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Fall and Winter Microhabitat Use and Suitability for Spring Chinook Salmon Parr in a U.S. Pacific Northwest River

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Abstract

Habitat degradation has been implicated as a primary threat to Pacific salmon *Oncorhynchus* spp. Habitat restoration and conservation are key toward stemming population declines; however, winter microhabitat use and suitability knowledge are lacking for small juvenile salmonids. Our objective was to characterize microhabitat use and suitability for spring Chinook Salmon *Oncorhynchus tshawytscha* parr during fall and winter. Using radiotelemetry techniques during October–February (2009–2011), we identified fall and winter microhabitat use by spring Chinook Salmon parr in Catherine Creek, northeastern Oregon. Tagged fish occupied two distinct gradient reaches (moderate and low). Using a mixed-effects logistic regression resource selection function (RSF) model, we found evidence that microhabitat use was similar between free-flowing and surface ice conditions. However, habitat use shifted between seasons; most notably, there was greater use of silt substrate and areas farther from the bank during winter. Between gradients, microhabitat use differed with greater use of large wood (LW) and submerged aquatic vegetation in the low-gradient reach. Using a Bayesian RSF approach, we developed gradient-specific habitat suitability criteria. Throughout the study area, deep depths and slow currents were most suitable, with the exception of the low-gradient reach where moderate depths were optimal. Near-cover coarse and fine substrates were most suitable in the moderate- and low-gradient reaches, respectively. Near-bank LW was most suitable throughout the study area. Multivariate principal component analyses (PCA) indicated co-occurring deep depths supporting slow currents near cover were intensively occupied in the moderate-gradient reach. In the low-gradient reach, PCA indicated co-occurring moderate depths, slow currents, and near-bank cover were most frequently occupied. Our study identified suitable and interrelated microhabitat combinations that can guide habitat restoration for fall migrant and overwintering Chinook Salmon parr in Catherine Creek and potentially the Pacific Northwest.

In the northwestern United States, abundance levels exhibited by Pacific salmon *Oncorhynchus* spp. stocks have declined to historic lows, and numerous stocks are threatened with extinction (Nehlsen et al. 1991). By the 1990s, 13% of native, naturally spawning Chinook Salmon *Oncorhynchus tshawytscha* stocks in the U.S. Pacific Northwest were extinct, and 77% of those remaining exhibited a moderate to high extinction risk (Nehlsen et al. 1991). Numerous anthropogenic sources of Pacific salmon mortality have been identified including overfishing (Fulton 1968), migration barriers (Raymond 1979; Williams et al. 2001), aberrant migration cues (Raymond

1988; Tiffan et al. 2009), supplementation programs (Hilborn 1992; Chilcote et al. 2011), nonindigenous species (Zimmerman 1999), natal stream nutrient deficits (Achord et al. 2003), climate change (Beamish and Bouillon 1993; Hare et al. 1999), and habitat degradation (Dauble et al. 2003).

Habitat loss and degradation have been implicated as the largest threat to endangered species in the United States (Richter et al. 1997; Wilcove et al. 1998) and are viewed as a primary cause of extinction (Ehrlich and Ehrlich 1981). Streams and rivers are among Earth's most altered ecosystems, and freshwater fauna extinction rates are five times higher than those of terrestrial biota (Bernhardt et al. 2005; Brierley and Fryirs 2008). Due to habitat loss and large-scale degradation, nearly 45% of historically accessible Pacific salmon habitat is currently unavailable in the contiguous United States (McClure et al. 2008).

Reversal of anthropogenic habitat degradation exacted on lotic ecosystems has become a mainstay fisheries management tool (Bond and Lake 2003; Bernhardt et al. 2005). Recently, efforts to preserve and enhance salmon populations in the Columbia River basin have transitioned from an intense focus on mortality within the Snake and Columbia river hydrosystem (e.g., Townsend et al. 2006; Skalski et al. 2014) toward also increasing production and survival of juvenile life stages upstream from the hydrosystem (Williams et al. 1999; NMFS 2008; Monzyk et al. 2009). Specifically, in the U.S. Pacific Northwest, millions of dollars are allocated annually toward watershed and stream restoration to restore threatened and endangered salmonid populations (NRC 1996; Roni et al. 2002). Strategically, restoration objectives routinely include restoring winter rearing habitats because severe winter conditions have been associated with high mortality in natal streams (Huusko et al. 2007; Brown et al. 2011).

Diverse and complex rearing habitats are critical to lotic fishes during winter (Cunjak 1996). Rearing habitat quality and quantity have the potential to limit winter survival and spring smolt production in natal streams (Nickelson et al. 1992; Solazzi et al. 2000). In natal streams exhibiting adequate spawner abundance, winter habitat functions as the primary bottleneck limiting smolt production (Nickelson et al. 1992). In degraded natal streams, habitat restoration can be a beneficial component toward restoring natural processes and a diverse suite of available habitats (Roni et al. 2002; Beechie et al. 2008).

In general, fish habitat is composed of physical and biological components necessary to complete life histories and sustain a population (Newcomb et al. 2007). Habitat use refers to the way fish utilize the physical and biological resources available within an occupied landscape. Habitat availability is the accessibility and procurability of physical and biological resources by a fish (Johnson 1980).

Habitat suitability is a measure of the capacity of a specific available habitat to support a fish, with those habitats most suitable being optimal (Bovee 1986). Routinely, available habitats are hierarchically characterized employing a spectrum ranging from least suitable (i.e., avoided) to most suitable (i.e., optimal). Habitat selection is the process of choosing a physical or biological component from a suite of available habitats (Johnson 1980). In general, habitat use is considered random (i.e., no preference) if habitat use is proportionally equivalent to habitat availability. However, preferred habitat refers to a specific physical or biological component that is preferentially selected under equal availabilities (e.g., laboratory experiment: Johnson 1980). Lastly, critical habitat areas exhibit characteristics important to sensitive life stages (e.g., early life history: Pitlo 1989; Newcomb et al. 2007).

In healthy ecosystems, available habitats can range from avoided areas to optimal core areas that are critical to population viability (e.g., keystone habitat). A keystone habitat is an area vital to the perpetuity of a population (Power 2001). For salmonids, damage to keystone habitats greatly harms dependent populations, and the effect is disproportionate to the fraction of the basin such habitats occupy (Power 2001). To effectively plan and implement successful habitat restoration, resource managers must understand the seasonal habitat requirements of the target species (Nickelson et al. 1992). Establishing predictable relationships among appropriate microhabitat variables and the target species should be foundational to any stream restoration strategy (Bovee 1986; Rabeni and Sowa 1996). Due to harsh winter field conditions (e.g., surface ice), few researchers have empirically characterized microhabitat use and suitability for Pacific salmon parr during winter (Huusko et al. 2007).

After a precipitous decline during the 20th century, the spring Chinook Salmon population in Catherine Creek, Oregon, a population within the Snake River Spring–Summer Chinook Salmon Evolutionary Significant Unit, was listed as threatened under the U.S. Endangered Species Act (ESA) in 1992 (NMFS 1992). Naturally produced juveniles from Catherine Creek exhibit smaller sizes, lower abundances, and lower survival compared with neighboring populations (Jonasson et al. 2016). Furthermore, even at very small adult recruitment levels (~100 spawners), naturally produced Catherine Creek juveniles have exhibited strong density-dependent relationships (e.g., low number of smolts per spawner: Jonasson et al. 2016). Cumulatively, these long-term trends suggest that overwintering habitat in Catherine Creek may function as a primary bottleneck limiting smolt production.

In response to the 2008 Biological Opinion (BiOp) by the National Oceanic and Atmospheric Administration (NOAA) Fisheries, the U.S. Bureau of Reclamation (USBR) began implementing habitat restoration in specific

Columbia River basin natal tributaries to benefit anadromous fishes (Booth et al. 2016). In 2009, USBR identified Catherine Creek for habitat restoration (USBR 2012), but optimal Chinook Salmon parr winter habitat was undefined. Thus, we used radiotelemetry techniques to identify and characterize fall and winter microhabitat use and suitability for Catherine Creek spring Chinook Salmon parr in an effort to guide stream restoration efforts. Specifically, our objectives were to (1) characterize fall and winter microhabitat use and suitability for spring Chinook Salmon parr during free-flowing and surface ice conditions and (2) characterize co-occurring microhabitat variables identified as fall and winter rearing habitat.

METHODS

Study area.— Catherine Creek originates in the southern slopes of the Wallowa Mountains of Oregon and flows northwest until entering the Grande Ronde Valley to join the Grande Ronde River (Figure 1), a tributary of the Snake River. Catherine Creek drains approximately 1,045 km^2 and typically exhibits fall and winter base flow discharges ranging from 0.9 to 1.4 m^3/s (available online at http://apps.wrd.state.or.us/apps/sw/hydro_near_real_time/display_hydro_graph.aspx?station_nbr=13320000).

Prior to European settlement (early 17th century), the Grande Ronde Valley ecosystem was markedly different (Duncan 1998; Gildemeister 1998). Historically, the Grande Ronde Valley supported vast grasslands, wetlands, and a 6.5- to 9.3-km^2 lake called Tule Lake (Beckham 1995; Gildemeister 1998). North American beaver *Castor canadensis*, a keystone ecosystem engineer (Jones et al. 1997; Wright and Jones 2006), were abundant in lower Catherine Creek and the upper Grande Ronde Valley (USBR 2012). In 1869, Catherine Creek was channelized, and Tule Lake and connected marshlands were drained to accommodate agriculture expansion (Gildemeister 1998).

Upstream from the Grande Ronde Valley, Catherine Creek has a moderate gradient (0.62% slope) exhibiting run–riffle–pool sequences and unembedded substrates (Bach 1995). At Catherine Creek's alluvial fan, near the mouth of Pyles Creek (Figure 1), the stream transitions to a low-gradient (0.02% slope) system characterized by slow velocities, fine substrates, and deep depths lacking cover. Upper Catherine Creek flows through a moderate-gradient coniferous forest landscape; however, deciduous vegetation is present within the riparian zone. Conversely, lower Catherine Creek meanders through the Grande Ronde Valley, which has been devoted to agriculture. Currently, despite historic anthropogenic activities, Catherine Creek rearing habitat is not severely degraded for Chinook Salmon parr and supports a diverse fish assemblage including steelhead *Oncorhynchus mykiss* and Bull Trout *Salvelinus confluentus* (USBR 2012).
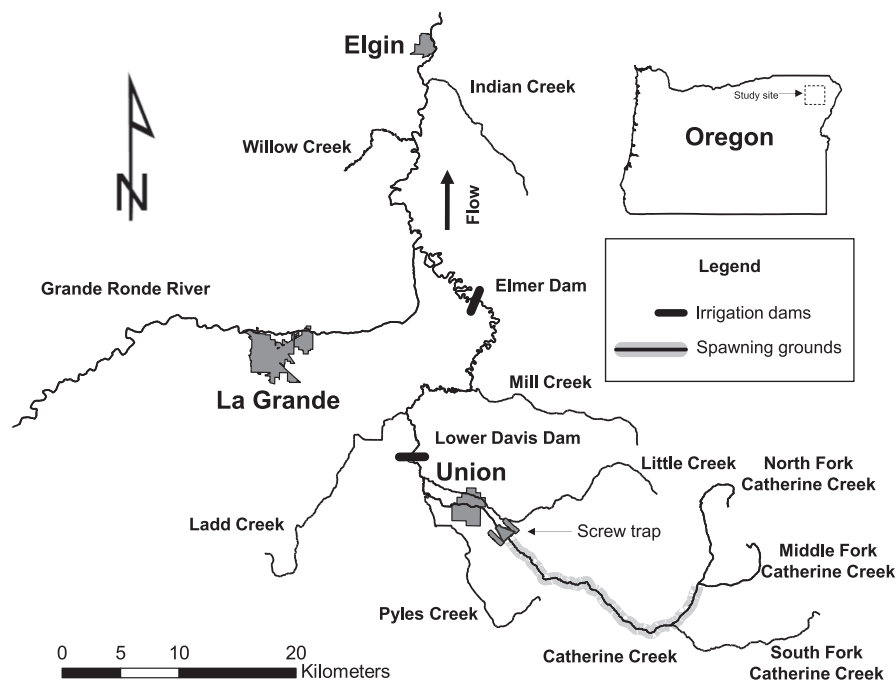

FIGURE 1. Study area in the Grande Ronde Valley, Oregon, bounded downstream by the mouth of Indian Creek near Elgin and upstream by the Catherine Creek rotary screw trap site near Union. The mouth of Pyles Creek was designated as the breakpoint between the moderate-gradient reach (upstream) and low-gradient reach (downstream). Shaded areas near Elgin, La Grande, and Union depict municipality limits.

