroat trout were present during 1277 of the surveys, and their occupancy rate was higher if brook trout *Salvelinus fontinalis* were absent (0.48) than if brook trout were present (0.31). During surveys where cutthroat trout were present, mean density was 1.81 fish/100 m^2. Underlying lithology was associated with westslope cutthroat trout distribution but not their abundance, suggesting that lithology may influence broader habitat features that affect their ability to fulfill a component of their life history, such as spawning or overwinter survival, more so than characteristics that affect their abundance, such as microhabitat suitability. Not surprisingly, westslope cutthroat trout occupancy was negatively influenced by the abundance of nonnative brook trout, but in central Idaho this effect is tempered by the limited distribution of brook trout. Both the occupancy and the abundance of westslope cutthroat trout were related in a nonlinear, dome-shaped manner to site elevation; considering that elevation was included as a surrogate for stream water temperature (which is also commonly related to trout occupancy and abundance in a dome-shaped manner), intermediate stream elevations (in central Idaho, 800 to 1600 m) currently seem to provide an ideal thermal regime for westslope cutthroat trout.

RESUMEN.—Los salmónidos nativos residentes en toda América del Norte han sufrido la disminución de sus poblaciones, el comprender los factores que influyen en la distribución y abundancia actual podría ayudar a conservar y gestionar estas especies. Examinamos la influencia de varios factores ambientales en la distribución y abundancia actual de la trucha degollada de westslope *Oncorhynchus clarkii lewisi* en el centro de Idaho, basados en los datos obtenidos a través de muestreo con esnórquel entre 2010 y 2019. En total, se realizaron 2758 muestreos con esnórquel en 1000 sitios. La trucha degollada estuvo presente en 1277 de los muestreos, y su tasa de ocupación fue mayor cuando la trucha de arroyo *Salvelinus fontinalis* no se encontró (0.48), en compasión de cuando si estuvo presente (0.31). Durante los muestreos en los que la trucha común estuvo presente, la densidad media fue de 1.81 peces/100 m^2. La litología subyacente se asoció con la distribución de la trucha degollada de westslope, pero no con su abundancia, lo que sugiere que la litología podría influir en características más amplias del hábitat, que afectan su capacidad para cumplir con un componente de su historia de vida, tal como el desove o la supervivencia durante el invierno, más que las características que afectan su abundancia, como la idoneidad del microhábitat. No es de extrañar que la ocupación de la trucha degollada de westslope fuera influida negativamente por la abundancia de la trucha de arroyo no autóctona. Sin embargo, en el centro de Idaho este efecto se vió atenuado por la distribución limitada de la trucha de arroyo. Tanto la ocupación como la abundancia de la trucha degollada de westslope se relacionaron de manera no lineal y en forma de parábola con la elevación del sitio; considerando que la elevación se incluyó como un sustituto de la temperatura del agua del arroyo, que también se relaciona comúnmente en forma de parábola con la ocupación y la abundancia de truchas, lo anterior sugiere que las elevaciones intermedias del arroyo (en el centro de Idaho, 800 a 1600 m) proporcionan actualmente un régimen térmico ideal para la trucha degollada de westslope.

Native resident salmonids throughout North America have experienced declines in distribution and abundance, including species in the Pacific Northwest such as westslope cutthroat trout *Oncorhynchus clarkii lewisi* (Shepard et al. 2005). In response to these declines, fisheries managers and various partners have developed recovery plans, multistate conservation agreements and strategies, and restoration projects (e.g., Lohr et al. 2000, Hirsch et

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al. 2006). However, for management actions to be effective, they must be developed with a good understanding of factors contributing to the status of the species (Milner et al. 1993).

Factors limiting the distribution and abundance of westslope cutthroat trout have been repeatedly investigated across their range (e.g., Sloat et al. 2005, D'Angelo and Muhlfeld 2013, Peterson et al. 2014, Heckel et al. 2020, Heinle et al. 2021). However, the relationship between environmental conditions and the status of this species can vary among populations. For example, road density has been reported to be positively associated with westslope cutthroat trout abundance in the St. Maries River basin, Idaho (Heckel et al. 2020) but was identified as a key limiting factor in British Columbia streams (Valdal and Quinn 2011). Such regional disparities in factors associated with the status of this species highlight the importance of determining limiting factors at geographic scales appropriate for regional management.

The Salmon and Clearwater River basins of central Idaho comprise a large contiguous network of stream habitats in mountainous terrain that is dominated by coniferous forests at higher elevations (up to 3800 m in elevation) and sagebrush-grass steppe at lower elevations. Over 80% of the study area is publicly owned, and nearly 25% is designated wilderness, with many large expanses functioning as de facto wilderness. Due to the high elevation, remoteness, and relatively pristine nature of this ecosystem, central Idaho serves as a stronghold for westslope cutthroat trout (Kennedy and Meyer 2015). Nevertheless, the distribution and abundance of the species in this area is patchy (Shepard et al. 2005). To better understand what biotic and abiotic factors contribute to this patchiness, we investigated landscape-level factors that might be influencing the contemporary distribution and abundance of westslope cutthroat trout in central Idaho.

