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ARTICLE

Distribution and Abundance of Westslope Cutthroat Trout in Relation to Habitat Characteristics at Multiple Spatial Scales

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Abstract
The distribution and relative abundance of Westslope Cutthroat Trout (WCT) *Oncorhynchus clarkii lewisi* in relation to habitat characteristics remain unknown across large portions of the species' range. The goals of this research were to provide a foundational understanding of WCT distribution and relative abundance related to habitat characteristics in tributaries of the St. Maries River, Idaho—a highly altered watershed. The basin drains an area of approximately 1,863 km^2 and has a longitudinal elevation difference of about 207 m. Backpack electrofishing and habitat assessments were conducted at 68 reaches in 35 different tributaries of the St. Maries River in 2017 and 2018. Habitat was measured at small (reach-level) and large (watershed-level) scales. A total of 652 WCT was sampled from 52 of 68 total reaches. Habitat characteristics varied by age-class, but most WCT were estimated to be age 0 and age 1. Logistic regression models indicated that the presence of age-0 WCT was positively related to stream gradient and elevation, but negatively related to water temperature, road density, fine substrate, stream depth, and the presence of Brook Trout (BKT) *Salvelinus fontinalis*. The relative abundance of age-0 WCT was positively associated with road density and inversely related to wetted width, canopy cover, and elevation. The presence of age-1 and older (age-1+) WCT was positively related to gradient, canopy cover, and elevation, but negatively associated with road density, temperature, stream depth, and the presence of BKT. Relative abundance of age-1+ WCT was positively associated with gradient, large substrate, canopy cover, and road density. Conversely, the relative abundance of age-1+ WCT was inversely related to wetted width and elevation. This research indicates that WCT populations can persist in response to altered landscapes when suitable habitat exists. However, unmitigated threats, such as nonnative species competition (e.g., BKT), hybridization with Rainbow Trout *O. mykiss*, habitat loss, and habitat fragmentation, pose persistent complications to WCT abundance in locations where populations appear robust but their actual abundance is unknown.

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Westslope Cutthroat Trout (WCT) *Oncorhynchus clarkii lewisi* occupy coldwater systems varying from high-elevation, low-productivity headwater streams to high-productivity, large river systems (Rieman and Apperson 1989; Shepard et al. 2005; Sloat et al. 2005). Westslope Cutthroat Trout is a species of high social importance due to its popularity among anglers, a species of high ecological importance due to its role in aquatic ecosystems, and a species of special concern in most of western North America (Fredericks et al. 1997; Shepard et al. 2005). Historically, WCT were one of the most widely distributed of all Cutthroat Trout subspecies (Allendorf and Leary 1988; Behnke 1992; Young et al. 2018). Their range included portions of the Fraser and South Saskatchewan River basins in Canada; the Missouri and Columbia River basins in Montana, Idaho, and Washington; the John Day River basin in Oregon; and the Methow River and Lake Chelan basins in Washington (Shepard et al. 2005; Young et al. 2018). In Idaho, WCT occupied nearly all waters in the central and northern parts of the state (Rieman and Apperson 1989). However, a variety of factors has limited WCT distribution and abundance. Introduction of nonnative fishes, hybridization, overharvest, and habitat loss have contributed to a reduction of WCT distribution throughout Idaho and the western United States (Allendorf and Leary 1988; Rieman and Apperson 1989; Behnke 1992; Schmetterling 2001; Shepard et al. 2005; Muhlfeld et al. 2009b). To aid population recovery, managers require information on where WCT are located and where they are absent to understand factors limiting their distribution and abundance. In addition, managers are tasked with prioritizing where restoration projects will occur based on large- and small-scale habitat characteristics.

The historically broad distribution of WCT can be linked to their highly migratory behavior, with individual fish moving more than 100 km in a single year (Bjornn and Mallet 1964; Schoby and Keeley 2011). All life history strategies contain mobile life stages, whether it is a resident fish moving between summer and winter habitat within a single stream, a fluvial migrant moving throughout a river network, or an adfluvial fish migrating from a lake to a stream. As such, habitat heterogeneity is important for successful production. Mortality and competition for resources are high early in life (Knight et al. 1999; McGrath et al. 2008). Habitat thought to be important for subadult and adult WCT may have limited suitability for age-0 WCT (Behnke 1992). To make informed management decisions about WCT populations, it is important to gain an understanding of habitat used by all age-classes of WCT. Therefore, understanding the distribution of WCT at different life stages and how it relates to habitat characteristics is important for fisheries and habitat managers focused on protecting and restoring aquatic habitats.

Limited fishery research and monitoring have occurred in the St. Maries River basin in northern Idaho. The Idaho Department of Fish and Game (IDFG) conducted creel surveys and distribution studies on WCT throughout the watershed in the 1980s (Apperson et al. 1988; Horton and Mahan 1988; Rieman and Apperson 1989). Authors of those studies found that WCT were distributed throughout the watershed and were often the dominant salmonid in tributaries, and they hypothesized that multiple life history strategies existed (i.e., resident, fluvial, and adfluvial) in the watershed (Apperson et al. 1988; Horton and Mahan 1988). Although WCT were historically distributed throughout the watershed, several factors have been hypothesized as responsible for the currently poor fishery that only provides angling opportunities in the spring; factors include nonnative salmonids (i.e., Brook Trout [BKT] *Salvelinus fontinalis* and Rainbow Trout [RBT] *O. mykiss*), high water temperatures, and poor habitat. Over a century of intensive timber harvest, agricultural use, mining, road building, and piscicide treatments (i.e., Squoxin; Goodnight and Mauser 1974) have occurred on the main stem of the St. Maries River (Apperson et al. 1988). Coupled with fishery investigations conducted in the 1980s, cursory habitat assessments were conducted to create a baseline index of habitat conditions in tributaries to the St. Maries River. Some land use practices were deemed deleterious, particularly intensive logging, livestock grazing, and roads (Apperson et al. 1988). However, improved forest and water management practices have been implemented over the past two decades (IDL 2018).

In the neighboring Coeur d'Alene River watershed, habitat restoration projects were conducted to mitigate land use practices (i.e., logging and roads) that were implicated as limitations to the WCT population in addition to angler noncompliance with regulations (Lewynsky 1986; Hunt and Bjornn 1995; Dunnigan et al. 1998; IDEQ 2001; DuPont et al. 2004). To mediate the effects of land use practices, efforts were made to rectify the declining WCT population by implementing habitat restoration projects and establishing land easements in the Coeur d'Alene River basin (DuPont et al. 2004). The St. Maries River watershed is a highly altered system, but changes in land and water use practices have occurred since the original population and habitat evaluations were conducted by IDFG. Managers are interested in conducting habitat restoration and land easement projects in the St. Maries River basin similar to those that were conducted in the Coeur d'Alene River basin. However, before restoration projects and easements can be planned, a better understanding of where different life stages of WCT are distributed throughout the St. Maries River basin and how that distribution relates to habitat is needed. Knowledge of WCT distribution and how it relates to habitat characteristics can be used for guiding fishery and habitat management actions throughout the watershed. The objectives of this study were to provide an understanding of current WCT distribution and relative abundance in tributaries of the St. Maries River and to evaluate how the distribution and relative abundance of WCT in tributaries of the St. Maries River were related to habitat characteristics at small (i.e., reach-level) and large (i.e., watershed-level) scales. The desired outcomes of this research are to provide managers with details about where WCT are present and absent and to provide details about what habitat characteristics are related to the current distribution of WCT in the St. Maries River basin.

METHODS

Study area.— The St. Maries River is a 71-km-long, sixth-order tributary of the St. Joe River located in the panhandle of Idaho (Figure 1). The St. Maries River joins the St. Joe River approximately 24 km upstream from Coeur d'Alene Lake. Water levels in Coeur d'Alene Lake are influenced by Post Falls Dam located on the Spokane River, which is the sole outflow of Coeur d'Alene Lake. The construction of Post Falls Dam was completed in the early 20th century, and the dam is owned and operated by Avista Corporation. Due to the operation of Post Falls Dam, the water level of Coeur d'Alene Lake was raised by approximately 2.5 m (DuPont et al. 2004; Walrath et al. 2015). From late spring to autumn, the lower portion of the St. Maries River (about 15 km) is inundated by the elevated water level in Coeur d'Alene Lake (Parametrix 2006). The St. Maries River basin drains an area of approximately 1,863 km^2, extends into four counties (Benewah, Clearwater, Latah, and Shoshone), and is characterized by alluvial sedimentary deposits resulting from the formation of ancient Lake Clarkia (Ladderud et al. 2015). Elevations in the basin vary from about 670 to 1,600 m, and the main-stem St. Maries River has a longitudinal elevation difference of 207 m.