Radiotelemetry.— During October–December 2009, 2010, and 2011, radio tags were implanted into 98, 129, and 73 naturally produced spring Chinook Salmon parr from Catherine Creek, respectively. Half-duty cycle (i.e., signal transmission, 12 h/d) coded radio tags (model NTQ-1, Lotek Wireless) were used to extend battery life and differentiate individual fish during daytime. All tags were weighed with an electronic analytical balance accurate to 0.1 mg (model EP64, Explorer Pro, Ohaus, Parsippany, New Jersey). Mean tag weight was 0.27 g (SD, 0.006; range, 0.25–0.30 g). During 2009, tags exhibited a 5-s burst rate (typical life = 21 d); however, a burst rate of 10 s (typical life = 33 d) was implemented during 2010 and 2011 to extend tag life.

Following a 24-h collection period, fall migrant parr were obtained using a 1.5-m rotary screw trap located downstream from core summer spawning areas (Figure 1). Prior to tag implantation, fish were placed into a 6-L container with freshwater treated with tricaine methanesulfonate (MS-222) at 70 mg/L and buffered with sodium bicarbonate. To ensure sufficient sedation, fish were exposed to the anesthetizing solution for an additional 60 s following loss of equilibrium (i.e., stage 4 anesthesia: Summerfelt and Smith 1990). Following anesthetic exposure (mean, 5.6 min; SD, 1.4), FL (mm) and weight (to 0.1 g) were recorded. A conservative minimum size criterion of 8.5 g was established to minimize tag burden to approximately 3%, which accords with available tag burden guidance for small juvenile salmonids (Adams et al. 1998a, 1998b; Chittenden et al. 2009; Brown et al. 2010).

Surgery protocol was similar to that of Adams et al. (1998a, 1998b). During surgery, diluted anesthetic solution (MS-222, 35 mg/L) was continuously administered through silicone tubing (4-mm inner diameter). A 5-mm incision was made anterior to the pelvic girdle and offset 2 mm left of and parallel to the ventral midline. An antenna outlet was created in the body wall using the shielded-needle technique (Ross and Kleiner 1982). Following antenna placement, a sterilized radio tag coated with oxytetracycline (200 mg/mL Vetrimycin 200) was inserted into the body cavity. Sterile, synthetic absorbable, monofilament surgical suture (Maxon 6–0) with a 9-mm, 3/8 circle, tapered needle was used to close the incision (Wagner and Cooke 2005). For each tagged fish, the sutured incision was coated with antibacterial ointment (Vetropolycin). In total, mean surgery time was 4.7 min (SD, 1.7). After surgery, tagged fish were placed into a covered, 19-L, aerated recovery container until normal equilibrium was exhibited (mean recovery time, 4.8 min; SD, 3.5). All tagged fish successfully recovered and were immediately released 50 m downstream from the collection site.

From October through February 2009–2011, daytime mobile tracking was conducted weekly from the release site to the mouth of Indian Creek (distance = 93 river kilometers; Figure 1). Mobile tracking was accomplished on foot or by boat using a Lotek SRX-400 W5XG receiver and a three-element foldable Yagi antenna. Upon detecting a tagged fish, zero-point tracking techniques (i.e., successive gain reductions) were initiated to localize the signal's origination point. Following signal localization, trackers used triangulation techniques (Cooke et al. 2012; Eiler 2012) to identify the occupied location. Catherine Creek is relatively narrow (5–20 m) during winter discharges and icing conditions; thus, trackers were typically able to approach tagged fish to within 5 to 10 m prior to initiating triangulation techniques. Triangulation techniques are more accurate when the distance between the transmitter and receiver is short (Simpkins and Hubert 1998), and triangulation techniques can yield accuracies ranging from 0.5 to 1.0 m^2 (David and Closs 2001, 2003). Caution was practiced during zero-point tracking and triangulation techniques not to disturb tagged fish and introduce fright bias (Cooke et al. 2012; Eiler 2012).

Microhabitat use and availability.— Microhabitat use data were collected weekly from ≥30 randomly selected fish using a weekly generated random tag code list. During 2009, microhabitat use data were only collected during free-flowing conditions; however, during 2010 and 2011, a 0.2-m-diameter, hand-powered, ice auger was used to obtain microhabitat use data when surface ice was present. Microhabitat variables measured included total depth (m), bottom velocity (m/s), mean column velocity (m/s), dominant substrate, dominant cover type, distance from cover (m), and distance from bank (m). During 2010 and 2011, additional variables measured included presence–absence of anchor ice, presence–absence of frazil ice, surface ice coverage (%), and surface ice thickness (m). Frazil ice is a cluster of ice crystals suspended in supercooled (<0.0°C) riverine waters and is called anchor ice when it adheres to substrates (Brown et al. 2011).

Microhabitat availability data were collected using line-transect survey techniques, which can minimize measurement error and are more repeatable than visual techniques (McMahon et al. 1996; Stanfield and Jones 1998). Microhabitat availability data were collected during free-flowing base flow conditions. Microhabitat variables measured at each transect point corresponded to microhabitat use variables. Evenly spaced transects placed at right angles to the flow and positioned two mean stream widths apart were divided into evenly spaced points from which measurements were obtained (Simonson et al. 1994). For each reach evaluated, points represented equal-sized cells; on average, cell area was 2.03 m^2 (SD, 2.04; range, 0.36–6.25 m^2). A total of 147 transects were surveyed yielding 1,816 survey points, resulting in approximately 12 points per transect.

For both microhabitat use and availability, a top-set wading rod was used to measure depth to the nearest centimeter. A Marsh–McBirney digital flow meter (model

2000) was used to measure bottom and mean column velocity (m/s). Mean column velocity was measured at a depth 60% from the surface when depths were ≤0.75 m. For depths >0.75 m, velocity was measured at depths 20% and 80% from the surface and averaged to produce mean column velocity (McMahon et al. 1996). Dominant substrate was visually determined using a modified Wentworth particle size classification (Bovee 1986). Nearest dominant cover type was visually determined by establishing the presence–absence of cover and then determining distance from cover. Cover types used were "no cover," large wood (LW), small wood (SW), rootwad, emersed aquatic vegetation, submersed aquatic vegetation, terrestrial vegetation, undercut bank, and boulder. Large wood was defined as wood ≥10 cm in diameter, while SW was <10 cm in diameter (Meehan 1991). Cover type was considered associated with fish occurrence when cover was ≤2 m from the triangulated fish location.

Microhabitat analyses.— For microhabitat availability, all continuous moderate and low gradient microhabitat data distributions were compared using the Kolmogorov–Smirnov (KS) two-sample test (Sokal and Rohlf 1998). For categorical variables, an analogous likelihood-ratio chi-square test was used to detect differences in microhabitat availability between gradients. Dominant substrate and cover were treated as categorical variables for all analyses. Microhabitat use and availability were characterized by gradient type (moderate and low). Onset of winter was meteorologically based, rather than using the astronomical designation of winter (Huusko et al. 2007). Specifically, the first day of winter was determined based on water temperature (≤1.0°C) and ice presence. Subsequently, winter began on November 13, 20, and 2 during 2009, 2010, and 2011, respectively.

We evaluated the relationship between microhabitat use and availability using resource selection functions (RSF; Johnson et al. 2006). A RSF is any function that describes the relative probability of occupying resource units (i.e., relative probability of use) that exhibit varying characteristics (Boyce et al. 2002; Manly et al. 2002). Using this method, we evaluated the relationship between relative use and availability using logistic regression, where use and availability were coded as 1 and 0, respectively. As a function of employing radiotelemetry techniques, multiple observations were made on individual fish possibly violating independence assumptions. Observations of habitat use made within a year also were potentially dependent. To incorporate potential fish- and year-level dependence, logistic regression models included random effects (Gillies et al. 2006). All RSF models were fit using the statistical package lme4 (Bates et al. 2015) implemented in R statistical software (R Core Team 2015).

Prior to model selection, we calculated Pearson correlations between all pairs of continuous habitat measures (e.g., depth, current velocity). The categorical predictor variables for substrate and cover were binary coded (0, 1) with baseline categories of clay and no cover, respectively. Three additional binary predictors were created for season, gradient type, and ice presence with fall, the moderate-gradient reach, and ice present as baseline categories, respectively.

Our goal was to obtain the simplest, best-predicting RSF model for fall migrant and overwintering Chinook Salmon parr in Catherine Creek. Thus, we began our modeling by constructing a global RSF model using pairwise uncorrelated habitat variables based on previous habitat use studies (Hillman et al. 1987; Allen 2000). The global model did not contain main effects for season and gradient because the parameters would only reflect the relative differences in the number of detections of tagged fish between seasons and gradients and were not of interest. To account for potential within-year and fish dependence, we evaluated the fit of global models containing randomly varying intercepts and slopes corresponding to year and individual fish. These random effects were added to the model one at a time and were kept in the model if they decreased Akaike's information criterion with the small-sample bias adjustment (AIC_c) by at least two (Burnham and Anderson 2002). Random effects that were found to improve model fit were then used during model selection. To obtain the best approximating model, we fit all possible subsets of the global model with random effects (including all two-way interactions) using mixed-effects logistic regression. The best approximating RSF model was then selected using AIC_c. Goodness of fit of the global model with random effects and the best approximating model were assessed by examining residuals. Specifically, residuals were examined using (1) normal probability plots of the lower (site) level residuals, (2) plots of lower level residuals ordered by individual fish, and (3) plots of the empirical Bayes residuals by their corresponding chi-square scores (Raudenbush and Bryk 2002).

We based all inferences and predictions on the best-fitting model. The precision of the parameter estimates was assessed by calculating profile confidence limits using the R package lmerTest (Kuznetsova et al. 2014). Scaled odds ratios were calculated for selected parameter estimates to facilitate interpretation (Hosmer and Lemeshow 2000). Relative probability of use was calculated using the parameters from the best approximating model (Manly et al. 2002).

We used Bayesian statistical methods to construct gradient-specific microhabitat suitability models using RSFs (Thomas et al. 2004; Hightower et al. 2012). Microhabitat use and suitability can be drastically different; thus, pooled fall and winter moderate and low gradient microhabitat use data were compared with spatially analogous

microhabitat availability data to yield type III univariate habitat suitability criteria (HSCs; Bovee 1986; Newcomb et al. 2007). Microhabitat use data were pooled among years to yield all HSCs. Typically, pooling of multiyear biotelemetry data for analysis purposes is discouraged as this technique cannot account for potential fish- and year-level dependence; however, we justified pooling microhabitat use data because we randomly collected few observations from many individuals (Rogers and White 2007), and traditional HSC-type analyses will enable comparisons with previous Chinook Salmon HSC studies (Raleigh et al. 1986; Hillman et al. 1987; Rubin et al. 1991; Allen 2000; McHugh and Budy 2004; Holecek et al. 2009; Bidlack et al. 2014).

Microhabitat use and availability data were spatially (moderate and low gradient) stratified for all HSC analyses because microhabitat availability differed significantly between gradient types. Model parameters were estimated by comparing microhabitat use with landscape-wide availability (Boyce et al. 2002). We modeled fall and winter microhabitat use with a multinomial distribution, following the approach developed by Thomas et al. (2004). A multinomial distribution is used in instances where a trial produces one of several possible outcomes, such as a fish's selection of cobble (rather than clay or silt, for example) substrates for winter concealment (Hightower et al. 2012).

Binning is a requirement of using continuous data in a multinomial model, and data availability dictated our bin sizes. We incorporated Sturges (1926) equation as an objective approach to determine bin widths for all continuous variables (Newcomb et al. 2007), with the exception of variable distance from cover, as our data collection methods dictated that the maximum distance not exceed 2 m. Values considered at the ends of the suitability spectrum were grouped to increase sample size and reduce bin quantity (Harris and Hightower 2011). We rescaled relative use probabilities to a maximum value of 1 for all microhabitat variables, as scaled relative use probabilities represent microhabitat suitability estimates (Harris and Hightower 2011; Hightower et al. 2012).