METHODS

Study Area

The current study incorporated data from the Clearwater and Salmon river basins of central Idaho (Fig. 1). The Clearwater River originates in the Bitterroot Mountains and has a drainage area of approximately 25,000 km^2 and a mean basin elevation of 1311 m. Originating in the Sawtooth Mountains, the Salmon River has a larger drainage area of approximately 37,000 km^2 and a higher mean basin elevation of 2020 m. Salmonid species present in these river basins include westslope cutthroat trout, bull trout *Salvelinus confluentus*, brook trout *S. fontinalis*, lake trout *S. namaycush*, mountain whitefish *Prosopium williamsoni*, Chinook salmon *O. tshawytscha*, coho salmon *O. kisutch*, and resident and anadromous forms of *O. nerka* and *O. mykiss*.

Fish Surveys

Westslope cutthroat trout distribution and abundance were assessed via daytime snorkel surveys conducted from 2010 to 2019 as part of the Idaho Department of Fish and Game's Natural Production Monitoring and Evaluation Program. These surveys typically occurred from June to August each year. Sites were selected either subjectively to represent the general habitat of the waterbody of interest, or using a generalized random-tessellation stratified design (see Apperson et al. 2015 for details). Survey crews attempted to survey approximately 100 linear meters of stream, but upstream and downstream site boundaries were adjusted to fit within hydraulic controls (Apperson et al. 2015). Because these data were from a long-term monitoring program, some sites (38%) were surveyed more than once during the study period. The frequency with which each site was surveyed was subjective depending on crew size, annual streamflow variation, and regional fisheries' management emphasis.

For each snorkeling survey, fish counting protocols followed those described in Thurow (1994). In short, one or more snorkelers moved upstream or downstream, visually observing and recording fish in all available habitat. Maximum underwater visibility at each site was measured with a tape measure prior to the snorkel survey. The measurement of maximum underwater visibility was used to determine how many snorkelers were required to ensure that the distance between snorkelers did not exceed the visibility. Snorkel surveys were predominantly conducted in an upstream direction except on occasions (approximately 10% of the surveys) when water velocities were too high or when the water was too deep for the snorkelers to survey in that direction.