Historical and current land use practices in the basin (e.g., railroad construction, timber harvest, mining, and agriculture) have altered stream channels, removed riparian vegetation, increased sediment input, and polluted streams that WCT occupied. Land ownership in the St. Maries River watershed is mixed between private, state, federal, and tribal parcels. Land managers in the basin consist of the U.S. Forest Service, state of Idaho, IDFG, Coeur d'Alene Tribe, U.S. Bureau of Land Management, Potlatch Corporation, Stimson Lumber, and Bennett Lumber. Most drainages in the St. Maries River basin have had timber harvested over much of their area during the 20th century, and logging continues to occur throughout the watershed. Logging companies originally used waterways as a log transport system. Splash dams created migration barriers, and log drives caused structural damage to waterways; river channels became straighter and less complex as log jams, woody debris, large boulders, and sharp channel bends were removed (Schott 1950; Strong and Webb 1970; IDEQ 2003; DuPont et al. 2004). Cattle grazing in the St. Maries River basin occurs in the river valley and low-gradient sections of tributary streams. Cattle grazing influences bank stability and riparian growth and can affect fish populations (Peterson et al. 2010). Cattle grazing occurs on Emerald, Carpenter, Santa, Charlie, and Gold Center creeks and the West Fork, Middle Fork, and main stem of the St. Maries River (Figure 1). As a result of historical and current land use practices in the St. Maries River basin, water quality in the St. Maries River, its forks, and the majority of its tributary streams was considered impaired (Clean Water Act section 303[d] listed) based on sediment, temperature, habitat alteration, nutrients, bacteria, and dissolved oxygen (IDEQ 2003). Relatively few site-specific actions have occurred to improve water quality, and none of the actions have been part of an integrated program to improve full beneficial use throughout the basin.

Field sampling.— Fishes and physical habitat characteristics were sampled from tributaries in the St. Maries River basin (Figure 1). Habitat characteristics were examined at large and small scales to investigate how large-scale (e.g., elevation) and small-scale (e.g., instream cover) factors were related to the distribution of fishes (Quist et al. 2005). A stratified sampling design was used to select the locations of sampling reaches. Streams that were within the 19 drainages with perennial flow that connected to the St. Maries River were considered tributaries that could be occupied by WCT. These tributaries of the St. Maries River were considered strata, and sampling reaches were randomly selected in each stratum. Reaches varied in length based on the average wetted stream width (Lyons 1992; Simonson 1995); a minimum reach length was not used. Reaches were selected using a random point generator in ArcMap version 10.5.1 (Esri, Redlands, California). Reaches were delineated into macrohabitats (i.e., pools, riffles, runs, off-channel units) and began and ended at the nearest macrohabitat transition (Quist et al. 2003; Sindt et al. 2012). In 2017, sampling was conducted from May to August on 44 reaches in 33 tributaries. In 2018, sampling was conducted from June to August on 24 reaches in 20 tributaries.

Fish were sampled in each reach using single-pass pulsed-DC electrofishing (Model LR-24 backpack electrofisher; Smith-Root, Inc., Vancouver, Washington; Simonson and Lyons 1995). For all backpack electrofishing, two netters each used a 6.4-mm-mesh dip net to collect fishes. Seconds of electrofishing were recorded for each macrohabitat and were used to calculate CPUE (fish/min of electrofishing). All fish were identified to species

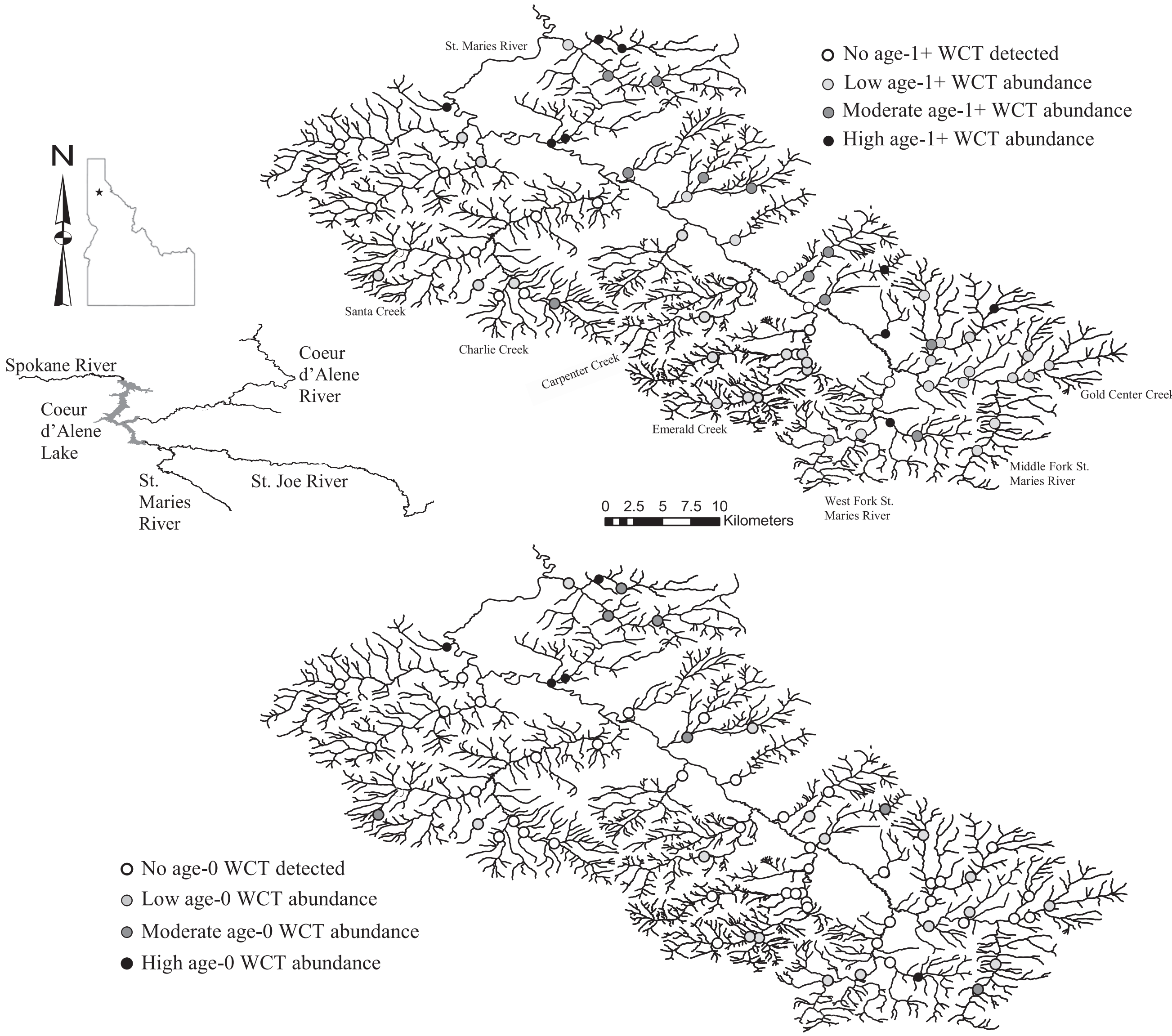

FIGURE 1. Detection and relative abundances of age-0 (bottom panel) and age-1 and older (age-1+; top panel) Westslope Cutthroat Trout (WCT) in 68 stream reaches of the St. Maries River basin, Idaho. The mean CPUE (fish/min of electrofishing) standardized to 100 m for age-0 WCT was 0.24 fish/min (SD = 0.65; range = 0.00–3.96 fish/min). For age-0 WCT, low abundance was CPUE ≤ 0.25 fish/min, moderate abundance was 0.25 fish/min < CPUE ≤ 1.00 fish/min, and high abundance was CPUE >1.00 fish/min. The mean CPUE standardized to 100 m for age-1+ WCT was 0.56 fish/min (SD = 1.09; range = 0.00–6.56 fish/min). For age-1+ WCT, low abundance was CPUE ≤ 0.5 fish/min, moderate abundance was 0.50 fish/min < CPUE ≤ 1.00 fish/min, and high abundance was CPUE >1.00 fish/min.

and measured for TL. Up to 10 WCT per 10-mm length-group were sacrificed, sagittal otoliths were extracted, and age was estimated. Sagittal otoliths were mounted (sulcus acusticus side facing up) onto a microscope slide using Crystalbond 509-3 (Aremco, Valley Vintage, New York) and were examined using transmitted light under a dissecting microscope. Annuli were enumerated by one reader that possessed previous experience in aging hard structures. A subsample of fish was cross-validated by a second reader, and age estimates between readers were within >95% concordance. Disagreement between readers occurred on where the last annulus was located near the edge. An age–length key was then used to infer the ages of all WCT that were caught in tributaries.