Bayesian statistics combine prior information with new data to produce refined parameter estimates (McCarthy 2007). Alternatively, we used uninformative prior distributions to produce new HSCs based solely on the data. Uncertainty for each HSC was characterized using a 95% Bayesian credible interval. For each microhabitat variable, we estimated the probability of no preference (Bayesian P-value) by comparing the observed and simulated data sets produced under the null hypothesis of no preference (Thomas et al. 2004; Hightower et al. 2012). We used Markov chain Monte Carlo methods to sample posterior distributions, including three mixing chains with ≤100,000 iterations each, and a ≤ 50,000-iteration burn-in period with no thinning. Model convergence was assessed by calculating the r statistic (Gelman and Hill 2007). OpenBUGS open-source software was used for all Bayesian statistical analyses (Spiegelhalter et al. 2010). OpenBUGS was called through program RStudio via the R2OpenBUGS package (Sturtz et al. 2005; R Core Team 2015).

In a multivariate approach, all continuous microhabitat variables were analyzed with a principal component analysis (PCA) to provide a visual representation for evaluating random or nonrandom habitat use. Principal component analysis allows collective interaction among multiple microhabitat variables to be ranked by importance by creating sequential uncorrelated linear combinations (i.e., principal component) that maximize variation explanation (Kwak and Peterson 2007). Principal components (PCs) with eigenvalues ≥ 1.0 were retained as a practical breakpoint (Kwak and Peterson 2007). Habitat availability scoring coefficients were used to calculate microhabitat use PC scores. Due to the variability of microhabitat availability between the moderate- and low-gradient reaches, PCAs were performed separately for each gradient reach. The statistical software package SAS/STAT 9.2 (SAS Institute 2009) was used to conduct all PCA analyses. A significance level (α) of 0.05 was applied to all statistical tests.

RESULTS

Fish Tagging

From 2009 to 2011, the total number of fish collected exhibited a mean length of 80.7 mm (SD, 8.7; range, 48–108 mm) and mean weight of 6.0 g (SD, 1.9; range, 1.2–14.2 g). In total, 300 juvenile Chinook Salmon fall migrants were radio-tagged. Tagged fish had a mean length of 95.5 mm (SD, 5.8; range, 89–107 mm) and mean weight of 9.8 g (SD, 1.1; range, 8.5–14.2 g). Average tag burden was 2.7% (SD, 0.003; range, 1.8–3.3%). During tagging, water temperatures ranged from 0.0°C to 14.0°C. Implanted tags exhibited a mean tag life of 99.3 d (SD, 14.8; range, 46–123 d), 83.1 d (SD, 21.2; range, 35–118 d), and 81.6 d (SD, 24.3; range, 40–120 d) for fish relocated during 2009, 2010, and 2011, respectively. Cumulatively, 13 (4.3%) tagged fish were confirmed mortalities (bird and mink predation) or were cases of tag expulsion (i.e., recovered tags). Fifteen (5.0%) tagged fish were not relocated following release.

Ice Conditions and Microhabitat Availability

During winter 2010 and 2011, frazil ice was observed at 36 (6.2%) locations. Surface and anchor ice were present at 124 (21.3%) and 32 (5.5%) locations, respectively. Mean surface ice thickness was 0.03 m (range, 0.01–0.25 m).

Moderate and low gradient microhabitat availability frequency distributions were significantly different for all variables (KS test: $D \geq 0.12$, $P < 0.0001$; chi-square: $\chi^2 \geq 709.27$, df ≤ 7, $P < 0.0001$). The moderate-gradient reach exhibited shallower depths with swifter currents flowing over coarser substrates. Dominant substrates available in the moderate-gradient reach ranged from clay to bedrock, while dominant substrates in the low-gradient reach ranged from clay to sand (Table 1). Dominant cover type within the moderate-gradient reach was SW, while "no cover" was the dominant cover type in the low-gradient reach (Table 1). Specifically, cover was absent from

19.2% and 46.3% of moderate- and low-gradient reaches, respectively.

Microhabitat Use and Gradient

During fall and winter, fish occupied deeper water in the low-gradient reach than in the moderate-gradient reach (Table 1). The use of slow bottom and mean column velocities was prevalent in both reaches (Table 1). Cobble was the modal dominant substrate used in the moderate-gradient reach, while silt was the modal dominant substrate used in the low-gradient reach (Table 1). For both reaches, occupancy typically occurred near the

TABLE 1. Sample size, mean, SD, minimum, and maximum statistics for fall and winter microhabitat use and availability from moderate- and low-gradient reaches of Catherine Creek for fall-migrant spring Chinook Salmon.

Variable and statistic	Moderate gradient		Low gradient	
	Use	Available	Use	Available
Depth (m)				
N	497	793	432	1,020
Mean	0.64	0.27	0.83	0.81
SD	0.34	0.24	0.37	0.68
Minimum–maximum	0.04–2.20	0.00–1.30	0.12–2.50	0.00–3.20
Bottom velocity (m/s)				
N	471	793	422	1,020
Mean	0.08	0.16	0.05	0.08
SD	0.11	0.19	0.09	0.09
Minimum–maximum	0.00–0.74	0.00–1.50	0.00–0.57	0.00–0.45
Mean velocity (m/s)				
N	470	793	425	1,020
Mean	0.17	0.29	0.12	0.22
SD	0.18	0.29	0.12	0.19
Minimum–maximum	0.00–0.96	0.00–2.00	0.00–0.65	0.00–0.76
Dominant substrate				
N	500	793	432	1,020
Mode	Cobble	Gravel	Silt	Silt
SD	1.05	1.28	0.85	0.73
Minimum–maximum	Clay–bedrock	Clay–bedrock	Clay–boulder	Clay–sand
Distance from bank (m)				
N	499	793	435	1,021
Mean	2.09	2.10	2.36	3.75
SD	1.44	1.59	1.85	3.25
Minimum–maximum	0.00–10.00	0.00–6.80	0.00–12.00	0.00–12.50
Cover				
N	505	793	432	1,020
Mode	Boulder	SW	LW	No cover
Distance from cover (m)				
N	448	642	374	548
Mean	0.57	0.63	0.45	0.52
SD	0.64	0.62	0.56	0.60
Minimum–maximum	0.00–2.00	0.00–2.00	0.00–2.00	0.00–2.00

riverbank (Table 1). Boulders were most frequently used as cover within the moderate-gradient reach, while LW was predominantly used in the low-gradient reach. Most fish relocations occurred in close proximity to cover in the moderate- and low-gradient reaches, and a majority (65%) were ≤0.5 m from cover.

During fall and winter, mean total depth use was greater than that available for both the moderate- and low-gradient reaches (Table 1), indicating that spring Chinook Salmon parr disproportionally occupied the deepest water available during fall and winter rearing. Moderate-gradient mean bottom velocity use was slower than that available, indicating that fish occupied the slower bottom velocities available, and to a lesser extent, a similar trend was present for the low-gradient reach (Table 1). A similar relationship of slower velocities being used than were available was documented for variable mean column velocity for both reaches (Table 1). Modal available dominant substrate in the moderate gradient was gravel, while the modal dominant substrate used was cobble, indicating that coarser available substrates were occupied. Silt was most commonly available and used by overwintering fish in the low-gradient reach (Table 1). Mean distance from the bank of occupied locations was similar to the corresponding availability mean for the moderate-gradient reach (Table 1). In contrast, fish occupied locations disproportionately closer to the bank in the low-gradient reach (Table 1). Fish occupying the moderate-gradient reach most frequently used boulders as cover, while LW was most commonly used in the low-gradient reach (Table 1). For both gradient types, mean distance from cover use was less than the corresponding availability (Table 1).

Relative Probability of Use Model

Bottom velocity and mean column velocity were strongly correlated (Pearson $r = 0.82$). Therefore, we fit two global models with each current measure and selected the global model containing mean column velocity because it fit better than bottom velocity ($\Delta AIC_c = 201$). The random effects that best explained variation in habitat use among fish and years in the global RSF model included a randomly varying intercept corresponding to individual fish and a depth parameter that varied among years.

The best approximating Chinook Salmon parr microhabitat RSF model contained total depth and a quadratic term, tag burden, mean column velocity, distance from cover and bank, three substrate categories, three cover categories, and five two-way interactions between total depth and tag burden, distance from bank and winter, silt substrate and winter, and low-gradient reach with LW and submerged aquatic vegetation (Table 2).

Tag burden did not appear to have an influence on microhabitat use, with the exception of a possible interaction with depth (Figure 2). For the entire study area, parameter estimates suggested that the greatest occupied depth for Chinook Salmon parr was between 1.0 and 1.5 m, and fish with a heavy tag burden tended to use more moderate depths (Figure 2). Throughout the study area, substrate appeared to have a considerable influence on fish rearing locations (Figure 2). Scaled odds ratios suggested that Chinook Salmon parr were 11.2 times more likely to use cobble substrates relative to other substrates, whereas fish were 4.1 times less likely to use silt substrates (Table 2). However, the interaction between silt and winter indicated that fish were more likely to use silt substrates during winter (Table 2). For the study area, cover also appeared to have a very strong influence; compared with other cover types, use was 7.5, 6.5, and 4.1 times more likely for rootwad, LW, and undercut bank, respectively (Table 2; Figure 2). Use of LW and submerged aquatic vegetation was greater in the low-gradient reach. For both gradient reaches cumulatively, model predictions suggested that distance from bank had a weaker influence on the relative probability of use by Chinook Salmon parr, and the influence was lower during winter (Figure 2).

Bayesian Suitability Models

The probability of observing these gradient-specific patterns under the null hypothesis of no preference was estimated to be $P \leq 0.001$ for all variables, with the exception of the observed dominant substrate pattern in the low-gradient reach ($P = 0.010$). Despite our pooled microhabitat use, data sets exhibiting a degree of dependence on year and fish (i.e., suggestive of narrow credibility intervals), our Bayesian suitability scores displayed wide 95% credibility intervals, indicating that dependence may have been minimal.

Deep depths (≥ 1.15 m) were most suitable in the moderate-gradient reach, while moderate depths (0.69–0.92 m) were most suitable in the low-gradient reach (Figure 3). Slow bottom velocities (0.00–0.11 m/s) were most suitable for both reaches (Figure 3). Similarly, slow to moderate mean column velocities (0.0–0.3 m/s) were most suitable in both reaches (Figure 3). Cobble and boulder substrates were most suitable within the moderate-gradient reach, while silt and clay were most suitable in the low-gradient reach (Figure 3). Large wood, undercut bank, and rootwad were the most suitable cover types in the moderate-gradient reach, while LW was most suitable in the low-gradient reach (Figure 3). Small to moderate distances to cover (0.0–1.5 m) were most suitable in both the moderate- and low-gradient reaches (Figure 3). For both gradient types, distances near the riverbank (0.91–2.73 m) were most suitable (Figure 3).

TABLE 2. Parameter estimates (SE in parentheses), lower and upper limits of 95% CIs, unit scalers, and scaled odds ratios of the best approximating resource selection function for Catherine Creek fall-migrant and overwintering Chinook Salmon parr. Parameter estimates are on a logit scale, and random effect estimates are SDs.

Parameter[a]	Estimate	Lower	Upper	Unit scaler	Scaled odds ratio
Fixed effects					
Total depth	14.92 (1.100)	12.763	17.083		
Total depth^2	−5.179 (0.239)	−5.644	−4.711		
Tag burden	1.153 (0.295)	0.571	1.716		
Mean column velocity	−5.432 (0.275)	−5.976	−4.883	0.1	0.58
Distance from cover	−0.190 (0.044)	−0.275	−0.102	0.5	0.91
Distance from bank	−0.500 (0.037)	−0.572	−0.427	0.5	0.78
Cobble substrate	2.413 (0.108)	2.206	2.620	1.0	11.17
Gravel substrate	1.481 (0.118)	1.252	1.715	1.0	4.40
Silt substrate	−1.403 (0.173)	−1.747	−1.068	1.0	0.25
Large wood	1.809 (0.120)	1.571	2.043	1.0	6.10
Rootwad	2.015 (0.179)	1.663	2.367	1.0	7.50
Undercut bank	1.408 (0.202)	1.006	1.800	1.0	4.09
Submerged aquatic vegetation	−3.751 (0.712)	−5.116	−2.383	1.0	0.02
Total depth × tag burden	−1.235 (0.351)	−1.911	−0.546		
Distance from bank × winter	0.163 (0.031)	0.101	0.223		
Winter × silt	1.051 (0.179)	0.693	1.393		
Low-gradient reach × large wood	1.931 (0.158)	1.629	2.233		
Low-gradient reach × submerged aquatic vegetation	3.532 (0.744)	2.074	4.980		
Random effects					
Individual fish	0.042 (0.011)	0.026	0.063		
Total depth (varied by year)	0.531 (0.049)	0.444	0.616		
Total depth^2 (varied by year)	0.344 (0.030)	0.286	0.400		

[a]Baseline substrate categories included clay, bedrock, and boulder; baseline cover categories included no cover, emergent aquatic vegetation, terrestrial vegetation, boulder, and undercut bank.