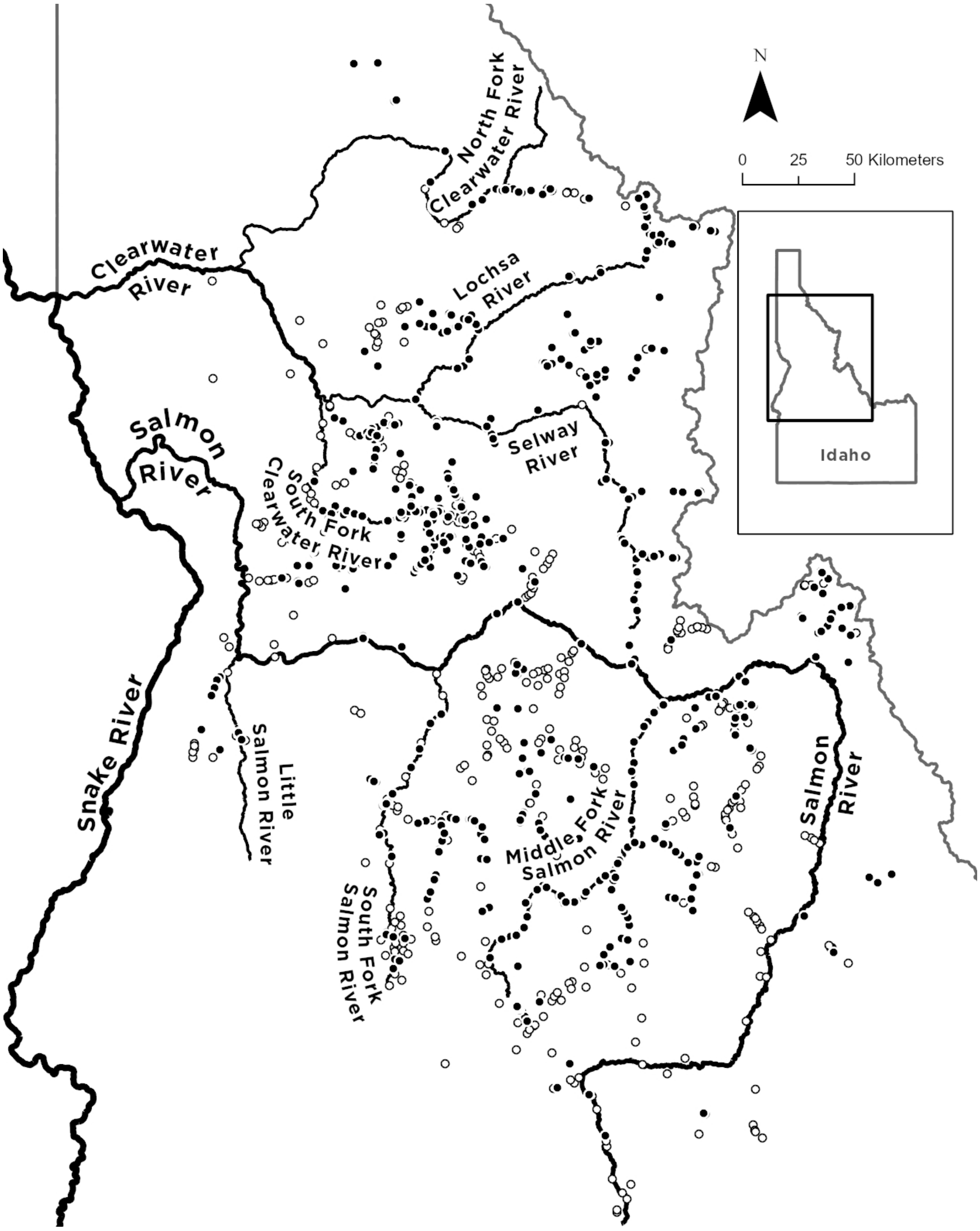

Fig. 1. Map of the Clearwater and Salmon River basins, Idaho, including major subbasins. Dots represent locations where stream snorkel surveys were conducted during 2010–2019 and where westslope cutthroat trout were either absent (white dots) or present (black dots).

Each snorkeler recorded all observed fish, identifying fish to species based on phenotypic characteristics and recording fish length to the nearest 25 mm (total length). Snorkelers did not record any observed fish <50 mm due to difficulty in identifying those fish to species. Fish density for each survey was standardized to fish per 100 m^2, but it should be recognized that densities of stream-dwelling salmonids as determined from snorkel surveys are inherently underestimated because detection probability is not 100% (Thurow and Schill 1996, Mullner et al. 1998, Korman et al. 2010). However, we assumed that the bias in abundance estimates was equivalent across all surveys.

Environmental Variables

Several site-level and landscape-level measurements were made either in the field at the time of snorkeling or later using a geographic information system (GIS) to characterize stream or watershed environmental conditions. During each field survey, instantaneous water temperature (°C) was recorded and included in our analyses because water temperature influences daytime concealment behavior in salmonids, which can directly alter their detection probability and thus their visual abundance (O'Neal 2007). Stream width (m) at the site was estimated by averaging wetted width measurements collected every 10 m throughout the reach; this measurement was included because stream size influences habitat complexity and biotic integrity (Fausch et al. 1984). The density of brook trout (fish/100 m^2) was included as an explanatory variable because this species consistently has a negative effect on westslope cutthroat trout occupancy and abundance (Dunham et al. 2002, Shepard 2004, Heckel et al. 2020).

Using a GIS, stream slope (%) at each site was estimated using NHDPlus (National Hydrography Dataset Plus) Version 2 (McKay et al. 2012); stream slope was included in our analyses to account for its influence on stream habitat characteristics (Bozek and Hubert 1992, Isaak and Hubert 2000, Wenger et al. 2011). However, sites where slope exceeded 15% were not included in the analysis ($n = 1$) because they rarely support salmonid populations (Isaak et al. 2018). NHDPlus was also used to estimate stream order. Similar to wetted width, stream order was included as a measure of stream size (Vannote et al. 1980) to account for its effect on fish assemblage (Fausch et al. 1984) and abundance (Eklöv et al. 1999).

Elevation (m) at each site was estimated using a digital elevation model in Arcmap 10.6 (Environmental Systems Research Institute, Redlands, CA) and was included in our analyses to account for the influence it often has on stream-dwelling salmonids (Jowett et al. 1996, Dunham and Rieman 1999, Rieman et al. 2006). Conductivity was estimated at each site using the GIS-based model constructed by Olson and Cormier (2019) and included due to its influence on stream productivity (McFadden and Cooper 1962, Scarnecchia and Bergersen 1987). Lithology was included because it influences stream morphology (Hack 1957, Minshall et al. 1985), substrate particle size (Connolly and Hall 1999), primary productivity (Minshall et al. 1985, Sanderson et al. 2009), and the availability of physical habitat (Baxter and Hauer 2000), all of which can influence salmonid communities (Lanka et al. 1987). Lithology at each of our snorkel sites was estimated using the Geologic Map of Idaho at a scale of 1:750,000 (Lewis et al. 2012) and was categorized as acid volcanic (rhyolite), basalt, sedimentary (including alluvium, sandstone, and quartzite), shale, and shield (metamorphic and plutonic rock; Suchet et al. 2003).

Road density was included because western native trout are usually less likely to occur and less abundant where there are roads near streams (Eaglin and Hubert 1993, Valdal and Quinn 2011). The 2019 Topologically Integrated Geographic Encoding and Referencing (TIGER) database (United States Census Bureau 2019) was used to map all the roads in Idaho, and road density was estimated by summing the total length of road within a 1.78-km radius (i.e., a 10-km^2 area) of each survey site. Slope, conductivity, elevation, lithology, and road density measurements were all taken from the downstream end of the snorkel survey site and were considered to be representative of the entire site, as it is unlikely that these factors varied greatly given the relatively short length of the sites ($\bar{x} = 95.7$ m, range 40.0 to 300.0).