Large-scale habitat characteristics (i.e., gradient, elevation, road density, and land use) were estimated at the basin level using ArcMap and Terrain Navigator Pro version 9.1 (MyTopo, Billings, Montana; Meyer et al. 2003; Sindt et al. 2012). Elevation and gradient were estimated from U.S. Geological Survey topographic maps (1:24,000 scale) using Terrain Navigator Pro. The distance (m) between the two contour lines that bounded the sampling reach was traced. Gradient was calculated as the elevational increment (12.192 m) between those two contour lines divided by the traced distance (Meyer et al. 2003). Road density was estimated using a raster layer in ArcMap and calculated as kilometers of roads per square kilometer surrounding a reach (km/km^2; Valdal and Quinn 2011). Dominant land use was estimated in the field and categorized as timberland (land that had recently been [e.g., lack of new tree growth, new access roads, drag lines] or was currently being clear-cut for timber); mineral (land that was managed and used for mineral extraction); private property (residential homes or summer camps); cattle-grazed (land where cattle grazing was occurring); forest (land that did not have noticeable effects from timber harvest); and thinned forest (forests that were not clear-cut, but had some timber harvested).

Small-scale habitat characteristics were quantified at the reach level for each macrohabitat. Water temperature (°C) and conductivity (μS/cm) measurements were taken prior to electrofishing using a handheld probe (DiST; Hanna Instruments, Woonsocket, Rhode Island). Although water temperature was taken prior to sampling, NorWeST stream temperature data were used in data analysis (Chandler et al. 2016). NorWeST stream temperature maps were developed at 1-km resolution using spatial statistical models based on observed temperature points throughout the watershed from August daily stream temperature summaries for 1993–2011. Coordinates of sampled sites in the St. Maries River were overlain onto the NorWeST map, and stream temperature was derived from those points. Total length of each macrohabitat was measured along the thalweg. If the macrohabitat length was less than 30 m, two transects at 25% and 75% of the macrohabitat length were established (Quist et al. 2003). If the macrohabitat length was greater than 30 m, transects at 25, 50, and 75% of the macrohabitat length were established. We did not establish a minimum length for macrohabitat units. At each transect, wetted stream width was measured. Depth, current velocity, and dominant substrate particle size were measured at four equidistant points and at the midpoint of each transect (20, 40, 50, 60, and 80%; Platts et al. 1983). Benthic current velocity and mean current velocity were taken using a portable water velocity meter (Marsh-McBirney Model 2000 Portable Flowmeter; Hach Company, Loveland, Colorado). Benthic current velocity was taken 0.03 m above the substrate. Mean current velocity was measured at 60% of the depth when depths were less than 0.75 m or at 20% and 80% of the depth when depths were greater than 0.75 m (Buchanan and Somers 1969). Substrate type was visually assessed and classified as wood, clay (<0.004 mm), silt (0.004–0.063 mm), sand (0.064–2.000 mm), gravel (2–16 mm), coarse gravel (16–64 mm), cobble (64–256 mm), boulder (>256 mm), or bedrock (Cummins 1962; Sindt et al. 2012). The percentage of substrate embeddedness was visually estimated (i.e., 25, 50, 75, and 100%; Platts et al. 1983) for coarse gravel, cobble, and boulder substrate types (Eaglin and Hubert 1993). Canopy cover (%) was estimated at each transect using a concave densiometer while standing at the stream margin and facing each bank and facing upstream and downstream at the midpoint of the channel (Quist et al. 2003). Bank characteristics were recorded for both banks at each transect. Bank characteristics were classified at each transect by the presence of woody vegetation, nonwoody vegetation, roots, boulders, rip-rap, eroding ground, and bare ground. All instream cover at least 0.3 m in length and in water at least 0.2 m deep was quantified by taking one length measurement, three width measurements, and three depth measurements. Instream cover was classified as undercut bank, overhanging vegetation, branch complex, log complex, rootwad, boulder, rip-rap, or aquatic vegetation (Quist et al. 2003).

For each macrohabitat, area was estimated using the thalweg length multiplied by the mean wetted width of all transects. Means were calculated for depth, current velocity, wetted width, substrate embeddedness, and canopy cover for each macrohabitat unit. Additionally, the mean coefficient of variation (CV) in depth, width, current velocity, and canopy cover was calculated ($CV = 100 \times [SD/mean]$) as an estimate of habitat heterogeneity. The proportions of each substrate type, bank characteristics, and instream cover type were calculated for each macrohabitat unit. All habitat characteristics except instream cover were then averaged across macrohabitat units in a reach. Averaged values were weighted by the proportion of the total stream reach area that was represented by the macrohabitat. Weighted values were summed to quantify habitat characteristics for the entire stream reach. Instream cover type was quantified as the proportion of reach area. Additional variables were created by combining two or more habitat variables (e.g., proportion of nonwoody cover, proportion of large substrate).

Data analysis.— Relative abundance and distribution related to habitat characteristics for different life stages were investigated by separating WCT into two groups: age-0 fish and age-1 and older (age-1+) fish (McGrath et al. 2008; Meyer et al. 2010). The TL of age-0 fish (≤61 mm) was used to discriminate age-0 from age-1+ WCT. Habitat relationships with WCT presence–absence and relative abundance data were investigated using a hurdle regression modeling approach (Welsh et al. 1996; Martin et al. 2005; Wenger and Freeman 2008; Smith et al. 2016).

Hurdle regression models consisted of two submodels. One submodel used logistic regression under a binomial distribution to predict the presence of WCT in relation to habitat characteristics across all reaches. The other submodel evaluated the relative abundance of WCT in relation to habitat characteristics under a negative binomial distribution for reaches where at least one WCT was present. The relative abundance of WCT was standardized to 100 m of linear stream length (Meyer et al. 2006). Presence–absence and relative abundance of age-0 WCT and age-1+ WCT were modeled separately to investigate whether habitat characteristics varied between life stages. Furthermore, habitat characteristics related to each age-group were summarized at both small (reach-level) and large (watershed-level) scales.

Hurdle models were constructed using the "glm" (R Core Team 2018) and "glm.nb" (Venables and Ripley 2002) functions in R statistical software. Models were assessed for overdispersion by visually examining diagnostic plots and estimating the dispersion parameter ($\hat{c}$). The dispersion parameter was calculated by dividing Pearson's residual deviance by the residual degrees of freedom. Models were considered overdispersed when $\hat{c}$ was greater than 1.0 (Burnham and Andersen 2002). Overdispersed models had an additional parameter added to adjust for the estimation of dispersion (Lawless 1987; Venables and Ripley 2002). McFadden's pseudo-R^2 was used to assess model fit (McFadden 1974; Hosmer and Lemeshow 1989). McFadden's pseudo-R^2 was calculated as 1 minus the difference in the log likelihood of a model with an intercept and explanatory variables and the log likelihood of an intercept-only model (McFadden 1974). McFadden's pseudo-R^2 values vary from 0.0 to 1.0, with values greater than 0.20 indicating good fit (Hox 2010); however, models with pseudo-R^2 values as low as 0.10 have also been shown to exhibit good model fit (Hosmer and Lemeshow 1989).

To avoid multicollinearity, Spearman's rank correlation coefficient (r_s) was used to further investigate relationships among habitat characteristics. Variables with r_s values greater than or equal to $|0.70|$ were considered highly correlated. When two variables were highly correlated, the most ecologically relevant and interpretable variable was retained for consideration in candidate models (Meyer et al. 2010; Sindt et al. 2012; Smith et al. 2016). For example, the sum of all instream cover in a reach was highly correlated with the sum of all nonwoody cover and the sum of all woody cover ($r_s \geq 0.70$). The sum of all instream cover was deemed the most ecologically important variable and was retained in candidate models; the other variables were removed. Habitat variables that were used to develop hurdle models included 4 large-scale variables and 16 small-scale variables (Table 1). The relationships between WCT presence–absence and relative abundance related to large-scale habitat characteristics were assessed with 14 candidate models that were created a priori for each submodel. Small-scale habitat characteristics were assessed with 39 candidate models that were created a priori for each submodel. Competing multiple regression models were evaluated using an information theoretic approach to rank submodels using Akaike's information criterion adjusted for small sample size (AIC_c; Burnham and Anderson 2002). The top model was the model that had the lowest AIC_c value. Models that had an AIC_c score within 2.0 AIC_c units of the top model were also considered top models and retained for interpretation (Burnham and Anderson 2002). Additionally, the sum of Akaike weights (w) for all models in which a variable was present was used to assess the relative importance of independent variables (Burnham and Anderson 2002; Quist et al. 2005; Meyer and High 2011).