Multivariate Microhabitat Use

For the moderate- and low-gradient reaches, multivariate PCA identified two contrasting habitat gradients each. For the moderate-gradient reach, PC1 characterized a habitat gradient of slow velocities near cover (low scores), increasing to swift velocities lacking cover (high scores; Table 3; Figure 4). Principal component 2 characterized a habitat gradient from shallow near-bank water (low scores) to deep midchannel water (high scores; Table 3; Figure 4). For the low-gradient reach, PC1 described a habitat gradient of slow mean column currents close to cover and the riverbank (low scores) to swift midchannel mean column currents lacking cover (high scores; Table 3; Figure 4). Principal component 2 described a habitat gradient of slow bottom currents and deep depths (low scores) increasing to fast bottom currents and shallow depths (high scores; Table 3; Figure 4). For the moderate- and low-gradient reaches, PC1 explained a cumulative variance of 45.6% and 64.0%, respectively (Table 3). For the moderate- and low-gradient reaches, PC2 explained a cumulative variance of 70.5% and 84.1%, respectively (Table 3).

In the moderate-gradient reach, fish occupied habitat in slow currents near cover (low PC1 scores) and rarely occupied swift currents lacking cover (high PC1 scores; Table 3; Figure 4). In addition, fish were associated with moderate to deep midchannel depths (moderate to high PC2 scores; Table 3; Figure 4). In the low-gradient reach, fish primarily occupied moderate to deep depths when slow currents and near-bank cover co-occurred (low PC1 and PC2 scores) and avoided highly available deep midchannel water exhibiting moderate to swift currents lacking cover (high PC1 scores; Table 3; Figure 4).

DISCUSSION

Using radiotelemetry and habitat assessment techniques, we successfully addressed our study objectives and determined spatial and temporal microhabitat use and suitability of fall migrant and overwintering spring Chinook Salmon parr. Radiotelemetry enabled the collection of minimally biased microhabitat use data during surface ice conditions, which permitted the comprehensive and
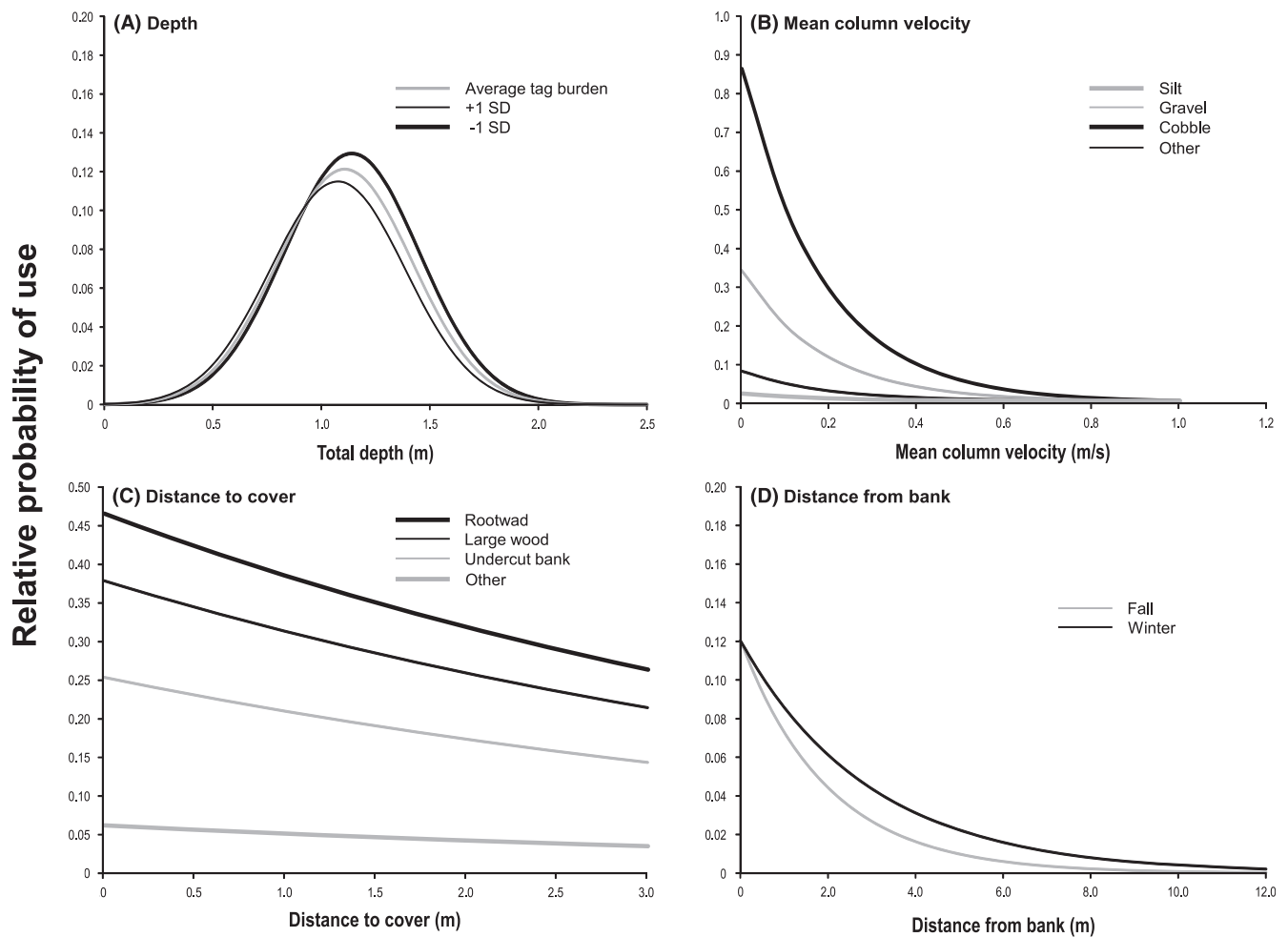
FIGURE 2. Predicted relative probability of use versus **(A)** depth for average tag burden, **(B)** mean column velocity for specific substrates, **(C)** distance from cover for specific cover types, and **(D)** distance from bank during specific seasons. Predictions were made using the best approximating model and average observed values of continuous microhabitat variables, fall season, moderate-gradient reach, no cover, and clay substrate.

quantitative characterization of Chinook Salmon fall migration and overwintering critical habitat. The findings of this thorough study substantially advance juvenile salmonid overwintering ecology and are critical to guide habitat conservation and restoration of this and other spring Chinook Salmon populations.

Microhabitat Use and Availability

Our mixed-effects logistic regression RSF model indicated that winter microhabitat use by Catherine Creek Chinook Salmon parr during free-flowing and surface ice conditions were not considerably different throughout the study area. Similarly, Whalen et al. (1999) reported that overwintering Atlantic Salmon *Salmo salar* parr occupied similar depths and velocities during free-flowing and surface ice conditions, exemplifying a degree of microhabitat use specificity. However, winter microhabitat use

specificity may not be universal among juvenile salmonids (Simpkins et al. 2000).

Generally, microhabitat use was spatially (moderate and low gradient) and temporally (fall and winter) similar during free-flowing conditions, indicating fall migrant and overwintering Chinook Salmon parr exhibit specific habitat preferences despite seasonal- and reach-specific diverse microhabitat availability. Highly suitable winter habitats minimize energetic cost, while simultaneously maximizing protection from environmental inconsistency (Cunjak 1996; Brown et al. 2011). Moderate to swift winter currents and associated forced swimming events increase energy depletion and mortality (Simpkins et al. 2004). To maximize energy conservation, overwintering juvenile salmonids are typically described as preferring a narrow range of habitats composed of deep pools supporting slow velocities and coarse substrates (Huusko et al. 2007;
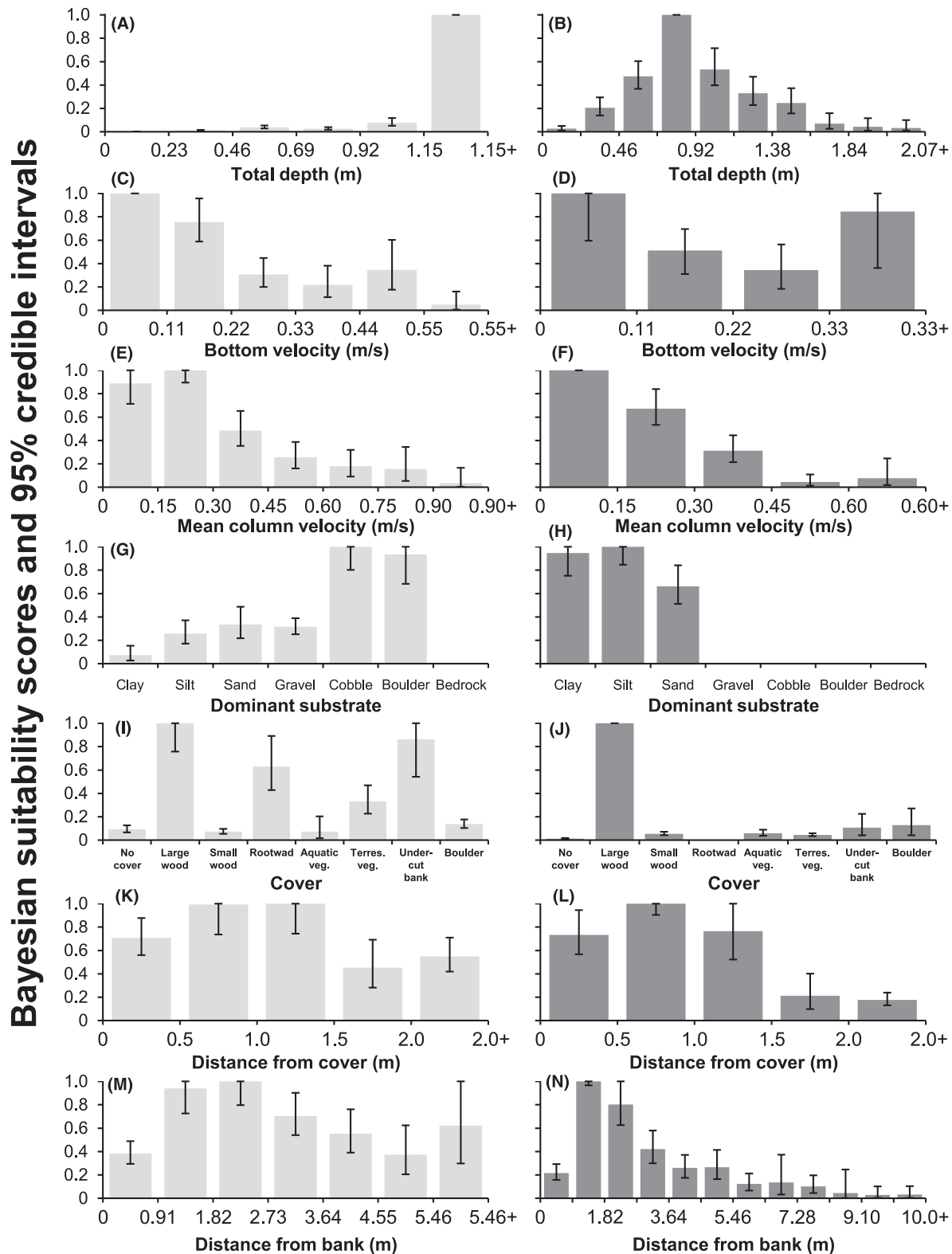
FIGURE 3. Moderate- and low-gradient Bayesian microhabitat suitability scores and 95% credible intervals for Catherine Creek spring Chinook Salmon for variables **(A, B)** total depth, **(C, D)** bottom velocity, **(E, F)** mean column velocity, **(G, H)** dominant substrate, **(I, J)** cover, **(K, L)** distance from cover, and **(M, N)** distance from bank during fall and winter. The light gray Bayesian suitability histograms represent the moderate-gradient reach, and the dark gray histograms represent the low-gradient reach.

TABLE 3. Fall and winter principal component (PC) loadings for spring Chinook Salmon parr microhabitat use and availability, eigenvalues, and cumulative variance explained for specified gradients (moderate and low). Principal components were derived based on microhabitat availability data during winter base flows; seasonal PC scores were calculated for both moderate- and low-gradient available microhabitat and corresponding microhabitat use. Loadings in bold italics were interpreted to have significantly influenced the corresponding PC.