Statistical Analysis

Evaluation of factors affecting westslope cutthroat trout occupancy and abundance was conducted using generalized linear models. Prior to any model construction, we excluded all data collected in the Potlatch River subbasin—although cutthroat trout are present in a few locations in the subbasin, they were never encountered in the snorkel surveys conducted in that subbasin. Multicollinearity among all continuous predictor variables was evaluated with pairwise Pearson correlation

TABLE 1. Correlation matrix for continuous predictor variables used to explain westslope cutthroat trout occupancy and abundance during snorkel surveys conducted in streams throughout the Clearwater and Salmon river basins of central Idaho.

	ELEV	SLOPE	COND	SO	TEMP	ROAD	WIDTH	BKT
Elevation (ELEV)	1.00							
Slope (SLOPE)	0.16	1.00						
Conductivity (COND)	0.26	0.04	1.00					
Stream order (SO)	−0.42	−0.62	−0.11	1.00				
Instantaneous water temperature (TEMP)	−0.46	−0.36	−0.16	0.55	1.00			
Road density (ROAD)	−0.03	−0.18	0.12	−0.01	0.02	1.00		
Mean wetted width (WIDTH)	−0.44	−0.38	−0.28	0.65	0.42	0.02	1.00	
Brook trout density (BKT)	0.13	−0.01	0.06	−0.15	0.05	0.11	−0.09	1.00

coefficients (r), but no comparisons exceeded $|r| > 0.70$ (Table 1), so we considered collinearity to be inconsequential (Dormann et al. 2013).

All variables were included in models as fixed effects. Fish density, instantaneous water temperature, and wetted width were averaged across all visits for survey sites with more than one visit during the study period. Averaging these variables across visits alleviated temporal autocorrelation (Sokal and Rohlf 1995) and pseudoreplication (Zar 1999) issues with the data. No such treatment was needed for conductivity, elevation, lithology, road density, stream slope, or stream order, as these values were all derived from GIS spatial layers and thus were static for each site. Instantaneous water temperature was assumed to potentially have a quadratic influence on westslope cutthroat trout distribution and abundance because at low temperatures, salmonid activity is diminished as concealment behavior is triggered (O'Neal 2007); but at high temperatures, activity for salmonids may also be reduced as the fish seek thermal refuge or cover (Thurow 1994). Elevation is often used as a surrogate for the water temperatures that stream-dwelling fish experience (e.g., Isaak et al. 2010, Eby et al. 2014), and as such, it was also assumed to potentially have a quadratic effect because salmonids such as westslope cutthroat trout have a thermal optimum and an upper thermal tolerance (Bear et al. 2007).

To relate westslope cutthroat trout occupancy to predictor variables, logistic regression was used with a dummy response variable of 1 if the fish species was present at a site and 0 if it was absent. To relate cutthroat trout abundance to predictor variables, a general linear model (GLM) was used. For both logistic and GLM models, we constructed the following models for comparison: a null (intercept-only) model; a full model with all 9 predictor variables included; and 9 reduced models, with each model systematically missing one of the predictor variables. Plausible models were considered to be those with Akaike's information criterion (AIC; Akaike 1973) scores within 2.00 of the best (i.e., most parsimonious) model. Akaike weights (w_i) were used to rank the relative plausibility of the candidate models (Burnham and Anderson 2004), whereas adjusted coefficient of determination (R^2; for GLMs) and adjusted pseudo-R^2 ($\tilde{R}^2$;

Nagelkerke 1991; for logistic regression) were used to assess the amount of variation explained by the models. The Hosmer and Lemeshow goodness-of-fit statistic (Hosmer et al. 2013) was used to check that the most plausible logistic regression models adequately fit the data, whereas diagnostic analyses of residuals were used for checking the adequacy of model fit for GLMs. Natural log transformations of the fish density data were needed to normalize the residuals of the GLM models. Scaling predictor variables that were continuous data—such that their means were equal to 0 and such that a 1 unit increase in each variable was equal to 1 standard deviation (Schroeder et al. 1986)—did not alter model fit, direction of relationships, or any conclusions regarding which variables were considered influential (see below), so scaling was omitted.

For both logistic and GLM models, model-averaged coefficient estimates and 95% confidence intervals (CIs) were derived only from the plausible models (i.e., those with AIC scores within 2.00 of the best model) and were calculated according to the formulas in Burnham and Anderson (1998). We considered model-averaged coefficient estimates with 95% CIs that did not overlap 0 to be influential in the occupancy and abundance models. For all statistical analyses, SAS statistical software (SAS Institute 2009) was used.

TABLE 2. Summary statistics of various site characteristics where westslope cutthroat trout were either absent or present during 2758 individual snorkeling surveys conducted from 2010 to 2019 in streams throughout the Clearwater and Salmon River basins of central Idaho.