RESULTS

In tributaries of the St. Maries River basin, 5,690 individual fish representing 15 different species were sampled from 35 different tributaries. Westslope Cutthroat Trout occurred at most sites, with a total of 652 WCT sampled from 52 of 68 reaches (76%). Ages of WCT varied from 0 to 5 years, and the most frequent ages were 0 and 1 year (Figure 2). The average CPUE for age-0 WCT was 0.24 fish/min (SD = 0.65), and catch rates varied from 0.00 to 3.96 fish/min. The average CPUE for age-1+ WCT was 0.56 fish/min (SD = 1.09), and catch rates varied from 0.00 to 6.56 fish/min. Total length of WCT varied from 23 to 406 mm, and the average TL was 110 mm (SD = 57; Figure 3). Age-0 WCT occurred at 28 reaches (41%) and were sampled as early as June 7 in 2017 and June 19 in 2018.

Reach length varied from 40 to 311 m, and the average reach length was 114 m (SD = 53). Habitat characteristics varied among sites where WCT were present and where they were absent (Table 2). The relationships between age-0 WCT and habitat characteristics were investigated at watershed- and reach-level scales. Logistic regression models evaluating large-scale habitat characteristics indicated that the presence of age-0 WCT was positively related to gradient and elevation but negatively related to road density (Table 3). The second component of the hurdle regression models (i.e., relative abundance) indicated that the relative abundance of age-0 WCT was positively related to road density, but negatively related to elevation. At the reach level, mean depth, fine substrate, water temperature, and the presence of BKT were negatively related to the presence of age-0 WCT. Furthermore, catch rates of age-0 WCT were negatively related to wetted width and canopy cover.

TABLE 1. Large- and small-scale habitat variables for 68 stream reaches in 35 different tributaries of the St. Maries River, Idaho. Variables were used as independent variables in candidate models (min = minimum; max = maximum).

Variable	Description	Mean	SD	Min	Max
	Large-scale variables				
Elevation	Elevation (m) of the upstream end of the stream reach	891.10	94.34	671.00	1,302.00
Gradient	Reach length divided by the elevation change (%)	1.75	1.38	0.14	7.30
Road density	Kilometers of roads per square kilometer (km/km^2)	1.49	0.58	0.42	2.51
Land use	Cattle grazing, timberland, forest, thinned forest, private property, mineral extraction				
	Small-scale variables				
Runs	Proportion of reach area as run	0.30	0.17	0.00	0.73
Pool : riffle	Mean pool-to-riffle ratio	1.73	2.79	0.00	12.65
Depth	Mean water depth (m)	0.26	0.13	0.06	0.62
Width	Mean wetted width (m)	3.33	1.67	1.04	8.68
Current velocity	Mean current velocity (m/s)	0.26	0.17	0.02	0.89
CV.Velocity	Mean coefficient of variation (CV) of current velocity	28.84	14.16	3.47	70.71
Canopy cover	Mean canopy cover (%)	65.41	19.56	17.18	98.10
Temperature	NorWeST mean August stream temperature (°C)	13.62	1.40	10.24	17.07
Substrate_{Fine}	Proportion of substrate that is silt or sand	0.22	0.24	0.00	1.00
$\text{Substrate}_{Gravel}$	Proportion of substrate that is gravel or coarse gravel	0.66	0.40	0.02	1.00
Substrate_{Large}	Proportion of substrate that is cobble or boulder	0.90	0.40	0.00	1.00
Embeddedness	Proportion of substrate that is covered in silt or sand	0.31	0.17	0.00	0.73
Total cover area	Mean sum of the area of all instream cover in a reach (m^2)	50.06	43.79	0.00	203.03
Distance to road	Distance to the nearest road (m)	316.06	532.83	3.58	3,096.42
BKT presence	Percentage of reaches where Brook Trout (BKT) occurred	29.00	46.00	0.00	100.00
Proportion cover	Proportion of reach with instream cover	0.16	0.13	0.00	0.51

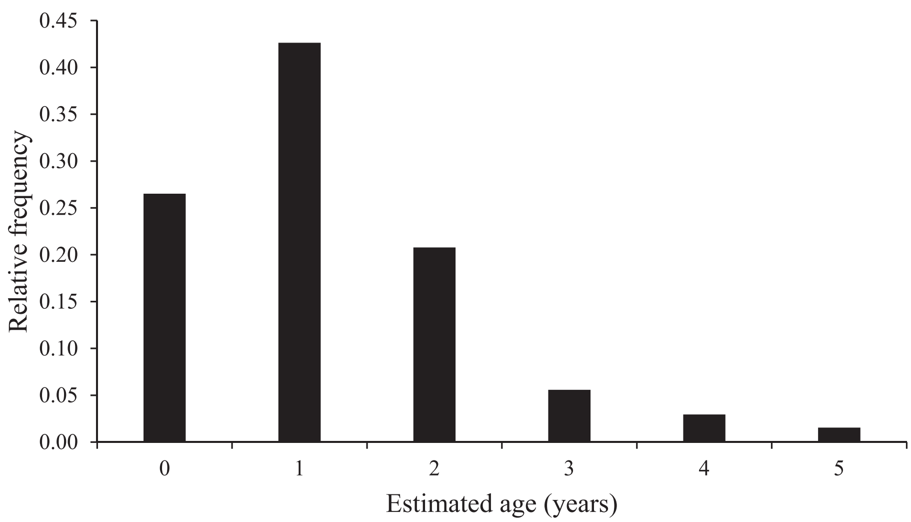

FIGURE 2. Age-frequency distribution of Westslope Cutthroat Trout (WCT) captured in tributaries of the St. Maries River, Idaho. A subsample of WCT was aged, and an age–length key developed from the subsample was used to infer ages of all WCT.

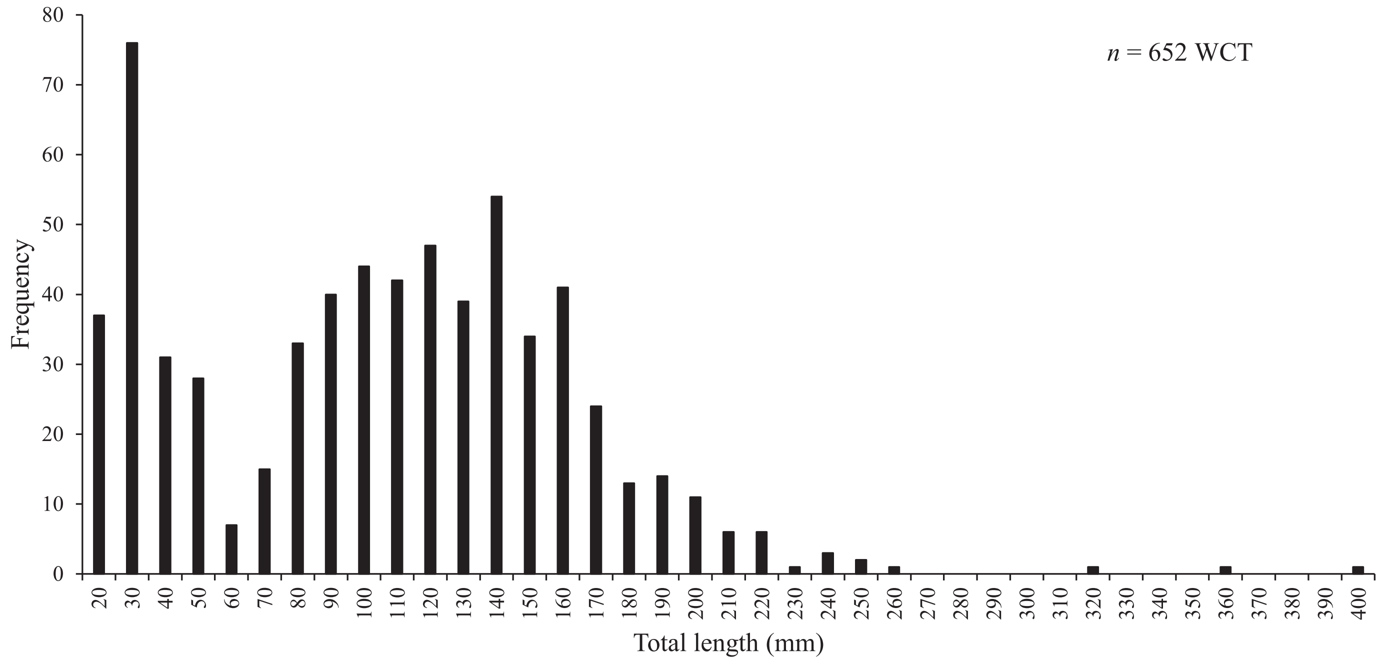

FIGURE 3. Length-frequency distribution of Westslope Cutthroat Trout (WCT) caught in tributaries of the St. Maries River, Idaho, 2017–2018.