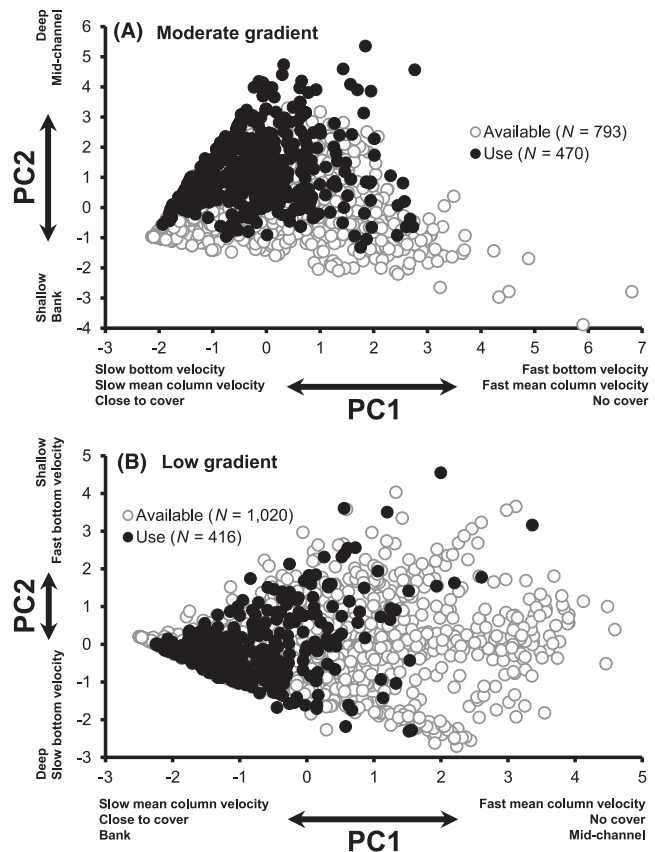| Variable or statistic	Moderate gradient		Low gradient	
	PC1	PC2	PC1	PC2
N				
Available	793		1,020	
Use	470		416	
Depth (m)	0.249	*0.681*	0.445	*−0.438*
Bottom velocity (m/s)	*0.562*	−0.318	0.384	*0.681*
Mean column velocity (m/s)	*0.605*	−0.179	*0.476*	0.422
Distance from cover (m)	*0.407*	−0.162	*0.446*	−0.270
Distance from bank (m)	0.299	*0.613*	*0.479*	−0.305
Eigenvalue	2.28	1.24	3.20	1.01
Cumulative variance explained (%)	45.6	70.5	64.0	84.1

FIGURE 4. Plots of PC scores for Chinook Salmon parr microhabitat use and available microhabitat during fall emigration and winter rearing in Catherine Creek, northeastern Oregon: **(A)** moderate gradient, **(B)** low gradient. Principal component loadings are provided in Table 3.

Brown et al. 2011). In contrast, Hillman et al. (1987) and Allen (2000) reported that overwintering Chinook Salmon parr occupied a wide range of depths and substrates during winter compared with summer and fall, but likewise reported strict occupancy of absent to slow winter currents. Similarly, Catherine Creek fall migrants and overwintering parr exhibited stricter occupancy of slow velocities, while other microhabitat variables demonstrated greater levels of variation. Based on previous research (Hillman et al. 1987; Allen 2000) and our HSC and PCA results, slow currents appear essential to highly suitable fall migration and overwintering habitat, while co-occurring depth and substrate size, although important, appear less critical.

Microhabitat Suitability

Careful thought and application must be implemented during the analytical stages of generating HSC models, because HSCs are widely considered to be the biological underpinning in professional conclusions pertaining to habitat quality and large-scale habitat management decisions (Cheslak and Garcia 1988; Newcomb et al. 2007). When producing type III HSCs, pooling data from different reaches can introduce bias and reduce precision as a function of temporal and spatial differences, as well as unequal representation from the data sources (Bovee

1986). Owing to the vast differences in microhabitat availably between the moderate- and low-gradient reaches of Catherine Creek, our gradient-specific suitability HSCs slightly diverge from our best-fitting, mixed-effect, logistic regression RSF model results, as these are representative of the entire study area. The largest discrepancy between these two complementary analyses occurred for the microhabitat variable, total depth. Our best-fitting, mixed-effect, logistic regression RSF model indicated that relative probability of use begins to decrease between depths of 1.0 and 1.5 m, while our Bayesian total depth HSC indicated that depths in this range are optimal in the moderate-gradient reach. Thus, we recommend that fisheries managers and restoration ecologists place strong emphasis on our best-fitting, mixed-effect, logistic regression RSF model's total depth results when addressing large areas exhibiting variable gradients; however, our gradient-specific depth HSCs may be most appropriate pertaining to smaller reaches exhibiting specific gradient types. Our Bayesian suitability and mixed-effects logistic regression RSF model results should be viewed as complementary.

Our Bayesian moderate-gradient HSC for depth indicated deep depths ($\geq$0.92 m) were most suitable (i.e., optimal) for overwintering Chinook Salmon parr, while the low-gradient reach depth HSC designated moderate depths (0.69–0.92 m) as optimal. In accord with our low-gradient reach depth HSC, Allen (2000) reported that shallow to moderate depths (~0.3–0.9 m) were optimal in the Yakima River basin, Washington, and that few fish were observed overwintering in deep depths > 1.2 m. During the present study, microhabitat availability surveys revealed that deep depths were typically associated with slow velocities and cover in the moderate-gradient reach, while deep depths in the low-gradient reach were associated with swift currents and no cover. We postulate that Catherine Creek low-gradient reach depths $\geq$ 0.92 m were less suitable for overwintering Chinook Salmon parr because co-occurring variables (midchannel swift currents lacking cover) cumulatively created unsuitable overwintering conditions. Suitable concurrent variables likely explain why we observed fish overwintering in deep depths in the moderate-gradient reach, while Allen (2000) did not, and emphasize that multiple interrelated microhabitat variables influence habitat selection.

Habitat selection and suitability are considerably influenced by habitat availability (Newcomb et al. 2007). Dominant substrate HSCs indicated that cobble and boulders were most suitable in the moderate-gradient reach, while fine substrates were most suitable in the low-gradient reach. Generally, winter use and high suitability of coarse substrates accord with previous research (Van Dyke et al. 2009); however, our finding of highly suitable fine substrates in the low-gradient reach is relatively novel. During winter, use of fine substrates is presumed to be a consequence of juvenile salmonids occupying cover as slow-velocity refuge or unembedded coarse substrates are rare (Hillman et al. 1992; Allen 2000). A plausible explanation for highly suitable fine substrates in the low-gradient reach is that coarser substrates were extremely rare. The absence of coarse concealment substrates and scarce refuge cover in the Grande Ronde Valley during dynamic and energetically taxing winter hydrological conditions may directly contribute to high mortality levels exhibited by Catherine Creek Chinook Salmon parr (Jonasson et al. 2016). Furthermore, parr that survive winter in the Grande Ronde Valley may exhibit low condition levels associated with a lack of concealment substrates, which could contribute to high delayed smolt mortality associated with seaward migration during high spring flows (March–June: Monzyk et al. 2009).

Parr did exhibit greater use of aquatic vegetation (e.g., American waterweed *Elodea canadensis*) as concealment cover in the Grande Ronde Valley, which may indicate historic predisturbance habitat use patterns in Catherine Creek. However, aquatic vegetation was relatively rare in the Grande Ronde Valley, functioning as dominant cover in only 5% of the study area. Several factors may be currently inhibiting aquatic vegetation in the Grande Ronde Valley, including presence of nonindigenous species (e.g., Common Carp *Cyprinus carpio*) and irrigation withdrawals (e.g., summer stream dewatering; authors' personal observations). Generally, Common Carp have detrimental effects on native fishes, water quality, macrophytes, and aquatic invertebrate communities (Forester and Lawrence 1978; Lougheed et al. 1998; Parkos et al. 2003; Miller and Crowl 2006). Future research designed to elucidate the degree of aquatic vegetation degradation in the Grande Ronde Valley and any associated negative consequences to juvenile Chinook Salmon may be justified.

Cover HSCs indicated that the cover types LW, undercut bank, and rootwad were most suitable in the moderate-gradient reach, while LW was most suitable in the low-gradient reach. Salmonid winter habitat occupancy is largely dependent on LW presence (Heifetz et al. 1986; Cederholm et al. 1997; Solazzi et al. 2000). In addition to LW being highly suitable juvenile salmonid winter cover, fall and early winter movement is lower when pools exhibiting LW cover are sufficiently available (Bjornn 1971; Tschaplinski and Hartman 1983; Martin et al. 1986; McMahon and Hartman 1989). Decreased movement during harsh winter conditions can be energetically beneficial and increase survival of juvenile salmonids (Lucas and Baras 2001; Brown et al. 2011).

Habitat Suitability Criteria and Transferability

Habitat suitability criteria, adjusted for habitat availability, can be considerably different from utilization criteria (Baldridge and Amos 1981; Newcomb et al. 2007). There are multiple commonalities between our Catherine Creek type III HSCs and the utilization HSCs (type II) reported by Allen (2000); however, discrepancies associated with depth and substrate are present. Criteria curves based solely on microhabitat use are type II criteria and therefore only reliably applicable to the water body of origin (Bovee 1986). Establishing site- and population-specific HSCs are prohibitively expensive and time consuming, so HSCs that exhibit a high degree of transferability are extremely valuable (Newcomb et al. 2007). Our type III HSCs may potentially be applied to overwintering Chinook Salmon parr (stream-type: Wydoski and Whitney 2003) throughout their current range owing to the high transferability of type III HSCs (Bovee 1986; Newcomb et al. 2007).

Typically, HSCs exhibiting a high degree of transferability can be used throughout a species' regional geographic range (Bovee 1986; Newcomb et al. 2007). In contrast, several researchers have demonstrated that HSCs can exhibit low transferability (Sheppard and Johnson 1985; Kwak et al. 1992; Rosenfeld et al. 2005). Reasons

that HSCs may fail convergence analyses and ultimately exhibit poor transferability are numerous and include prey availability differences (Rosenfeld et al. 2005), competition (Gatz et al. 1987; Schlosser 1987), seasonal microhabitat use shifts (Hillman et al. 1987; Holecek et al. 2009), size-class differences (Moyle and Baltz 1985), microhabitat availability differences (DeGraaf and Bain 1986), fish density differences (Rosenfeld et al. 2005), predation differences (Orth 1987), homogeneous microhabitat availability (Bovee 1986; Freeman et al. 1997), and insufficient sample sizes (Thomas and Bovee 1993). However, successful convergence between our moderate- and low-gradient HSCs and previously reported criteria (e.g., Allen 2000) are indicative of local and regional high transferability potential. Nevertheless, caution should be employed to prohibit uncritical across-stream use of general microhabitat models (e.g., HSCs) before possible convergence and transferability limitations are realized (McHugh and Budy 2004; Newcomb et al. 2007).

Multivariate Microhabitat Use and Habitat Restoration

Fish occupy habitat based on concurrent and interrelated microhabitat conditions (Heggenes et al. 1991; Mäki-Petäys et al. 2002). Our multivariate analyses (PCA) indicated that deep depths exhibiting slow currents and cover were occupied within the moderate-gradient reach, while moderate to deep depths supporting slow currents near cover and the riverbank were occupied in the low-gradient reach. Thus, habitat restoration designed to increase the quality and quantity of moderate-gradient winter habitat for Chinook Salmon parr could focus on implementation of alcoves, main-channel pools, backwaters, side channels, and beaver ponds (Arend 1999). Similarly, restoration efforts that create debris jams and beaver ponds are likely to provide suitable winter habitat in low-gradient portions of Catherine Creek and the Grande Ronde Valley.

Generally, fish habitat restoration approaches attempt to engineer solutions to environmental degradation (e.g., Meffe 1992); however, engineered habitats rarely replace the full suite of lost original habitat conditions (Bisson et al. 1997) and typically fail to fully mitigate losses to fisheries (Hilborn and Winston 1993; Roni et al. 2002). Instream habitat restoration limitations highlight the importance of restoring and conserving natural processes that encourage physical and biological health and resilience (Reeves et al. 1991; Waples et al. 2009). Often though, even when species-, life stage-, and season-specific HSCs and multivariate habitat use analyses are available, constructing instream habitat structures that create habitat exhibiting concurrent suitable microhabitats can be a challenge (Sedell and Beschta 1991; Bisson et al. 1997). Placement of LW structures that mimic natural processes by incorporating materials consistent in size, type, location,

and orientation to those occurring in natural channels is paramount (Bisson et al. 1997; Roni et al. 2002). Anecdotally, we observed a pattern pertaining to flow direction, channel morphology, and riparian vegetation that was associated with highly occupied pools. Generally, occupied pools were preceded by a 30–50-m straight riffle and positioned at the base of a large live tree (e.g., black cottonwood *Populus trichocarpa*) or a cluster of trees where stream flow abruptly changed flow direction (e.g., 90° turn). In addition to engineered LW structures, stream restoration ecologists attempting to restore mainstream pools for overwintering Chinook Salmon parr may consider incorporating existing live large trees by redirecting the stream channel into existing rootwads followed by a 90° turn in flow direction.

