

SPATIAL VARIABILITY IN SPAWNING HABITAT SELECTION BY CHINOOK SALMON
(*ONCORHYNCHUS TSHAWYTSCHA*) IN A WILDERNESS RIVERE. J. HAMANN^{a*}, B. P. KENNEDY^{a,b}, D. C. WHITED^c AND J. A. STANFORD^c^a Department of Fish & Wildlife Sciences, University of Idaho, Moscow, Idaho, USA^b Departments of Biological Sciences and Geological Sciences, University of Idaho, Moscow, Idaho, USA^c Flathead Lake Biological Station, University of Montana, Polson, Montana, USA

ABSTRACT

Chinook salmon (*Oncorhynchus tshawytscha*) survival during early life stages depends largely on spawning habitat selection by adults, which has been linked to biophysical stream variables (e.g. stream flow, velocity and substrate composition) as well as hyporheic exchange associated with riffle/pool and run/pool transitions. To examine how physical habitat variables influenced spawning habitat choice in one central Idaho (USA) wilderness stream, we used remote sensing techniques to classify and quantify the total amount of each aquatic habitat type present to assess how habitat quantity changed as stream order increased. Additionally, we measured physical habitat variables at each reach throughout the entire stream length for one spawning season to assess whether Chinook salmon selected for the same habitat parameters at varying spatial scales. Run, riffle and pool habitat types contributed similar proportions to the total area in both the upper and lower basins. However, 'transitional zones' (i.e. pool-riffle and pool-run transitions) accounted for 16% of the total area in the upper basin and only 4% in the lower. Redds were built in multiple habitat types in each of the three primary spawning locations, but transitional zones were chosen most frequently only in the upper basin. Significant differences in habitat variables were seen between spawning groups, with stream wetted width and velocity accounting for the majority of the variation. The techniques described here could be used to locate features that serve as indicators of potential spawning habitat, although caution should be exercised when extrapolating spawning habitat needs over large spatial extents. Copyright © 2013 John Wiley & Sons, Ltd.

KEY WORDS: Chinook salmon; spawning habitat; remote sensing; object-oriented classification; Big Creek; Middle Fork Salmon River

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INTRODUCTION

The scientific and societal need for identifying and preserving critical habitat for threatened and endangered species has become increasingly necessary (Scott *et al.*, 1993; Noss *et al.*, 1995; Noss, 1996). In riverine environments, anthropogenic impacts have fundamentally altered or eliminated habitat necessary for the growth, survival and reproduction of many aquatic species. For salmonids (members of the family Salmonidae), habitat degradation has been implicated as one of the primary factors contributing to population declines from historical levels (Nehlsen *et al.*, 1991; Frissell, 1993; Montgomery, 2004), and Endangered Species Act (ESA) requirements have focused conservation approaches on protecting and restoring the quality of critical habitats that still remain (Thurow, 2000; Beechie *et al.*, 2003; Good *et al.*, 2007). Additionally, the USA ESA requires the preparation and implementation of recovery plans that includes designation of critical habitat for each primary life stage of a listed

organism (Geist *et al.*, 2002). As human populations expand along river corridors and global energy needs continue to place demands on river flows, there is increasing value in knowing how fundamental life history stages will be most impacted by changes to critical habitat.

One critical habitat type for salmonids is defined by the spawning phase of their life histories. Chinook salmon (*Oncorhynchus tshawytscha*) characteristically return to natal rearing streams as sexually mature adults to reproduce and die. Female Chinook salmon choose suitable sites within the stream and begin building the structures in which they will deposit their eggs, termed redds (Bjornn and Reiser, 1991). They displace gravel and excavate pits in the stream bed by the downward-sweeping action of the tail, and fine particles are displaced downstream. The remaining coarse, sorted gravels allow for adequate flow through interstitial spaces that provide oxygen to developing embryos (Healey, 1991). Site selection is crucial because significant lifetime mortality occurs during the incubation period (Quinn, 2005).

Site selection for redd construction is thought to be influenced primarily by biophysical characteristics of the stream (Bjornn and Reiser, 1991). Researchers have focused