	Absent				Present			
Variable	Mean	SD	Min	Max	Mean	SD	Min	Max
Length (m)	95.7	23.3	40.0	226.6	95.9	24.8	40.0	300.0
Wetted width (m)	9.9	8.5	0.8	59.6	11.5	8.7	1.4	64.6
Elevation (m)	1423	495	278	2413	1284	362	443	2431
Slope (%)	2.0	1.9	0.0	10.6	1.8	1.7	0.0	11.2
Conductivity (µS/cm)	78	40	30	327	62	23	30	189
Instantaneous water temperature (°C)	12.7	3.1	4.0	24.0	13.3	3.0	5.0	24.0
Road density (km/10 km^2)	7.7	8.2	0.0	53.2	7.0	8.3	0.0	50.8
Brook trout density (fish/100 m^2)	0.58	3.00	0.00	41.43	0.10	0.66	0.00	12.36

RESULTS

During 2010–2019, a total of 2758 snorkel surveys were conducted at 1000 sites in the Clearwater and Salmon river basins. Across both basins, conductivity at the survey sites averaged 69 µS/cm (range 30 to 327 µS/cm), elevation averaged 1345 m (range 278 to 2431 m), total kilometers of road in a 10-km^2 radius around survey sites averaged 7.3 km (range 0 to 53.2 km^2), stream slope averaged 1.9% (range 0.0% to 11.2%), water temperature at the time of the survey averaged 13.0 °C (range 4.0 °C to 24.0 °C), and mean wetted width averaged 10.8 m (range 0.8 to 64.6 m; Table 2). The most common lithology across all sites was shield (46%), followed by shale (21%), sedimentary (17%), basalt (9%), and acid volcanic (6%).

Westslope cutthroat trout were observed during 1277 (46%) surveys. They were present during at least one survey at 560 sites; among the 279 occupied sites that were surveyed

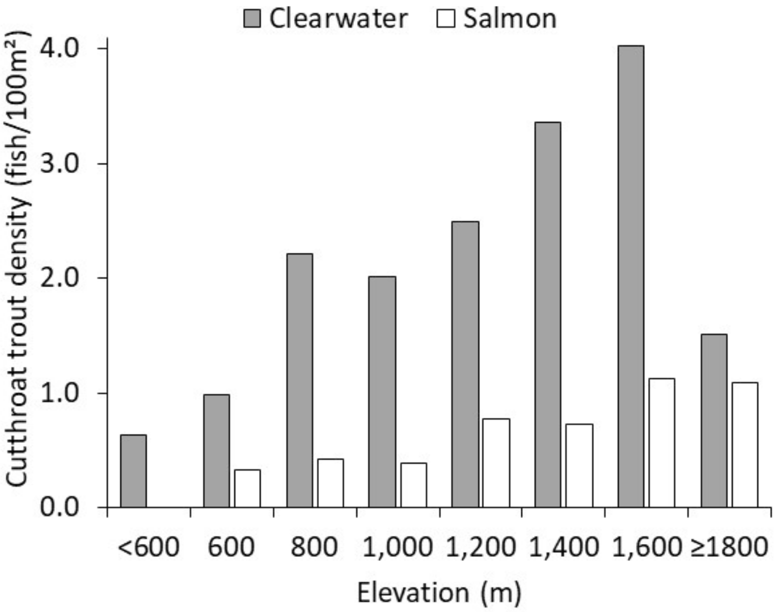

Fig. 2. Mean westslope cutthroat trout density (as determined from snorkel surveys) in relation to site elevation in streams throughout the Clearwater and Salmon river basins of central Idaho.

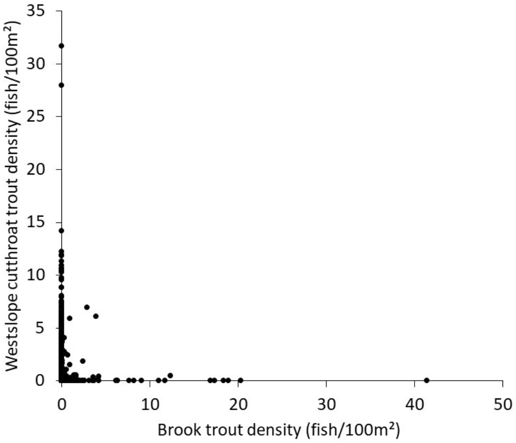

Fig. 3. Paired estimates of westslope cutthroat trout density and brook trout density (as determined from snorkel surveys) at stream sites throughout the Clearwater and Salmon river basins of central Idaho.

more than once, westslope cutthroat trout were more often intermittently present (198 sites) than always present (81 sites). However, even at sites where westslope cutthroat trout were observed intermittently, they were present 65% of the time on average. Brook trout were observed during 288 (10%) surveys and at 176 (18%) sites, and westslope cutthroat trout were more likely to be present during surveys in which brook trout were absent (48% of the time) than when brook trout were present (31%).

At the sites occupied by cutthroat trout, mean cutthroat trout density was 1.81 fish/100 m^2, but this varied from a low of 0.02 fish/100 m^2 to a high of 31.68 fish/100 m^2. Mean cutthroat trout density was higher in the Clearwater River basin (2.32 fish/100 m^2) than in the Salmon River basin (0.86 fish/100 m^2; Fig. 2). In comparison, brook trout mean density (at sites they occupied) was 1.71 fish/100 m^2, and this varied from a low of 0.01 fish/100 m^2 to a high of 41.43 fish/100 m^2. Mean density was >1.0 fish/100 m^2 for both species at only 3 sites (Fig. 3).