Historically, lower Catherine Creek and the Grande Ronde Valley supported extensive beaver complexes and lentic-like habitats (e.g., Tule Lake) before their removal during the late-1800s (Gildemeister 1998). Space is the primary factor regulating lotic fishes during winter, and habitats such as large backwater areas and beaver ponds are preferred salmonid winter habitats that exhibit concurrent highly suitable microhabitats (Cunjak 1996). Compared with other overwintering habitats such as tributaries and sloughs, extensive loss of beaver pond habitat can drastically decrease winter smolt production capacity (Pollock et al. 2004). Beaver reintroduction, management, and protection may be a low-cost and sustainable tool to enhance salmonid winter habitat (Pollock et al. 2004; Kemp et al. 2012) throughout Catherine Creek and the Grande Ronde Valley.

Recently, salmonid habitat improvement techniques, such as beaver dam support and beaver dam analogue structures, have been developed to encourage, maintain, and mimic beaver activity in predefined areas (Beechie et al. 2010). In the short term, beaver dam support and beaver dam analogue structures facilitate pools and increase complexity; however, in the long term, these structures promote streambed aggradation, elevate the floodplain water table, increase summer flows, lower water temperatures, narrow the stream channel, increase sinuosity, and increase riparian vegetation (Pollock et al. 2003, 2007; Beechie et al. 2010; Kemp et al. 2012). Restoration actions that reactivate floodplain habitat increase hydraulic retention time through increased habitat complexity and hyporheic flow (Lamberti et al. 1989; Pearsons et al. 1992; Johnson 2004), which are beneficial to juvenile salmonids occupying off-channel habitat during winter low-flow periods (White et al. 1987; Evans et al. 1998; Clark et al. 1999; Johnson 2004).

Beaver pond complexes and associated marshlands facilitate concurrent and interrelated microhabitat conditions (deep depths with slow velocities and cover: Collen and Gibson 2001) that correspond to those identified as

highly suitable and concurrently used during the current study. The magnitude and value of suitable habitat provided by historic upper Grande Ronde Valley beaver complexes and marshlands to overwintering Chinook Salmon parr is uncertain. Based on our HSC and PCA results, we propose that the predisturbance marshland ecosystem in the Grande Ronde Valley may have been critical keystone habitat for overwintering Catherine Creek Chinook Salmon parr due to the diverse, complex, and heterogeneous qualities associated with lentic-like habitat nodes within lotic ecosystems (Collen and Gibson 2001; Power 2001). Degradation of critical keystone habitat negatively impacts dependent fish populations disproportionately relative to the proportion of the ecosystem that habitat comprises (Power 2001). Future restoration targeting reestablishment of a marshland ecosystem coupled with postrestoration evaluation research designed to investigate overwintering behavior (e.g., movement), habitat use, growth, and survival may prove valuable toward understanding the overwintering potential for Chinook Salmon parr in the upper Grande Ronde Valley.

Management and Restoration Implications

Over the past two centuries, anthropogenic modifications to Catherine Creek and the Grande Ronde Valley have resulted in altered habitat availability; thus, significant restoration initiatives will likely be required to restore ecological form and functions that represent the historical template. If upper Grande Ronde Valley marshlands, beaver complexes, and Tule Lake were historical critical keystone overwintering habitats, then restoration actions that successfully restore such an ecosystem to lower Catherine Creek could drastically benefit overwintering spring Chinook Salmon parr. However, extensive restoration of beaver complexes and marshland habitat within the upper Grande Ronde Valley may be an unrealistic immediate restoration objective due to current water (e.g., irrigation withdrawals) and land use practices (e.g., agriculture). Until large-scale restoration opportunities are available, multiple small-scale restoration actions that provide deep pools with slow velocities and cover (e.g., beaver complexes, off-channel ponds, and main-stem pools) could be pursued upstream from the Grande Ronde Valley.

Overwinter survival and smolt abundance have been correlated with slow-water habitat quantity and stream length (Bradford et al. 1997; Sharma and Hilborn 2001). Historical agriculture practices in the smaller valleys of upper Catherine Creek decreased stream sinuosity, stream length, and stream–floodplain connectivity (Nowak 2004), and these practices likely directly decreased slow-water habitat quantity. Vital to the concept of small-scale overwintering habitat restoration upstream from the Grande Ronde Valley is increasing the quantity of slow-water habitat. Restoration actions that restore sinuosity, increase stream length,

and reconnect the floodplain to promote off-channel ponds (e.g., beaver reservoir complexes) will likely increase overwinter rearing habitat quantity (Richards et al. 1992).

Freshwater rearing habitat is important for the recovery of Chinook Salmon populations in the Snake River basin (McHugh et al. 2004). Often though, the ecological and habitat needs of Pacific salmon are at odds with human activities, and co-existence is regularly a challenge (Quinn 2005). Instream restoration can be beneficial toward improving lotic system habitats (Hillman et al. 1987; Gowan et al. 1994) and increasing juvenile salmonid abundance and density (Quinn and Kwak 2000). But, to achieve maximum habitat restoration benefit, knowledge of critical habitats specific to species, life stage, and season are essential. We recommend habitat restoration objectives that intently focus on incorporating designs that yield concurrent and interrelated microhabitat combinations that collectively create critical habitats. Our fall and winter microhabitat use and suitability data provide fish managers and habitat restoration ecologists both moderate- and low-gradient habitat restoration guidance throughout Catherine Creek and the Grande Ronde Valley, and perhaps the Pacific Northwest.

REFERENCES

Achord, S., P. S. Levin, and R. W. Zabel. 2003. Density-dependent mortality in Pacific salmon: the ghost of impacts past? Ecology Letters 6:335–342.

Adams, N. S., D. W. Rondorf, S. D. Evans, and J. E. Kelly. 1998a. Effects of surgically and gastrically implanted radio transmitters on growth and feeding behavior of juvenile Chinook Salmon. Transactions of the American Fisheries Society 127:128–136.

Adams, N. S., D. W. Rondorf, S. D. Evans, J. E. Kelly, and R. W. Perry. 1998b. Effects of surgically and gastrically implanted radio transmitters on swimming performance and predator avoidance of juvenile Chinook Salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences 55:781–787.

Allen, M. A. 2000. Seasonal microhabitat use by juvenile spring Chinook Salmon in the Yakima River basin, Washington. Rivers 7:317–332.

Arend, K. K. 1999. Classification of streams and reaches. Pages 47–56 *in* M. B. Bain and N. J. Stevenson, editors. Aquatic habitat assessment. American Fisheries Society, Bethesda, Maryland.

Bach, L. B. 1995. River basin assessment: upper/middle Grande Ronde River and Catherine Creek. Oregon Department of Environmental Quality, Portland.

Baldridge, J. E., and D. Amos. 1981. A technique for determining fish habitat suitability criteria: a comparison between habitat utilization and availability. Pages 251–258 *in* N. B. Armantrout, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Bethesda, Maryland.

Bates, D., M. Mächler, B. Bolker, and S. Walker. 2015. Fitting linear mixed-effects models using lme4. Journal of Statistical Software 67:1–48.

Beamish, R. J., and D. R. Bouillon. 1993. Pacific salmon production trends in relation to climate. Canadian Journal of Fisheries and Aquatic Sciences 50:1002–1016.

Beckham, S. D. 1995. Grande Ronde River, Oregon: river widths, vegetative environment, and conditions shaping its condition, Imbler vicinity to headwaters. Interior Columbia Basin Ecosystem Management Project, Eastside Ecosystem Management Project, Walla Walla, Washington.

Beechie, T., G. Pess, P. Roni, and G. Giannico. 2008. Setting stream restoration priorities: review of approaches and a three-step process for identifying and prioritizing actions. North American Journal of Fisheries Management 28:891–905.

Beechie, T. J., D. A. Sear, J. D. Olden, G. R. Pess, J. M. Buffington, H. Moir, R. Roni, and M. M. Pollock. 2010. Process-based principles for restoring river ecosystems. BioScience 60:209–222.

Bernhardt, E. S., M. A. Palmer, J. D. Allan, G. Alexander, K. Barnas, S. Brooks, J. Carr, S. Clayton, C. Dahm, J. Follstad-Shah, D. Galat, S. Gloss, P. Goodwin, D. Hart, B. Hassett, R. Jenkinson, S. Katz, G. M. Kondolf, P. S. Lake, R. Lave, J. L. Meyer, T. K. O'Donnell, L. Pagano, B. Powell, and E. Sudduth. 2005. Synthesizing U.S. river restoration efforts. Science 308:636–637.

Bidlack, A. L., L. E. Benda, T. Miewald, G. H. Reeves, and G. McMahan. 2014. Identifying suitable habitat for Chinook Salmon across a large, glaciated watershed. Transactions of the American Fisheries Society 143:689–699.

Bisson, P. A., G. H. Reeves, R. E. Bilby, and R. J. Naiman. 1997. Watershed management and Pacific salmon: desired future conditions. Pages 447–474 *in* D. J. Stouder, P. A. Bisson, and R. J. Naiman, editors. Pacific salmon and their ecosystems: status and future options. Chapman and Hall, New York.

Bjornn, T. C. 1971. Trout and salmon movements in two Idaho streams as related to temperature, food, stream flow, cover, and population density. Transactions of the American Fisheries Society 100:423–438.

Bond, N. R., and P. S. Lake. 2003. Local habitat restoration in streams: constraints on the effectiveness of restoration for stream biota. Ecological Management and Restoration 4:193–198.

Booth, D. B., J. G. Scholz, T. J. Beechie, and S. C. Ralph. 2016. Integrating limiting-factor analysis with process-based restoration to improve recovery of endangered salmonids in the Pacific Northwest USA. Water [online serial] 8(5):174.

Bovee, K. D. 1986. Development and evaluation of habitat suitability criteria for use in the instream flow incremental methodology. U.S. Fish and Wildlife Service Biological Report 86(7).

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

Bradford, M. J., G. C. Taylor, and J. A. Allan. 1997. Empirical review of Coho Salmon smolt abundance and the prediction of smolt production at the regional level. Transactions of the American Fisheries Society 126:49–64.

Brierley, G. J., and K. A. Fryirs, editors. 2008. River futures: an integrative scientific approach to river repair. Island Press, Washington, D.C.

Brown, R. S., R. A. Harnish, K. M. Carter, J. W. Boyd, K. A. Deters, and M. B. Eppard. 2010. An evaluation of the maximum tag burden for implantation of acoustic transmitters in juvenile Chinook Salmon. North American Journal of Fisheries Management 30:499–505.

Brown, R. S., W. A. Hubert, and S. F. Daly. 2011. A primer on winter, ice, and fish: what fisheries biologists should know about winter ice processes and stream-dwelling fish. Fisheries 36:8–26.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York.

Cederholm, C. J., R. E. Bilby, P. A. Bisson, T. W. Bumstead, B. R. Fransen, W. J. Scarlett, and J. W. Ward. 1997. Response of juvenile Coho Salmon and steelhead to placement of large woody debris in a coastal Washington stream. North American Journal of Fisheries Management 17:947–963.

Cheslak, E. F., and J. C. Garcia. 1988. An evaluation of the effects of various smoothing and curve-fitting techniques on the accuracy of suitability functions. U.S. Fish and Wildlife Service Biological Report 88(11):259–283.

Chilcote, M. W., K. W. Goodson, and M. R. Falcy. 2011. Reduced recruitment performance in natural populations of anadromous salmonids associated with hatchery-reared fish. Canadian Journal of Fisheries and Aquatic Sciences 68:511–522.

Chittenden, C. M., K. G. Butterworth, K. F. Cubitt, M. C. Jacobs, A. Ladouceur, D. W. Welch, and R. S. McKinley. 2009. Maximum tag to body size ratios for an endangered Coho Salmon (*O. kisutch*) stock based on physiology and performance. Environmental Biology of Fishes 84:129–140.

Clark, E., B. W. Webb, and M. Ladle. 1999. Microthermal gradients and ecological implications in Dorset rivers. Hydrological Processes 13:423–438.