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on water velocity, water depth and substrate composition as a proxy for physical habitat variables required by fish and developing embryos (Knapp and Preisler, 1999). These measures can be incorporated into microhabitat models (physical habitat simulation system, etc.) designed to describe habitat suitability and deduce the effects of stream conditions on fish populations over varying spatial scales (Milhous *et al.*, 1989). These stream metrics alone do not correlate well with or otherwise explain redd site selection, however (Shirvell, 1989; McHugh and Budy, 2004). Broader, contextual issues at reach and river segment scales play a role in local habitat occupancy, as do nearby, complementary habitats for salmonids (Vronskii and Leman, 1991; Montgomery *et al.*, 1999; Baxter and Hauer, 2000; Fukushima, 2001; McHugh and Budy, 2004; Isaak *et al.*, 2007; McKean *et al.*, 2008). Chinook salmon spawn primarily at pool-riffle transitions, herein referred to as 'transitional zones' or 'transitional areas,' because of the hyporheic exchange that occurs in these areas as well as distributional sorting of appropriately-sized substrate that can be excavated free of silt and debris (Bjornn and Reiser, 1991). Temperatures and flow patterns are moderated in transitional areas (Brunke and Gonser, 1997) and intergravel flow rates are maximized, providing oxygen to developing embryos and removing waste from eggs and alevins in the gravel (McNeil, 1969). These transitional areas might also provide the greatest availability of microhabitats in terms of substrate, flow and depth combinations that are conducive for redd construction (Isaak *et al.*, 2007; McKean *et al.*, 2008).

Physical variables that determine habitat selection may vary from site to site along a river landscape, and therefore, our understanding of habit requirements has to consider hierarchical changes along a river corridor. Ecological studies are often constrained by the logistical considerations of site access and site replication as well as the ability to generalize inferences, and these considerations often limit research questions to those relevant over small spatial and short temporal scales that potentially overlook processes occurring over long time frames and wide spatial extents (Fausch *et al.*, 2002). In aquatic systems, stream survey work has traditionally been a labour intensive process that limits data collections at high resolution over the broad spatial scales needed to accurately characterize salmon ecology. Remote sensing tools and geographic information systems (GIS) make it possible to examine habitats in a continuous, spatially heterogeneous framework that would be difficult and/or challenging using traditional sampling methods (Wright *et al.*, 2000; Mertes, 2002; Johnson and Host, 2010; Whited *et al.*, 2012 and references therein). They provide the added advantage of removing some of the observer variability and subjectivity that accompanies ground-based surveys (Roper and Scarnecchia, 1995). These improved technologies allow for the study of habitats in a coarser spatial context that is

more relevant to fish population dynamics and life history diversity (Isaak and Hubert, 1997).

In this study, our overarching goals were threefold: (i) to delineate and classify aquatic habitat types in a salmon spawning stream; (ii) to predict spawning ground occupancy of Chinook salmon on the basis of the location of transitional zones; and (iii) to determine if those preferences change relative to stream size along a wilderness river corridor. Previous work in this system has quantified the occurrence and spatial scale of straying of adults from their natal habitats. This work has demonstrated that individuals originated in the lower stream reaches may stray to the upper-most sections of the watershed to spawn (Hamann and Kennedy, 2012). Given that philopatry may not operate in this system at a scale that overrides physical habitat selection in determining spawning habitat choice, we looked at how physical habitat metrics influence spawning habitat selection. We used remote sensing techniques to classify aquatic habitat into run, riffle and pool habitat types to determine if proximity to transitional zones was a useful predictor of redd occurrence. We quantified the total amount of each habitat type available to assess how habitat quantity changed as stream order increased. Additionally, we measured physical habitat variables (depth, velocity, substrate composition, floodplain width, wetted channel width and distance to pool) at each redd throughout the entire stream length for one spawning season to determine if the metrics selected by spawning salmon varied at multiple spatial scales.

METHODS

Study area

Big Creek, a tributary of the Middle Fork of the Salmon River (MFSR) in central Idaho, is one of few remaining pristine watersheds in the continental United States and represents one of the eastern and southern-most destinations for anadromous salmonids in their historic Pacific distribution (Figure 1). Nearly the entire watershed is located within the Frank Church-River of No Return Wilderness Area, the landscape is relatively undisturbed, and habitat quality remains virtually unchanged from that which supported fairly large historic runs of salmon. Hence, Big Creek serves as an ideal reference system for studying fish-habitat relationships in undisturbed rivers.

Big Creek is a fourth-order stream that drains 1543 km² of forested and mountainous terrain. Stream elevations range from 1754 m near the headwaters to 1030 m at the confluence with the MFSR 65-km downstream. The hydrograph is snowmelt-driven with peak flows occurring in June followed by baseflows from mid-July to March. The stream flows east through a combination of short open valleys with wide floodplains and more dominant narrow, constricted V-shaped