We further investigated the relationship between habitat characteristics and age-1+ WCT. Logistic regression models predicting the presence of age-1+ WCT followed a pattern similar to that of models predicting the presence of age-0 WCT. The presence of age-1+ WCT was positively related to stream gradient and elevation and negatively related to road density (Table 4). Relative abundance of age-1+ WCT was positively related to gradient and road density, but negatively correlated with elevation. At the reach level, logistic regression models indicated that the percentage of canopy cover was positively related to the presence of age-1+ WCT. However, the presence of age-1+ WCT was inversely related to water temperature, the presence of BKT, and mean depth. The relative abundance of age-1+ WCT at the reach level was inversely related to wetted width, but positively related to the proportion of large substrate and canopy cover.

The sum of Akaike weights for all top models in which an independent variable occurred provided additional evidence related to the importance of each variable (Table 5). The presence of BKT and gradient carried the most weight in the top models predicting presence–absence of age-0 WCT (Figure 4). The mean wetted stream width and canopy cover were equally weighted in predicting the relative abundance of age-0 WCT. The sum of Akaike weights for gradient and road density was highest for predicting the presence–absence of age-1+ WCT, followed by stream temperature (Figure 5). Gradient also had the highest sum of Akaike weights for predicting the relative abundance of age-1+ WCT, followed by mean wetted width.

DISCUSSION

The primary goals of this research were to (1) evaluate the distribution and relative abundance of WCT in tributaries of the St. Maries River and (2) evaluate how the distribution and relative abundance of WCT in tributaries of the St. Maries River were related to habitat characteristics. We identified locations where WCT were present and absent in tributaries of the St. Maries River basin. We estimated the ages of WCT in tributaries and related their distribution to small-scale (e.g., wetted width, BKT presence, and water temperature) and large-scale (e.g., gradient, elevation, and road density) habitat characteristics. Our results were consistent with and contrary to other studies on WCT. Tributaries, particularly headwater streams, are vital habitat for Cutthroat Trout at multiple life stages (Schlosser 1991; Northcote 1997; Fausch et al. 2002; Uthe et al. 2016). Smaller tributary streams are critical for reproductive success (Rieman and Apperson 1989; Behnke 1992; Magee et al. 1996; Northcote 1997; Shepard 2004), natal rearing (Northcote 1997; Rosenfeld et al. 2002), and thermal refuge (Kaeding 1996; Baird and Krueger 2003; D'Angelo and Muhlfeld 2013). Distribution and length frequencies of WCT in tributaries of the St. Maries River were somewhat consistent with what was observed by IDFG in the 1980s (Apperson et al. 1988; Horton and Mahan 1988). Apperson et al. (1988) estimated that WCT caught in tributaries were dominated by age-2 fish, suggesting that tributaries of the St. Maries River were important juvenile rearing areas. In the current study, the majority of WCT that we caught in St. Maries

TABLE 2. Large- and small-scale habitat variables for stream reaches where age-0 Westslope Cutthroat Trout (WCT) and age-1 and older (age-1+) WCT were present and absent in reaches of 35 different tributaries of the St. Maries River, Idaho. Variables (defined in Table 1) were used as independent variables in candidate models (BKT = Brook Trout). Values represent the mean (SD in parentheses) of each variable for the respective response of age-0 WCT present or absent and age-1+ WCT present or absent.

Variable	Age-0 present	Age-0 absent	Age-1+ present	Age-1+ absent
Large-scale variables				
Elevation (m)	906.46 (125.95)	880.25 (63.39)	901.83 (104.64)	856.00 (28.47)
Gradient (%)	2.15 (1.33)	1.46 (1.36)	2.05 (1.40)	0.76 (0.73)
Road density (km/km^2)	0.14 (0.06)	0.16 (0.06)	0.14 (0.06)	0.19 (0.04)
Small-scale variables				
Runs	0.31 (0.19)	0.29 (0.15)	0.32 (0.17)	0.23 (0.14)
Pool : riffle	1.65 (3.17)	1.78 (2.52)	1.31 (2.42)	3.07 (3.50)
Depth (m)	0.22 (0.12)	0.28 (0.13)	0.23 (0.10)	0.35 (0.16)
Width (m)	2.89 (1.27)	3.63 (1.86)	3.06 (1.39)	4.19 (2.21)
Current velocity (m/s)	0.25 (0.19)	0.27 (0.27)	0.29 (0.19)	0.18 (0.07)
CV.Velocity	32.40 (14.72)	26.36 (13.38)	30.57 (14.71)	23.22 (10.75)
Canopy cover (%)	72.10 (17.77)	60.72 (19.60)	69.83 (17.05)	51.05 (20.82)
Temperature (°C)	13.01 (1.17)	14.04 (1.41)	13.21 (1.18)	14.93 (1.28)
Substrate_{Fine}	0.15 (0.17)	0.27 (0.27)	0.17 (0.16)	0.41 (0.35)
$\text{Substrate}_{Gravel}$	0.65 (0.38)	0.67 (0.41)	0.64 (0.35)	0.72 (0.55)
Substrate_{Large}	1.00 (0.44)	0.86 (0.37)	0.96 (0.40)	0.78 (0.41)
Embeddedness	0.70 (2.10)	0.31 (0.18)	0.53 (1.54)	0.27 (0.17)
Total cover area (m^2)	40.47 (38.40)	56.77 (46.48)	48.89 (41.93)	53.87 (50.67)
Distance to road (m)	377.26 (527.53)	273.23 (538.99)	334.84 (567.67)	255.03 (409.01)
BKT presence (%)	14.29	40.00	26.92	37.50
Proportion cover	0.17 (0.14)	0.16 (0.12)	0.17 (0.14)	0.13 (0.09)

TABLE 3. The top logistic regression models investigating the presence–absence and relative abundance (i.e., CPUE = fish/min of electrofishing) of age-0 Westslope Cutthroat Trout at multiple spatial scales based on habitat assessments. Habitat assessments were conducted in reaches ($n = 68$) of 35 different tributaries in the St. Maries River basin, Idaho, in 2017 and 2018 (variables are defined in Table 1; BKT = Brook Trout). Akaike's information criterion adjusted for small sample size (AIC_c) was used to rank the candidate models. Delta AIC_c (ΔAIC_c) is the difference in AIC_c between the given model and the top model. Only candidate models within 2.00 AIC_c units were considered as a top model (Burnham and Anderson 2002). The total number of parameters (K) and Akaike weight (w_i) are included. McFadden's pseudo-R^2 was used to evaluate model fit, and the direction of effect for each covariate is indicated ([+] positive; [–] negative).

Response variable	Model parameters	AIC_c	ΔAIC_c	K	w_i	R^2
	Large-scale models					
Presence–absence	+ Gradient	92.10	0.00	2	0.31	0.76
	+ Gradient – Road density	93.20	1.06	3	0.18	0.76
	+ Gradient + Elevation	93.60	1.44	3	0.15	0.76
	Small-scale models					
	– BKT presence – Depth – Substrate_{Fine}	83.40	0.00	4	0.31	0.79
	– BKT presence – Temperature	83.90	0.46	3	0.24	0.79
	– BKT presence – Substrate_{Fine}	84.90	1.48	3	0.15	0.78
	Large-scale models					
Relative abundance	Null model	198.60	0.00	2	0.28	0.00
	+ Road density	199.20	0.61	3	0.21	0.01
	– Elevation	199.20	0.62	3	0.21	0.01
	Small-scale models					
	– Width – Canopy cover	185.40	0.00	4	0.69	0.09

TABLE 4. The top logistic regression models investigating the presence–absence and relative abundance (i.e., CPUE = fish/min of electrofishing) of age-1 and older Westslope Cutthroat Trout at multiple spatial scales based on habitat assessments. Habitat assessments were conducted in reaches (n = 68) of 35 different tributaries in the St. Maries River basin, Idaho, in 2017 and 2018 (variables are defined in Table 1; BKT = Brook Trout). Akaike's information criterion adjusted for small sample size (AIC_c) was used to rank the candidate models. Delta AIC_c (ΔAIC_c) is the difference in AIC_c between the given model and the top model. Only candidate models within 2.00 AIC_c units were considered as a top model (Burnham and Anderson 2002). The total number of parameters (K) and Akaike weight (w_i) are included. McFadden's pseudo-R^2 was used to evaluate model fit, and the direction of effect for each covariate is indicated ([+] positive; [–] negative).