The most plausible logistic regression models (of those we considered) explaining the variation observed in westslope cutthroat trout occupancy included all predictor variables except either instantaneous water temperature, stream slope, stream order, road density, or stream width (Table 3). Based on model-averaged parameter estimates (from the most plausible models only) with 95% CIs that did not overlap 0, results indicated that westslope cutthroat trout were more likely to occupy sites with lower conductivity, containing fewer

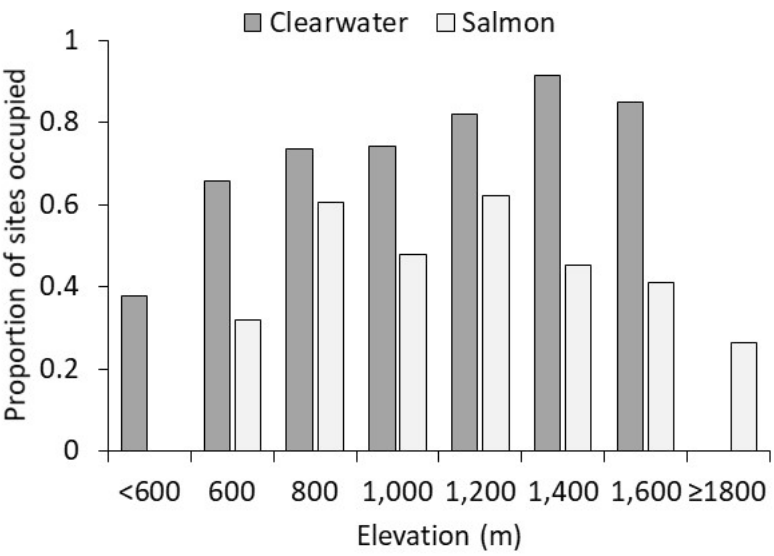

Fig. 4. Proportion of stream sites occupied by westslope cutthroat trout (as determined from snorkel surveys) in relation to site elevation throughout the Clearwater and Salmon river basins of central Idaho.

TABLE 3. Suite of logistic regression models explaining the variation we observed in westslope cutthroat trout occupancy in streams throughout the Clearwater and Salmon river basins of central Idaho. Plausible models were considered to be those with Akaike's information criterion (AIC) scores within 2.00 of the best model. Akaike weights (w_i) were used to rank the relative plausibility of the candidate models, and adjusted pseudo-coefficient of determination ($\tilde{R}^2$) was used to assess the amount of variation explained by the models.

Model	AIC	ΔAIC	w_i	$\tilde{R}^2$
Full model without temperature	1229.92	0.00	0.21	0.21
Full model without slope	1230.06	0.14	0.20	0.21
Full model without stream order	1230.19	0.27	0.19	0.21
Full model without road density	1230.26	0.34	0.18	0.21
Full model without stream width	1231.12	1.20	0.12	0.21
Full model	1232.00	2.08	0.08	0.21
Full model without lithology	1234.18	4.26	0.03	0.20
Full model without brook trout density	1240.38	10.46	<0.01	0.20
Full model without conductivity	1259.46	29.54	<0.01	0.18
Full model without elevation	1290.91	60.99	<0.01	0.14
Null (intercept-only) model	1373.86	143.94	<0.01	—

brook trout, and at an intermediate elevation (Table 4), with occupancy peaking at sites that were 800–1400 m in elevation and declining at lower or higher elevation (Fig. 4). Westslope cutthroat trout were also more likely to occupy sites with underlying lithologies of shield (59% occupancy rate) and acid volcanic (54%) rather than basalt (32%; Table 4).

The most plausible GLM models (of those we considered) explaining the variation observed in westslope cutthroat trout abundance included all predictor variables except either instantaneous water temperature, lithology, or stream slope (Table 5). Based on model-averaged parameter estimates (from the most plausible models only) with 95% CIs that did not overlap 0, results indicated that where westslope cutthroat trout were present, their density was higher in smaller streams with fewer brook trout and lower conductivity (Table 6). Cutthroat trout density peaked at sites that were 1400–1600 m in elevation and declined at lower and higher elevation (Fig. 2).

DISCUSSION

Westslope cutthroat trout remain widely distributed and abundant in central Idaho

Table 4. Model-averaged parameter estimates and 95% confidence intervals from logistic regression models predicting the distribution of westslope cutthroat trout in streams throughout the Clearwater and Salmon river basins of central Idaho. For lithology, shield was the reference condition.

			95% CI	
Parameter	Estimate	SE	Lower	Upper
Intercept	−1.64	1.04	−3.68	0.40
Brook trout density	−0.18	0.08	−0.34	−0.03
Conductivity	−0.014	0.003	−0.020	−0.009
Elevation	0.0053	0.0009	0.0035	0.0071
Elevation ^ 2	-2.2×10^{-6}	0.3×10^{-6}	-2.9×10^{-6}	-1.6×10^{-6}
Road density	-0.4×10^{-5}	0.7×10^{-5}	-1.7×10^{-5}	0.9×10^{-5}
Stream slope	0.006	0.034	−0.062	0.073
Instantaneous water temperature	0.01	0.11	−0.21	0.23
Instantaneous water temperature ^ 2	0.0007	0.0040	−0.0072	0.0086
Stream order	0.03	0.07	−0.10	0.16
Stream width	−0.009	0.009	−0.026	0.008
Lithology-basalt	−0.54	0.24	−1.00	−0.07
Lithology-acidic volcanic	0.51	0.22	0.08	0.94
Lithology-sedimentary	0.19	0.15	−0.10	0.47
Lithology-shale	−0.06	0.15	−0.36	0.24

Table 5. Suite of general linear regression models explaining the variation we observed in westslope cutthroat trout abundance in streams throughout the Clearwater and Salmon river basins of central Idaho. Plausible models were considered to be those with Akaike's information criterion (AIC) scores within 2.00 of the best model. Akaike weights (w_i) were used to rank the relative plausibility of the candidate models, and adjusted coefficient of determination (R^2) was used to assess the amount of variation explained by the models.