Collen, P., and R. J. Gibson. 2001. The general ecology of beavers (*Castor* spp.), as related to their influence on stream ecosystems and riparian habitats, and the subsequent effects on fish – a review. Reviews in Fish Biology and Fisheries 10:439–461.

Cooke, S. J., S. G. Hinch, M. C. Lucas, and M. Lutcavage. 2012. Biotelemetry and biologging. Pages 819–881 *in* A. V. Zale, D. L. Parrish and T. M. Sutton, editors. Fisheries techniques, 3rd edition. American Fisheries Society, Bethesda, Maryland.

Cunjak, R. A. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):267–282.

Dauble, D. D., T. P. Hanrahan, D. R. Geist, and M. J. Parsley. 2003. Impacts of the Columbia River hydroelectric system on main-stem habitats of fall Chinook Salmon. North American Journal of Fisheries Management 23:641–659.

David, B. O., and G. P. Closs. 2001. Continuous remote monitoring of fish activity with restricted home ranges using radiotelemetry. Journal of Fish Biology 59:705–715.

David, B. O., and G. P. Closs. 2003. Seasonal variation in diel activity and microhabitat use of an endemic New Zealand stream-dwelling galaxiid fish. Freshwater Biology 48:1765–1781.

DeGraaf, D. A., and L. H. Bain. 1986. Habitat use by and preferences of juvenile Atlantic Salmon in two Newfoundland rivers. Transactions of the American Fisheries Society 115:671–681.

Duncan, A. 1998. History, science, the law, and watershed recovery in the Grande Ronde: a case study. Oregon State University, Oregon Sea Grant, ORESU-O-97-001, Corvallis.

Ehrlich, P. R., and A. H. Ehrlich. 1981. Extinction: the causes and consequences of the disappearance of species. Random House, New York.

Eiler, J. H. 2012. Tracking aquatic animals with radiotelemetry. Pages 163–204 in N. S. Adams, J. W. Beeman, and J. H. Eiler, editors. Telemetry techniques: a user guide for fisheries research. American Fisheries Society, Bethesda, Maryland.

Evans, E. C., G. R. McGregor, and G. E. Petts. 1998. River energy budgets with special references to river bed processes. Hydrological Processes 12:575–595.

Forester, T. S., and J. M. Lawrence. 1978. Effects of Grass Carp and carp on populations of Bluegill and Largemouth Bass in ponds. Transactions of the American Fisheries Society 107:172–175.

Freeman, M. C., Z. H. Bowen, and J. H. Crance. 1997. Transferability of habitat suitability criteria for fishes in warmwater streams. North American Journal of Fisheries Management 17:20–31.

Fulton, L. A. 1968. Spawning areas and abundance of Chinook Salmon (Oncorhynchus tshawytscha) in the Columbia River basin: past and present. U.S. Fish and Wildlife Service Special Scientific Report Fisheries 571.

Gatz, A. J. Jr., M. J. Sale, and J. M. Loar. 1987. Habitat shifts in rainbow trout: competitive influences of brown trout. Oecologia 74:7–19.

Gelman, A., and J. Hill. 2007. Data analysis using regression and multilevel/hierarchical models. Cambridge University Press, New York.

Gildemeister, G. 1998. Watershed history, middle and upper Grande Ronde River subbasins of northeast Oregon. Report to the Oregon Department of Environmental Quality, U.S. Environmental Protection Agency, and the Confederated Tribes of the Umatilla Indian Reservation, La Grande, Oregon.

Gillies, C. S., M. Hebblewhite, S. E. Nielsen, M. A. Krawchuk, C. L. Aldridge, J. L. Frair, D. J. Saher, C. E. Stevens, and C. L. Jerde. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

Gowan, C., M. K. Young, K. D. Fausch, and S. C. Riley. 1994. Restricted movement in resident stream salmonids: a paradigm lost? Canadian Journal of Fisheries and Aquatic Sciences 51:2626–2637.

Hare, S. R., N. J. Mantua, and R. C. Francis. 1999. Inverse production regimes: Alaska and West Coast Pacific salmon. Fisheries 24(1):6–14.

Harris, J. E., and J. E. Hightower. 2011. Spawning habitat selection of Hickory Shad. North American Journal of Fisheries Management 31:495–505.

Heggenes, J., T. G. Northcote, and A. Peter. 1991. Spatial stability of Cutthroat Trout in a small, coastal stream. Canadian Journal of Fisheries and Aquatic Sciences 7:49–56.

Heifetz, J., M. L. Murphy, and K. V. Koski. 1986. Effects of logging on winter habitat of juvenile salmonids in Alaskan streams. North American Journal of Fisheries Management 6:52–58.

Hightower, J. E., J. E. Harris, J. K. Raabe, P. Brownell, and C. A. Drew. 2012. A Bayesian spawning habitat suitability model for American Shad in southeastern United States rivers. Journal of Fish and Wildlife Management 3:184–198.

Hilborn, R. 1992. Hatcheries and the future of salmon in the Northwest. Fisheries 17(1):5–8.

Hilborn, R., and J. Winston. 1993. Learning to enhance salmon production: lessons from the Salmonid Enhancement Program. Canadian Journal of Fisheries and Aquatic Sciences 50:2043–2056.

Hillman, T. W., J. S. Griffith, and W. S. Platts. 1987. Summer and winter habitat selection by juvenile Chinook Salmon in a highly sedimented Idaho stream. Transactions of the American Fisheries Society 116:185–195.

Hillman, T. W., J. W. Mullan, and J. S. Griffith. 1992. Accuracy of underwater counts of juvenile Chinook Salmon, Coho Salmon, and steelhead. North American Journal of Fisheries Management 12:598–603.

Holecek, D. E., K. J. Cromwell, and B. P. Kennedy. 2009. Juvenile Chinook Salmon summer microhabitat availability, use, and selection in a central Idaho wilderness stream. Transactions of the American Fisheries Society 138:633–644.

Hosmer, D. W., and S. Lemeshow. 2000. Applied logistic regression, 2nd edition. Wiley, New York.

Huusko, A., L. Greenberg, M. Stickler, T. Linnansaari, M. Nykänen, T. Vehanen, S. Koljonen, P. Louhi, and K. Alfredsen. 2007. Life in the ice lane: the winter ecology of stream salmonids. River Research and Applications 23:469–491.

Johnson, C. J., S. E. Niesen, E. H. Merrill, T. L. McDonald, and M. S. Boyce. 2006. Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. Journal of Wildlife Management 70:347–357.

Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 6:65–71.

Johnson, S. L. 2004. Factors influencing stream temperatures in small streams: substrate effects and a shading experiment. Canadian Journal of Fisheries and Aquatic Sciences 61:913–923.

Jonasson, B. C., E. R. Sedell, S. K. Tattam, A. B. Garner, C. Horn, K. L. Bliesner, J. W. Dowdy, S. D. Favrot, J. M. Hay, G. A. McMichael, B. C. Power, O. C. Davis, and J. R. Ruzycki. 2016. Investigations into the life history of naturally produced spring Chinook Salmon and summer steelhead in the Grande Ronde River subbasin. Annual Report to Bonneville Power Administration, Project 1992-026-04, Portland, Oregon.

Jones, C. G., J. H. Lawton, and M. Shachak. 1997. Positive and negative effects of organisms as physical ecosystem engineers. Ecology 78:1946–1957.

Kemp, P. S., T. A. Worthington, T. E. L. Langford, A. R. J. Tree, and M. J. Gaywood. 2012. Qualitative and quantitative effects of reintroduced beavers on stream fish. Fish and Fisheries 13:158–181.

Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2014. lmerTest: tests in linear mixed effects models. R package version 2.0–25. Available: http://cran.r-project.org/package=lmerTest. (August 2017).

Kwak, T. J., and J. T. Peterson. 2007. Community indices, parameters, and comparisons. Pages 677–763 in C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Kwak, T. J., M. J. Wiley, L. L. Osborne, and R. W. Larimore. 1992. Application of diel feeding chronology to habitat suitability analysis of warmwater stream fishes. Canadian Journal of Fisheries and Aquatic Sciences 49:1417–1430.

Lamberti, G. A., S. V. Gregory, L. R. Ashkenas, R. C. Wildman, and A. D. Stcinman. 1989. Influence of channel geomorphology on retention of dissolved and particulate matter in a Cascade Mountain stream. Pages 33–40 in D. L. Abell, editor. Proceedings of the California riparian systems conference. U. S. Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California.

Lougheed, V. L., B. Crosbie, and P. Chow-Fraser. 1998. Predictions on the effect of Common Carp (Cyprinus carpio) exclusion on water quality, zooplankton, and submergent macrophytes in a Great Lakes

wetland. Canadian Journal of Fisheries and Aquatic Sciences 55:1189–1197.

Lucas, M. E., and E. Baras. 2001. Migration of freshwater fishes. Blackwell Science, Ames, Iowa.

Mäki-Petäys, A., J. A. Huusko, J. Erkinaro, and T. Muotka. 2002. Transferability of habitat suitability of Atlantic Salmon (*Salmo salar*). Canadian Journal of Fisheries and Aquatic Sciences 59:218–228.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Dordrecht, The Netherlands.

Martin, D. J., L. J. Wasserman, and V. H. Dale. 1986. Influence of riparian vegetation on posteruption survival of Coho Salmon fingerlings on the west-side streams of Mount St. Helens, Washington. North American Journal of Fisheries Management 6:1–8.

McCarthy, M. A. 2007. Bayesian methods for ecology. Cambridge University Press, New York.

McClure, M. M., S. M. Carlson, T. J. Beechie, G. R. Press, J. C. Jorgensen, S. M. Sogard, S. E. Sultan, D. M. Holzer, J. Travis, B. L. Sanderson, M. E. Power, and R. W. Carmichael. 2008. Evolutionary consequences of habitat loss for Pacific salmonids. Evolutionary Applications 1:300–318.

McHugh, P., and P. Budy. 2004. Patterns of spawning habitat selection and suitability for two populations of spring Chinook Salmon, with an evaluation of generic versus site-specific suitability criteria. Transactions of the American Fisheries Society 133:89–97.

McHugh, P., P. Budy, and H. Schaller. 2004. A model-based assessment of the potential response of Snake River spring–summer Chinook Salmon to habitat improvements. Transactions of the American Fisheries Society 133:622–638.

McMahon, T. E., and G. F. Hartman. 1989. Influence of cover complexity and current velocity on winter habitat use by juvenile Coho Salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 46:1551–1557.

McMahon, T. E., A. V. Zale, and D. J. Orth. 1996. Aquatic habitat measurements. Pages 83–120 *in* B. R. Murphy and D. W. Willis, editors. Fisheries techniques, 2nd edition. American Fisheries Society, Bethesda, Maryland.

Meehan, W. R. 1991. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.

Meffe, G. K. 1992. Techno-arrogance and halfway technologies, salmon hatcheries on the Pacific coast of North America. Conservation Biology 6:350–354.

Miller, S. A., and T. A. Crowl. 2006. Effects of Common Carp (*Cyprinus carpio*) on macrophytes and invertebrate communities in a shallow lake. Freshwater Biology 51:85–94.

Monzyk, F. R., B. C. Jonasson, T. L. Hoffnagle, P. J. Keniry, R. W. Carmichael, and P. J. Cleary. 2009. Migration characteristics of hatchery and natural spring Chinook Salmon smolts from the Grande Ronde River Basin, Oregon, to Lower Granite Dam on the Snake River. Transactions of the American Fisheries Society 138:1093–1108.

Moyle, P. B., and D. M. Baltz. 1985. Microhabitat use by an assemblage of California stream fishes: developing criteria for instream flow determinations. Transactions of the American Fisheries Society 114:695–704.

Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2):4–21.

Newcomb, T. J., D. J. Orth, and D. F. Stauffer. 2007. Habitat evaluation. Pages 843–886 *in* C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Nickelson, T. E., J. D. Rogers, S. L. Johnson, and M. F. Solazzi. 1992. Seasonal changes in habitat use by juvenile Coho Salmon (*Oncorhynchus kisutch*) in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49:783–789.

NMFS (U.S. National Marine Fisheries Service). 1992. Endangered and threatened species; threatened status for Snake River spring/summer Chinook Salmon, threatened status for Snake River fall Chinook Salmon. Federal Register 57:78(22 April 1992):14653–14662.

NMFS (U.S. National Marine Fisheries Service). 2008. Remand of 2004 biological opinion of the Federal Columbia River Power System (FCRPS) including 19 Bureau of Reclamation projects in the Columbia basin (revised pursuant to court order, NWF v. NMFS, Civ. No. CV 01-640-RE [D. Oregon] 2005/05883). Seattle.