Response variable	Model parameters	AIC_c	ΔAIC_c	K	w_i	R^2
	Large-scale models					
Presence–absence	+ Gradient – Road density	52.00	0.00	3	0.64	0.39
	+ Elevation + Gradient – Road density	53.40	1.39	4	0.32	0.40
	Small-scale models					
	– Temperature + Canopy cover	56.30	0.00	3	0.26	0.33
	– Temperature	57.30	0.97	2	0.16	0.28
	– Temperature – Depth	57.70	1.35	3	0.13	0.31
	– Temperature – Depth + Canopy cover	57.90	1.57	4	0.12	0.34
	– Temperature – BKT presence	57.90	1.62	3	0.12	0.31
	Large-scale models					
Relative abundance	+ Gradient	350.70	0.00	3	0.37	0.05
	+ Gradient – Elevation	351.80	1.09	4	0.21	0.05
	+ Gradient + Road density	352.50	1.83	4	0.15	0.05
	Small-scale models					
	– Width + $Substrate_{Large}$	353.40	0.00	4	0.26	0.05
	– Width	354.60	1.19	3	0.14	0.04
	– Width + Canopy cover + $Substrate_{Large}$	354.90	1.48	5	0.12	0.05
	– Width + Canopy cover	355.20	1.76	4	0.11	0.04

River tributaries were less than 170 mm, with the highest frequencies of lengths at 30–39 and 140–149 mm. We estimated that WCT in tributaries were dominated by age-1 fish, followed by age-0 fish, suggesting that St. Maries River tributaries are important natal rearing areas. Although tributaries in the St. Maries River basin may not be typical high-elevation headwater streams, these tributaries function as headwaters by providing critical habitat for the early life history of WCT.

Previous research has indicated that certain habitat characteristics, such as gradient (Brown and Mackay 1995; D'Angelo and Muhlfeld 2013) and road density (Eaglin and Hubert 1993; Valdal and Quinn 2011), are important for the occurrence of WCT. In the current study, multiple large-scale habitat characteristics (e.g., gradient, road density, and elevation) were important for predicting the occurrence of age-0 and age-1+ WCT in tributaries of the St. Maries River. The positive association of WCT presence with gradient follows a similar finding in streams of Glacier National Park, Montana, where the occurrence of WCT was associated with gradient (D'Angelo and Muhlfeld 2013). Additionally, Kozel and Hubert (1989) observed that gradient had a substantial influence on stream habitat when predicting trout standing stock in Wyoming streams. Our observations in the St. Maries River basin corroborate these studies; gradient of a reach had a positive correlation with the presence of WCT. Moreover, gradient was also positively related to the relative abundance of age-1+ WCT. The sum of Akaike weights for gradient was high (≥0.50), suggesting that gradient was an important covariate for predicting those responses.

Regarding other large-scale habitat characteristics (i.e., elevation and road density), our findings were contrary to those of other studies. The effect of elevation on the relative abundance of WCT was negative, although elevation was positively related to presence. This pattern suggests that WCT are commonly encountered at higher-elevation reaches, but are most abundant at lower-elevation reaches. High and moderate relative abundances of both age-classes of WCT were scattered, but many sites at lower elevations had the highest abundances of WCT. Lower reaches of streams may have more abundant resources (e.g., prey availability) throughout the year and are able to support greater abundances of WCT (Berger and Gresswell 2009). Furthermore, migration to lower elevations has been observed when salmonids seek overwintering habitat (Bjornn and Mallet 1964; Lewynsky 1986; Brown and Mackay 1995; Dobos et al. 2016; Uthe et al. 2016), which is the likely pattern that WCT follow in the St. Maries River basin. Although we did not evaluate overwintering behavior of WCT in the St. Maries River basin,

TABLE 5. Sum of Akaike weights (w) and direction of relationship (positive or negative) for each independent variable in the top logistic regression models (variables are defined in Table 1; WCT = Westslope Cutthroat Trout; BKT = Brook Trout; age 1+ = age 1 and older). High values (in bold; e.g., $w \geq 0.50$) suggest that a variable is important for that life stage.

Response variable	Independent variable	w
Age-0 WCT presence–absence	BKT presence	(–) **0.70**
	Gradient	(+) **0.64**
	Substrate_{Fine}	(–) 0.46
	Road density	(–) 0.18
	Depth	(–) 0.31
	Elevation	(+) 0.15
	Temperature	(–) 0.24
Age-0 WCT relative abundance	Width	(–) **0.69**
	Canopy cover	(–) **0.69**
	Road density	(+) 0.21
	Elevation	(–) 0.21
Age-1+ WCT presence–absence	Gradient	(+) **0.96**
	Road density	(–) **0.96**
	Temperature	(–) **0.79**
	Canopy cover	(+) 0.38
	Elevation	(+) 0.38
	Depth	(–) 0.25
	BKT presence	(–) 0.12
Age-1+ WCT relative abundance	Gradient	(+) **0.73**
	Width	(–) **0.63**
	Substrate_{Large}	(+) 0.38
	Canopy cover	(+) 0.23
	Elevation	(–) 0.21
	Road density	(+) 0.15

additional research that is focused on understanding overwintering locations of WCT in the watershed may be warranted. We also found that road density increased at lower elevations, often where WCT densities were higher. Road density was inversely related to the occurrence of WCT, but positively related to the relative abundance of WCT. A positive relationship between the relative abundance of WCT and road density is contrary to many studies (Furniss et al. 1991; Eaglin and Hubert 1993; Valdal and Quinn 2011). Timber harvest and associated roads often influence stream habitat by accelerating sediment delivery to stream channels (Chamberlain et al. 1991; Furniss et al. 1991; Eaglin and Hubert 1993; Weaver and Fraley 1993). Seasonal roads for timber harvest in the St. Maries River watershed are abundant due to the long history of logging in the basin (Schott 1950; IDEQ 2003). The sum of Akaike weights for road density was much greater (0.96) when inversely related to presence–absence models than in other models (i.e., ≤0.21) containing the covariate. In other words, road density carried more weight when inversely related to the response than when it was positively related, thereby suggesting that road density may have a greater negative effect on the occurrence of WCT than a positive effect on the abundance of WCT. Furthermore, the positive relationship between the relative abundance of WCT and road density is explained by the highest density of roads that occurred at mid- to low-elevation sites, which were also the elevations where WCT were most abundant. Roads have been linked to increasing sediment delivery to stream channels (Chamberlain et al. 1991; Furniss et al. 1991; Eaglin and Hubert 1993; Weaver and Fraley 1993); increased sedimentation can affect spawning gravel embeddedness and fry emergence (Chamberlain et al. 1991; Weaver and Fraley 1993; Magee et al. 1996).

Westslope Cutthroat Trout were sampled in some tributaries ($n = 18$) that are Clean Water Act section 303(d) listed for sediment impairment (IDEQ 2003), and regression models indicated a negative relationship between the occurrence of WCT and fine substrates (i.e., silt and sand). A negative relationship between WCT occurrence and fine substrates, but a positive relationship with gradient indicates that WCT were found in streams with increased stream velocity and less fine substrates. Westslope Cutthroat Trout are widely distributed in the western United States within lands that have stringent habitat protections (Shepard et al. 2005), suggesting that land use can affect spatial distributions of WCT. For example, timber harvest, roads, and cattle grazing have been implicated in fragmentation of habitat, destabilization of streambanks, and increased sedimentation (Meehan 1991). Increased concentrations of fine sediments can prevent fry emergence and decrease growth and survival of juvenile salmonids (Chapman 1988; Suttle et al. 2004). Tributary sites where fine substrate (i.e., silt and sand) was the dominant substrate type were negatively related to the presence of age-0 WCT, whereas sites dominated by large substrate were positively related to the relative abundance of age-1+ WCT. Large substrate (e.g., boulders) is an important habitat characteristic for WCT because it increases channel complexity by providing instream cover and current breaks in high-gradient streams (Griffith and Smith 1993; Jakober et al. 2000; Rosenfeld et al. 2000; Dobos et al. 2016).