Model	AIC	ΔAIC	w_i	R^2
Full model without temperature	−70.18	0.00	0.37	0.36
Full model without lithology	−69.84	0.34	0.31	0.36
Full model without slope	−69.05	1.13	0.21	0.36
Full model	−67.54	2.64	0.10	0.36
Full model without ln(brook trout density)	−60.31	9.87	0.00	0.35
Full model without stream order	−51.95	18.23	0.00	0.34
Full model without elevation	−49.30	20.88	0.00	0.34
Full model without conductivity	−46.52	23.66	0.00	0.34
Full model without road density	−41.21	28.97	0.00	0.33
Full model without stream width	−6.24	63.94	0.00	0.29
Null (intercept-only) model	170.04	240.22	0.00	0.00

Table 6. Model-averaged parameter estimates and 95% confidence intervals from general linear regression models predicting the abundance of westslope cutthroat trout in streams throughout the Clearwater and Salmon river basins of central Idaho. For lithology, shield was the reference condition.

			95% CI	
Parameter	Estimate	SE	Lower	Upper
Intercept	0.19	0.38	−0.55	0.92
Brook trout density	−0.08	0.03	−0.14	−0.03
Conductivity	−0.0057	0.0012	−0.0080	−0.0035
Elevation	0.0010	0.0003	0.0003	0.0016
Elevation ^ 2	-0.05×10^{-5}	0.01×10^{-5}	-0.07×10^{-5}	-0.02×10^{-5}
Road density	-0.15×10^{-4}	0.03×10^{-4}	-0.20×10^{-4}	-0.09×10^{-4}
Stream slope	0.016	0.010	−0.004	0.036
Instantaneous water temperature	0.018	0.031	−0.042	0.078
Instantaneous water temperature ^ 2	−0.0009	0.0011	−0.0031	0.0012
Stream order	−0.10	0.02	−0.14	−0.06
Stream width	−0.028	0.003	−0.035	−0.022
Lithology-basalt	−0.18	0.12	−0.42	0.06
Lithology-acidic volcanic	0.06	0.10	−0.12	0.25
Lithology-sedimentary	0.04	0.06	−0.09	0.16
Lithology-shale	−0.08	0.06	−0.19	0.04

(Kennedy and Meyer 2015), especially in comparison to much of the rest of their native range (Shepard et al. 2005). Nevertheless, they are certainly not as widespread or as abundant as they were historically. While many biotic and abiotic factors have contributed to the historical decline of the species (Shepard et al. 2005), our results focus on several broad-scale environmental factors that appear to be influencing their contemporary distribution and abundance.

Our results suggest that in central Idaho, westslope cutthroat trout are more likely to be encountered in stream reaches underlain by shield and acid volcanic lithologies than in reaches with basalt lithology. Lithology influences stream morphology (Minshall et al. 1985), substrate particle size (Connolly and Hall 1999), the productivity of the waterbody (Minshall et al. 1985, Sanderson et al. 2009), and the availability of physical habitat (e.g., overhead cover, aquatic vegetation, and instream cover; Baxter and Hauer 2000), all of which can influence salmonid communities (Lanka et al. 1987). For westslope cutthroat trout, the lower probability of occurrence in stream reaches with basalt lithology could be due to the fact that basaltic landscapes tend to produce less complex drainage patterns and more riverine migration barriers than landscapes formed on softer underlying rock do (Guy et al. 2008), and both ecosystem complexity and connectivity have been shown to be important for westslope cutthroat trout populations (Pierce et al. 2014). Additionally, basalt lithology typically produces larger stream substrate particle sizes (Kaufmann and Hughes 2006, Kaufmann et al. 2009), and westslope cutthroat trout tend to spawn in areas with relatively small substrates (Magee et al. 1996) compared to other sympatric native salmonids in central Idaho (e.g., Riebe et al. 2014, Guzevich and Thurow 2017); thus, westslope cutthroat trout may have more difficulty successfully spawning in stream reaches with basalt lithology than in reaches with shield and acid volcanic lithologies. The fact that lithology was more influential for fish distribution than abundance suggests that lithology may influence broader habitat features that affect the ability of westslope cutthroat trout to fulfill a component of their life history, such as spawning or overwinter survival—more so than characteristics that affect fish abundance, such as microhabitat suitability. However, surprisingly little research has been conducted on the direct effects of lithology on fish distribution or abundance (but see Nelson et al. 1992); thus, further research is needed to establish better causative links between lithology and fish ecology.