Nowak, M. C. 2004. Grande Ronde Subbasin Plan. Prepared for the Northwest Power and Conservation Council, Portland, Oregon.

NRC (National Research Council). 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, D.C.

Orth, D. J. 1987. Ecological considerations in the development and application of instream flow-habitat models. Regulated Rivers: Research and Management 1:171–181.

Parkos, J. J., V. J. Santucci, and D. H. Wahl. 2003. Effects of adult Common Carp (*Cyprinus carpio*) on multiple trophic levels in shallow mesocosms. Canadian Journal of Fisheries and Aquatic Sciences 60:182–192.

Pearsons, T. N., H. W. Li, and G. A. Lamberti. 1992. Influence of habitat complexity on resistance to flooding and resilience of stream fish assemblages. Transactions of the American Fisheries Society 121:427–436.

Pitlo, J. Jr. 1989. Walleye spawning habitat in pool 13 of the upper Mississippi River. North American Journal of Fisheries Management 9:303–308.

Pollock, M. M., T. J. Beechie, and C. E. Jordan. 2007. Geomorphic changes upstream of beaver dams in Bridge Creek, an incised stream channel in the interior Columbia River basin, eastern Oregon. Earth Surface Processes and Landforms 32:1174–1185.

Pollock, M. M., M. Heim, and D. Werner. 2003. Hydrologic and geomorphic effects of beaver dams and their influence on fishes. Pages 213–233 *in* S. V. Gregory, K. Boyer, and A. Gurnell, editors. The ecology and management of wood in world rivers. American Fisheries Society, Bethesda, Maryland.

Pollock, M. M., G. R. Pess, T. J. Beechie, and D. R. Montgomery. 2004. The importance of beaver ponds to Coho Salmon production in the Stillaguamish River basin, Washington, USA. North American Journal of Fisheries Management 24:749–760.

Power, M. E. 2001. Field biology, food web models, and management: challenges of context and scale. Oikos 94:118–129.

Quinn, T. P. 2005. The behavior and ecology of Pacific salmon and trout. University of Washington Press, Seattle.

Quinn, J. W., and T. J. Kwak. 2000. Use of rehabilitated habitat by Brown Trout and Rainbow Trout in an Ozark tailwater river. North American Journal of Fisheries Management 20:737–751.

R Core Team. 2015. R: a language and environment for statistical computing, version 3.2.2. Available: http://www.R-project.org/. (January 2018).

Rabeni, C. F., and S. P. Sowa. 1996. Integrating biological realism into habitat restoration and conservation strategies for small streams. Canadian Journal of Fisheries and Aquatic Sciences 53(Supplement 1):252–259.

Raleigh, R. F., W. J. Miller, and P. C. Nelson. 1986. Habitat suitability index models and instream flow suitability curves: Chinook Salmon. U.S. Fish and Wildlife Service Biological Report 82(10.122).

Raudenbush, S. W., and A. S. Bryk. 2002. Hierarchical linear models: applications and data analysis methods. Sage Publications, Thousand Oaks, California.

Raymond, H. L. 1979. Effects of dams and impoundments on migrations of juvenile Chinook Salmon and steelhead from the Snake River, 1966–1975. Transactions of the American Fisheries Society 108:505–529.

Raymond, H. L. 1988. Effects of hydroelectric development and fisheries enhancement on spring and summer Chinook Salmon and steelhead in the Columbia River basin. North American Journal of Fisheries Management 8:1–24.

Reeves, G. H., J. D. Hall, T. D. Roelofs, T. L. Hickman, and C. O. Baker. 1991. Rehabilitating and modifying stream habitats. Pages 519–558 in W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.

Richards, C., P. J. Cernera, M. P. Ramey, and D. W. Reiser. 1992. Development of off-channel habitats for use by juvenile Chinook Salmon. North American Journal of Fisheries Management 12:721–727.

Richter, B. D., D. P. Braun, M. A. Mendelson, and L. L. Master. 1997. Threats to imperiled freshwater fauna. Conservation Biology 11:1081–1093.

Rogers, K. B., and G. C. White. 2007. Analysis of movement and habitat use from telemetry data. Pages 625–676 in C. S. Guy and M. L. Brown, editors. Analysis and interpretation of freshwater fisheries data. American Fisheries Society, Bethesda, Maryland.

Roni, P., T. J. Beechie, R. E. Bilby, F. E. Leonetti, M. M. Pollock, and G. R. Pess. 2002. A review of stream restoration techniques and a hierarchical strategy for prioritizing restoration in Pacific Northwest watersheds. North American Journal of Fisheries Management 22:1–20.

Rosenfeld, J. S., T. Leiter, G. Lindner, and L. Rothman. 2005. Food abundance and fish density alters habitat selection, growth, and habitat suitability curves for juvenile Coho Salmon (Oncorhynchus kisutch). Canadian Journal of Fisheries and Aquatic Sciences 62:1691–1701.

Ross, M. J., and C. F. Kleiner. 1982. Shielded-needle technique for surgically implanting radio-frequency transmitters in fish. Progressive Fish-Culturist 44:41–43.

Rubin, S. P., T. C. Bjornn, and B. Dennis. 1991. Habitat suitability curves for juvenile Chinook Salmon and steelhead development using a habitat-oriented sampling approach. Rivers 2:12–29.

SAS Institute. 2009. SAS online documentation, version 9.2. SAS Institute, Cary, North Carolina.

Schlosser, I. J. 1987. The role of predation in age- and size-related habitat use by fish. Ecology 68:651–659.

Sedell, J. R., and R. L. Beschta. 1991. Bringing back the "bio" in bioengineering. Pages 160–175 in J. Colt and R. J. White, editors. Fisheries bioengineering symposium. American Fisheries Society, Symposium 10, Bethesda, Maryland.

Sharma, R., and R. Hilborn. 2001. Empirical relationships between watershed characteristics and Coho Salmon (Oncorhynchus kisutch) smolt abundance in 14 western Washington streams. Canadian Journal of Fisheries and Aquatic Sciences 58:1453–1463.

Sheppard, J. D., and J. H. Johnson. 1985. Probability-of-use for depth, velocity, and substrate by subyearling Coho Salmon and steelhead in Lake Ontario tributary streams. North American Journal of Fisheries Management 5:277–282.

Simonson, T. D., J. Lyons, and P. D. Kanehl. 1994. Quantifying fish habitat in streams: transect spacing, sample size, and a proposed framework. North American Journal of Fisheries Management 14:607–615.

Simpkins, D. G., and W. A. Hubert. 1998. A technique for estimating the accuracy of fish locations identified by radiotelemetry. Journal of Freshwater Ecology 13:263–268.

Simpkins, D. G., W. A. Hubert, C. Martinez del Rio, and D. C. Rule. 2004. Factors affecting swimming performance of fasted Rainbow Trout with implications of exhaustive exercise on overwinter mortality. Journal of Freshwater Ecology 19:657–666.

Simpkins, D. G., W. A. Hubert, and T. A. Wesche. 2000. Effects of fall-to-winter changes in habitat and frazil ice on the movements and habitat use of juvenile Rainbow Trout in a Wyoming tailwater. Transactions of the American Fisheries Society 129:101–118.

Skalski, J. R., M. B. Eppard, G. R. Ploskey, M. A. Weiland, T. J. Carlson, and R. L. Townsend. 2014. Assessment of subyearling Chinook Salmon survival through the federal hydropower projects in the mainstem Columbia River. North American Journal of Fisheries Management 34:741–752.

Sokal, R. R., and F. J. Rohlf. 1998. Biometry, 3rd edition. Freeman, New York.

Solazzi, M. F., T. E. Nickelson, S. L. Johnson, and J. D. Rodgers. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 57:906–914.

Spiegelhalter, D., A. Thomas, N. Best, and D. Lunn. 2010. OpenBUGS user manual, version 3.1.2. MRC Biostatistics Unit, Cambridge, UK.

Stanfield, L. W., and M. L. Jones. 1998. A comparison of full-station visual and transect based methods of conducting habitat surveys in support of habitat suitability index models for southern Ontario. North American Journal of Fisheries Management 18:657–675.

Sturges, H. A. 1926. The choice of a class interval. Journal of the American Statistical Association 21:65–66.

Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: a package for running WinBUGS from R. Journal of Statistical Software [online serial] 12(3).

Summerfelt, R. C., and L. S. Smith. 1990. Anesthesia, surgery, and related techniques. Pages 216–218 in C. B. Schreck and P. B. Moyle, editors. Methods for fish biology. American Fisheries Society, Bethesda, Maryland.

Thomas, J. A., and K. D. Bovee. 1993. Application and testing of a procedure to evaluate the transferability of habitat suitability criteria. Regulated Rivers: Research and Management 8:285–294.

Thomas, D. L., C. Ianuzzi, and R. P. Barry. 2004. A Bayesian multinomial model for analyzing categorical habitat selection data. Journal of Agricultural, Biological, and Environmental Statistics 9:432–442.

Tiffan, K. F., T. J. Kock, C. A. Haskell, W. P. Connor, and R. K. Steinhorst. 2009. Water velocity, turbulence, and migration rate of subyearling fall Chinook Salmon in the free-flowing and impounded Snake River. Transactions of the American Fisheries Society 138:373–384.

Townsend, R. L., J. R. Skalski, P. Dillingham, and T. W. Steig. 2006. Correcting bias in survival estimation resulting from tag failure in acoustic and radiotelemetry studies. Journal of Agriculture, Biological, and Environmental Statistics 11:183–196.

Tschaplinski, P. J., and G. F. Hartman. 1983. Winter distribution of juvenile Coho Salmon (Oncorhynchus kisutch) before and after logging in Carnation Creek, British Columbia, and some implications for overwinter survival. Canadian Journal of Fisheries and Aquatic Sciences 40:452–461.

USBR (U.S. Bureau of Reclamation). 2012. The Catherine Creek Tributary Assessment. U.S. Bureau of Reclamation, Final Report, Boise, Idaho.

Van Dyke, E. S., D. L. Scarnecchia, B. C. Jonasson, and R. W. Carmichael. 2009. Relationship of winter concealment habitat quality on pool use by juvenile spring Chinook Salmon in the Grande Ronde River Basin, Oregon, USA. Hydrobiologia 625:27–42.

Wagner, G. N., and S. J. Cooke. 2005. Methodological approaches and opinions of researchers involved in the surgical implantation of telemetry transmitters in fish. Journal of Aquatic Animal Health 17:160–169.

Waples, R. S., T. Beechie, and G. R. Pess. 2009. Evolutionary history, habitat disturbance regimes, and anthropogenic changes: what do these mean for resilience of Pacific salmon populations? Ecology and Society [online serial] 14:3.

Whalen, K. G., D. L. Parrish, and M. E. Mather. 1999. Effect of ice formation on selection of habitats and winter distribution of post-young-of-the-year Atlantic Salmon parr. Canadian Journal of Fisheries and Aquatic Sciences 56:87–96.

White, D. S., C. H. Elzinga, and S. P. Hendricks. 1987. Temperature patterns within the hyporheic zone of a northern Michigan river. Journal of the North American Benthological Society 6:85–91.

Wilcove, D. S., D. Rothstein, J. Dubow, A. Phillips, and E. Losos. 1998. Quantifying threats to imperiled species in the United States. BioScience 48:607–615.

Williams, J. G., S. G. Smith, and W. D. Muir. 2001. Survival estimates for downstream migrant yearling juvenile salmonids through the Snake and Columbia rivers hydropower system, 1966–1980 and 1993–1999. North American Journal of Fisheries Management 21:310–317.

Williams, R. N., P. A. Bisson, D. L. Bottom, L. D. Calvin, C. C. Coutant, M. W. Erho, C. A. Frissell, J. A. Lichatowich, W. J. Liss, W. E. McConnaha, P. R. Mundy, J. A. Stanford, and R. R. Whitney. 1999. Return to the river: scientific issues in the restoration of salmonid fishes in the Columbia River. Fisheries 24(3):10–19.

Wright, J. P., and C. G. Jones. 2006. The concept of organisms as ecosystem engineers ten years on: progress, limitations, and challenges. BioScience 56:203–209.

Wydoski, R. S., and R. R. Whitney. 2003. Inland fishes of Washington, 2nd edition. University of Washington Press, Seattle.

Zimmerman, M. P. 1999. Food habits of Smallmouth Bass, Walleyes, and Northern Pikeminnow in the lower Columbia River basin during outmigration of juvenile anadromous salmonids. Transactions of the American Fisheries Society 128:1036–1054.