Additional reach-level habitat characteristics (e.g., wetted stream width, temperature, and canopy cover) were associated with the occurrence and abundance of WCT in our top models. Wetted stream width was an important covariate in models assessing the relative abundance of both age-classes of WCT. However, wetted stream width was inversely related to relative abundance, which is contrary to other studies that have typically found a positive relationship between stream width and trout presence or abundance (Clarkson and Wilson 1995; Kruse et al. 1997;

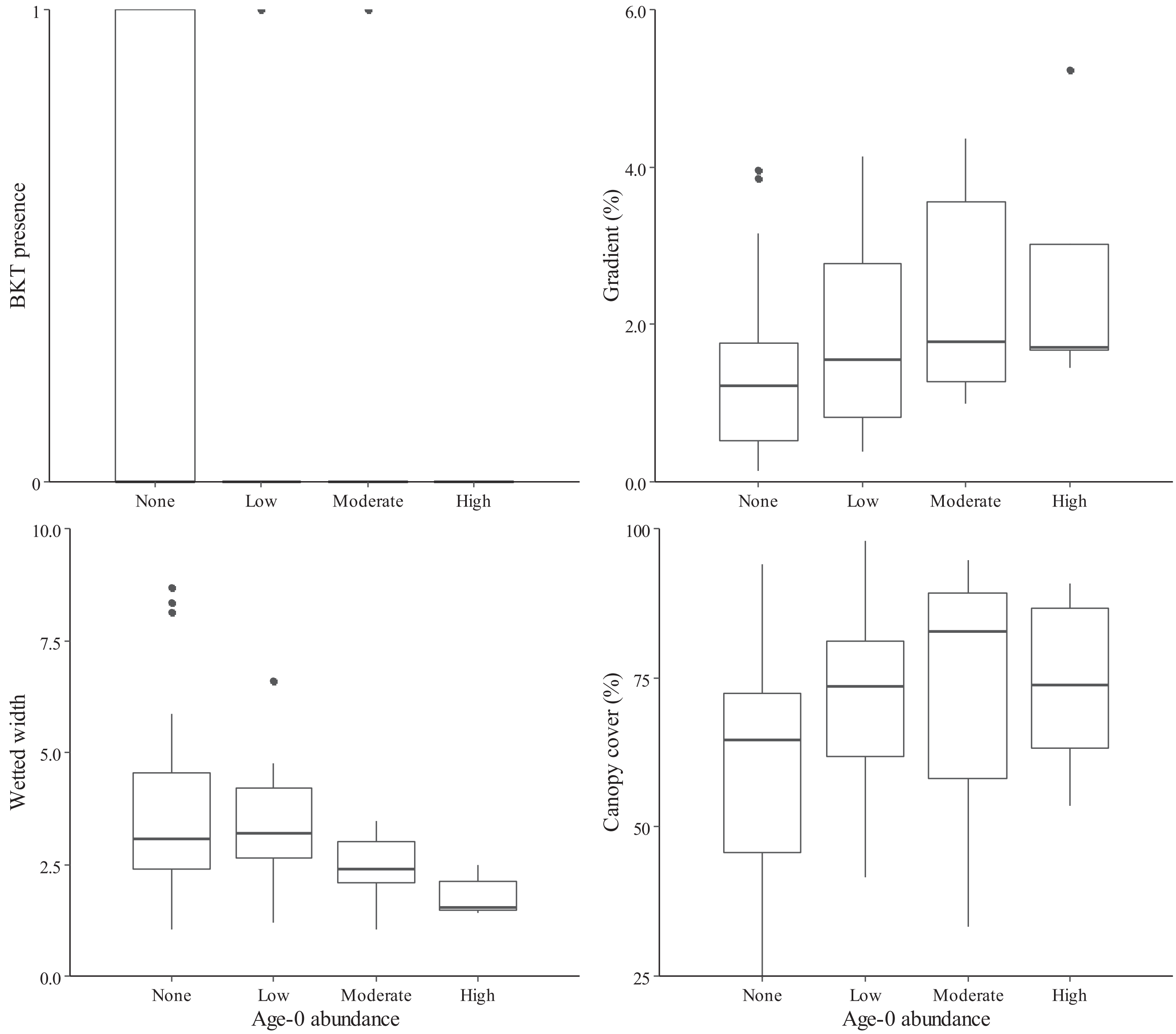

FIGURE 4. Age-0 Westslope Cutthroat Trout relative abundance in response to independent variables with the highest Akaike weights in the top logistic regression models (BKT = Brook Trout). Wetted width was measured in meters. The lower and upper hinges correspond to the first and third quartiles, respectively. The upper whisker extends from the hinge to largest value no further than 1.5× the interquartile range. The lower whisker extends from the hinge to the smallest value at most 1.5× the interquartile range of the hinge. The dots represent outliers. The line in the middle of the box represents the median.

Dunham and Rieman 1999). Capture efficiency was likely higher in narrow, smaller streams, and higher abundances of WCT occurred in narrower tributaries. Wider stream channels in the current study were typical of reaches where WCT were not detected. Narrower stream channels in the St. Maries River watershed often had more canopy cover than wider streams, which is important for regulating stream temperatures and providing cover from predators (Platts and Nelson 1989). Canopy cover was positively associated with age-1+ WCT presence and relative abundance, but negatively related to age-0 relative abundance. A denser canopy cover can help to maintain lower instream water temperatures and provide cover from predators, which may be more important for age-1+ WCT. However, for age-0 WCT, less canopy cover is providing more solar radiation, which increases periphyton biomass and ultimately provides more food resources for WCT fry (Hetrick et al. 1998). Although some sites had