The negative influence that brook trout abundance had on westslope cutthroat trout distribution and abundance in our study was not surprising, considering that such a pattern has been observed for many subspecies of cutthroat trout (reviewed *in* Dunham et al. 2002). A number of potential explanations exist for this relationship, but the most prevalent is competition (Dunham et al. 2002, Peterson et al. 2004). Competition from brook trout has often restricted cutthroat trout populations to small, steeper headwater streams where they are more protected from brook trout invasion (Shepard et al. 2005), but brook trout were present at only 83 (18%) of the 460 sites where westslope cutthroat trout were absent, indicating that in central Idaho, brook trout distribution is too limited to be a primary factor influencing contemporary westslope cutthroat trout occupancy. However, due to the relatively intact nature of riverscapes in the Salmon and Clearwater river basins (e.g., Schoby and Keeley 2011, Feeken et al. 2019), continued expansion of brook trout in central Idaho is likely to occur (e.g., Adams et al. 2002, Benjamin et al. 2007) without active suppression in streams where they currently exist.

Given the thermal requirements of westslope cutthroat trout (Bear et al. 2007, Macnaughton et al. 2021), water temperature clearly influences their distribution and abundance (e.g., Shepard 2004). While water temperature was included as a predictor variable in our model, it was based on instantaneous measurements at the time of each snorkel survey and therefore obviously did not represent the thermal regime that fish experienced over the course of each year. Rather, water temperature was included to account for its potential influence on fish behavior and thus fish detectability (O'Neal 2007), but it was not useful in explaining the variation we observed in westslope cutthroat trout occupancy or abundance. In contrast, both the occupancy and the abundance of westslope cutthroat trout were related to elevation in a nonlinear, dome-shaped manner. Elevation was included as a surrogate for stream water temperature (Isaak et al. 2010, Eby et al. 2014), which has previously been shown to be related to trout abundance in a dome-shaped manner (Isaak and Hubert 2004, Meyer et al. 2010). We speculate that in central Idaho there is a range of stream elevations (perhaps from 800 to 1600 m) that currently provides an ideal thermal regime for westslope cutthroat trout, though their distribution in the future will likely shift to higher elevations as stream temperatures continue to warm due to climate change (Isaak et al. 2012).

Road density apparently had no effect on westslope cutthroat trout distribution, but where this species was present, higher road density reduced its abundance, which concurs with previous studies reporting similar relationships (e.g., Muhlfeld et al. 2009, Valdal and Quinn 2011). Roads can negatively affect salmonid populations through sedimentation and habitat alteration (Dunham and Rieman 1999), as well as by creating barriers to fish movement (Simpkins and Mistak 2010). The influence of roads on fish occupancy and abundance can be difficult to ascertain using GIS data because the database used to map roads in Idaho has a lag on the inclusion of recently closed or decommissioned roads, and because closed and decommissioned roads, though not actively in use, can negatively affect salmonid communities through legacy effects of increased stream sedimentation—at least until vegetative regrowth can stabilize the soil (McCaffery et al. 2007).

Conductivity was negatively associated with both the distribution and abundance of westslope cutthroat trout, though conductivity is normally associated with the fertility of a water body (Rawson 1951, Welch 1952) and has been previously shown to be positively associated with trout abundance in streams (e.g., McFadden and Cooper 1962, Scarnecchia and Bergersen 1987). In the present study, conductivity at nearly all of the sites was <100 µS/cm, which is considered low for flowing waters (Griffith 2014); thus, the negative effect we observed for the limited range of low conductivities in central Idaho streams may have been more correlative than causative in nature. For example, conductivity is generally lower in smaller headwater streams (Wilcox et al. 1956) where we observed westslope cutthroat trout densities to be higher. Moreover, conductivity is correlated to other important cations and anions (e.g., alkalinity and water hardness) that can influence fish populations in a number of ways (Scarnecchia and Bergersen 1987).

In fact, we fully recognize that for many of the associations reported herein, correlation between predictor variables and the distribution and abundance of westslope cutthroat trout does not necessarily imply a causative relationship; this is a well-recognized weakness of any nonmanipulative ecological investigation (Hilborn 2016). In addition, our analyses included only some of the environmental characteristics that may influence the distribution and density of westslope cutthroat trout in central Idaho or elsewhere; thus, our models explained only a small amount of the overall variation we observed in westslope cutthroat trout occupancy and abundance. Nevertheless, assuming the general patterns that we observed at least suggest causative links, some findings relevant to the management of westslope cutthroat trout emerge. First, where westslope cutthroat trout were present, road density negatively influenced their abundance, suggesting that restoration of stream habitat impaired by roads could improve the status of the species in central Idaho (Pierce et al. 2013). Second, while management actions to improve degraded stream habitat usually target areas that are most degraded or where funding can be secured, it should also be recognized that in central Idaho improving habitat in stream reaches underlain with shield and acid volcanic lithology may provide the most benefit to westslope cutthroat trout. Third, efforts to control or eradicate brook trout populations would likely improve the security of westslope cutthroat trout populations in central Idaho. Lastly, while protecting central Idaho streams at intermediate elevation may currently provide the most benefit for westslope cutthroat trout, recognition of the future importance of upstream habitat as the climate continues to warm (Isaak et al. 2015) is critical for the long-term persistence of westslope cutthroat trout in central Idaho.

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