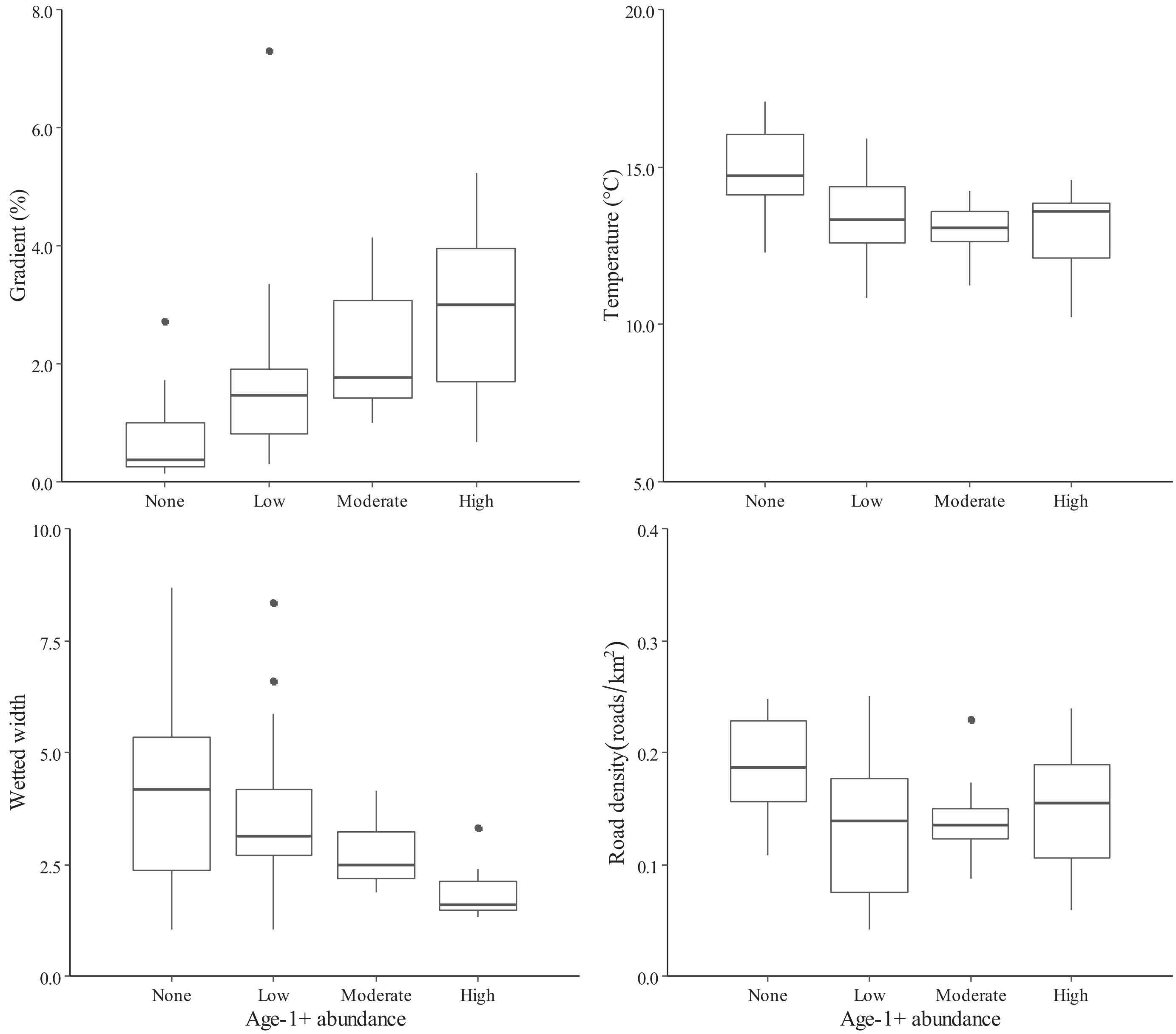

FIGURE 5. Age-1 and older (age-1+) Westslope Cutthroat Trout relative abundance in response to independent variables with the highest Akaike weights in the top logistic regression models. Wetted width was measured in meters. The lower and upper hinges correspond to the first and third quartiles, respectively. The upper whisker extends from the hinge to largest value no further than 1.5× the interquartile range. The lower whisker extends from the hinge to the smallest value at most 1.5× the interquartile range of the hinge. The dots represent outliers. The line in the middle of the box represents the median.

less canopy, more solar radiation (i.e., warmer water temperatures), and higher densities of age-0 WCT, water temperature was negatively associated with presence of age-0 WCT and age-1+ WCT. The presence of WCT in St. Maries River tributaries was associated with a stream temperature of about 13.0°C, which is close to the optimum growth temperature for WCT (i.e., 13.6°C; Bear et al. 2007). Stream temperature is an important factor limiting WCT distribution, and optimum stream temperatures exist in the St. Maries River basin, indicating highly suitable habitat (Sloat et al. 2005).

Westslope Cutthroat Trout in St. Maries River tributaries were associated with stream depths less than 0.4 m, which is contrary to research in the Coeur d'Alene River basin (DuPont et al. 2004; Stevens and DuPont 2011). DuPont et al. (2004) and Stevens and DuPont (2011) observed that adult WCT in the Coeur d'Alene River basin preferred water depths greater than 1.0 m. However, the current study predominantly sampled juvenile WCT, suggesting that stream depth of habitat used by WCT likely varies with age-class and (or) length. Moreover, we observed some sampling reaches that were predominately homogeneous stream channels comprised of pools over 50 m long and about 1 m deep. We did not encounter WCT in reaches of this type, which is evident in our models because of the negative association of depth to WCT occurrence. This finding is contrary to other work (Rosenfeld et al. 2000; Harig and Fausch 2002; D'Angelo and Muhlfeld 2013) in which observed pool density was positively associated with the occurrence and abundance of WCT. Persistence of WCT in a highly altered system such as the St. Maries River basin is a testament to the viability of the population and that there is connectivity throughout the watershed to habitat that supports critical components of WCT life history. Presence of pools and deeper water is still important for WCT, particularly as overwintering habitat (Brown and Mackay 1995; Schmetterling 2001; Dobos et al. 2016), but summer habitat use of WCT in St. Maries River tributaries was predominately in shallower water that is characteristic of most tributaries in the system. Our findings indicate that reaches dominated by deep, long pools were not associated with the presence of WCT; those habitats likely become more important for WCT in fall and winter.

Research on the relationship between Cutthroat Trout and BKT is well documented. Brook Trout compete with Cutthroat Trout and often displace native Cutthroat Trout (Griffith 1988; Behnke 1992; Dunham et al. 2002; Shepard 2004; Quist and Hubert 2005). The presence of BKT was negatively related to the presence of WCT in the St. Maries River basin. Brook Trout likely displaced WCT from Alder and Crystal creeks, where WCT were once the dominant salmonid species (Apperson et al. 1988). Shepard (2004) suggested that certain habitat characteristics may influence BKT invasion and their displacement of WCT. Shepard (2004) found that BKT invasion and displacement of WCT were influenced by water temperature, pool frequency, and erosion and deposition of fine sediments. Support for Shepard's (2004) findings was observed in the St. Maries River basin. The presence of WCT in the St. Maries River basin was negatively related to the presence of BKT, but also to fine sediments.

Hybridization between WCT and RBT has been identified as a limiting factor for WCT populations and their distribution (Shepard et al. 2005; Muhlfeld et al. 2009a). Some data on hybridization suggest that WCT in the St. Maries River may be altered (Shepard et al. 2005); however, no direct investigations into hybridization of WCT in the St. Maries River basin have been completed. Therefore, no genetic data are available on introgression and hybridization of WCT and RBT in the St. Maries River basin. Furthermore, IDFG has not stocked RBT in the St. Maries River since 2002 and those fish were triploid RBT. The present study did not investigate genetics of WCT captured in the St. Maries River basin, but an investigation of the current status of hybridization and introgression in WCT populations is needed. Although we identified one possible hybrid and zero RBT during this study, future research on hybridization and introgression between WCT and RBT in the sub-basins of the Coeur d'Alene Lake watershed may be useful for managers.

Additional research and continued monitoring should be conducted in the St. Maries River basin. Specifically, research on summer and winter habitat use and movement in the main stem would be beneficial in understanding movement patterns of various life stages of WCT in the system. We did not investigate overwintering fish behavior and habitat use, so we do not know WCT overwintering habitat requirements and what the limitations are in this system. In addition, we did not encounter many adult WCT in tributaries, so investigating adult WCT habitat use and movement in the watershed would be insightful. Adult WCT may only use tributaries for spawning, and juveniles may emigrate from tributaries after their first or second year. We described where WCT were distributed related to habitat characteristics in tributaries of the St. Maries River, with the majority of our sample describing habitat use by juvenile WCT. Understanding early life history is important because it indicates whether recruitment is occurring and whether suitable habitat exists to support early life stages. We provided information on habitat characteristics important for the distribution and abundance of juvenile WCT in a highly altered watershed. Generally, tributaries in the northeastern and southeastern portions of the watershed contained good habitat, with cold water throughout the summer, and moderate to high abundances of WCT. However, poor habitat was evident in reaches of tributaries draining the western and southwestern portions of the watershed. Monitoring the discharge and water temperature of larger tributaries draining the southwestern portion of the watershed (e.g., Emerald, Carpenter, Santa, and Alder creeks) would provide an understanding of how much warm water those drainages are contributing to the main-stem St. Maries River. Drainages in the southwest portion of the basin contained the poorest habitat, which is where habitat enhancement could be focused. Large portions of these drainages were cattle grazed, had poor riparian stability, and exhibited warm water temperatures. In response, barriers to fish movement were formed between the St. Maries River and headwaters in those drainages where WCT abundances were low to moderate. Therefore, understanding how those large drainages contribute to the St. Maries River is important in moving forward with habitat remediation projects in the main-stem river and in lower reaches of those tributaries.

The current study supports existing research suggesting that WCT populations appear robust and broadly distributed in headwaters (Shepard et al. 2005; D'Angelo and

Muhlfeld 2013) and tributaries (Sloat et al. 2005; McGrath et al. 2008) throughout their current distribution. Westslope Cutthroat Trout appeared to be present in most tributaries even though the St. Maries River basin has been negatively altered by land use practices. Although some of our findings were contrary to those of other studies, the St. Maries River basin is unlike many other systems where WCT have been studied; it is an altered watershed where most tributaries with WCT present are similar to small, narrow, high-gradient headwater streams, but at lower elevations than headwater streams in places like Glacier National Park, Montana. Westslope Cutthroat Trout had low abundances or were absent in some tributaries due to poor habitat conditions and (or) interactions with nonnative BKT. Conversely, moderate to high abundances of WCT in the St. Maries River basin were positively correlated with gradient, canopy cover, and large substrate, which are habitat characteristics that have been shown to be critical for the distribution and abundance of WCT in other portions of their distribution. However, unmitigated threats, such as competition with nonnative species (e.g., BKT), hybridization with RBT, habitat loss, and habitat fragmentation pose persistent complications to WCT abundance in locations where populations appear robust, but their actual abundance is unknown. Positive relationships between WCT abundance and certain habitat characteristics (i.e., gradient, instream cover, and temperature) indicate that suitable habitat exists in the watershed, and more suitable habitat could be created and protected if land easements and restoration projects are implemented. Even though land use practices like forest clearcutting and agricultural use occur in the St. Maries River watershed, their effects can be mitigated by maintaining and protecting habitat that promotes the occurrence and abundance of WCT.

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