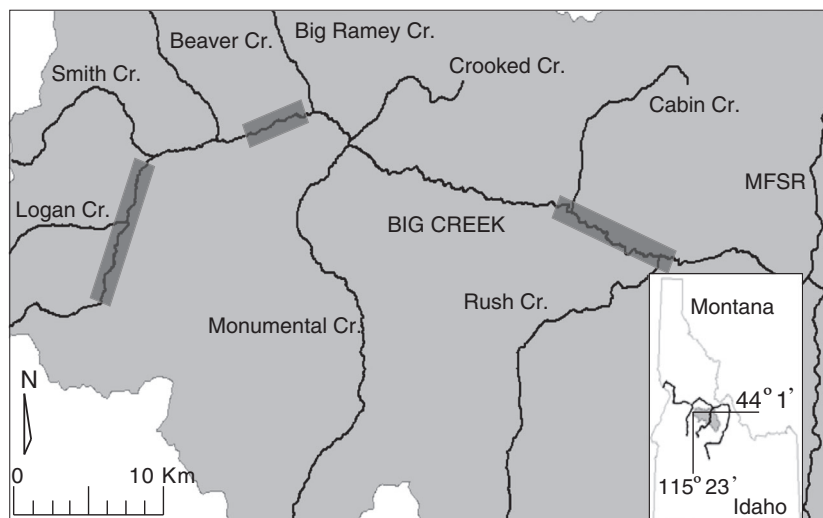


Figure 1. Map of Big Creek and major tributaries. Insets depict relative location within the Middle Fork Salmon River basin, and square shaded areas represent sampling locations where redds were measured and for which high-resolution images were acquired (UBC = upper Big Creek, MBC = middle Big Creek, LBC = lower Big Creek)

valleys, an arrangement that results in dispersed and non-continuous spawning habitat reaches. Geology is variable but is dominated by granites, granodiorites and rhyolitic volcanics of the Challis magmatic event (Lewis, unpublished data). High elevations and northern slopes are dominated by conifer spp., whereas sagebrush (*Artemisia* spp.), grasses and forbs predominate in low elevation areas and southern slopes. A thorough description of the Big Creek drainage can be found in Thurow (2000).

Population status

Snake River Chinook salmon in the Big Creek watershed are a wild, indigenous subpopulation that are characterized as spring/summer salmon on the basis of the timing of their adult upstream migration in the lower Columbia River (Matthews and Waples, 1991). Once part of the largest Chinook salmon runs in the world (Stanford *et al.*, 2010), the entire population experienced drastic declines from the late 19th to 20th centuries due to hydropower, over-harvest, habitat degradation and hatchery misuse (NRC, 1996; Montgomery, 2004). Snake River spring/summer Chinook salmon were identified as an evolutionary significant unit in 1991 and listed as threatened under the ESA in 1992 (Matthews and Waples, 1991; NMFS, 1992; Brown, 2002), and on the basis of various climate change scenarios, the Big Creek subpopulation faces a 50% chance of extirpation (Crozier *et al.*, 2008). Adult Chinook salmon enter the MFSR drainage by mid-summer, migrate to natal areas and build redds between late-July and mid-September (Isaak and Thurow, 2006). Other salmonids occurring in the basin include bull trout (*Salvelinus confluentus*), brook trout

(*Salvelinus fontinalis*), mountain whitefish (*Prosopium williamsoni*), steelhead/rainbow trout (*Oncorhynchus mykiss*) and westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) (Thurow, 1985).

Redd sampling

Trained observers conducted spawning ground surveys throughout Big Creek from late-July to mid-September 2009 to encompass the entire range of temporal and spatial variation in spawning activity. Although attempts were made to find and measure each active redd in the entire stream length, our efforts were most intensively directed towards areas that have been the focus of spawning ground surveys by tribal, state and federal agencies for several decades. Completed redds were identified by a number of characteristics, including evidence of significant scouring, horseshoe-shaped margins on the upstream edge of the redd and abrupt edges or trenching. The upstream edge of redd excavation was often characterized by large cobbles and pits, whereas the downstream edge was frequently evidenced by an elevated pillow with sorted gravels near the water surface.

Water depth and velocity were measured at the upstream edges of each redd; depth (cm) was measured with a top-setting wading rod, and velocity (m/sec) was measured at 10-s intervals with a SonTek FlowTracker at 60% of the total depth (Sontek/YSI, San Diego, California, USA). The intermediate axis of 10 randomly chosen substrate particles in undisturbed areas along the margins of each redd was recorded. This measurement was assumed to represent substrate conditions in the stream prior to redd construction,

and redd presence was assumed to be an indicator of substrate suitability. This sample size was chosen for logistical reasons to both minimize disturbance of the redd and lower the handling time of substrates. The surface area of each redd was also measured, and a global positioning system (GPS) coordinate was taken using a Trimble GeoXM (Trimble Navigation Limited, Sunnyvale, California, USA) with sub-metre resolution in most cases. Additional habitat variables, including floodplain width, channel wetted width and distance to pools, were measured at each redd using high-resolution digital images and satellite imagery of the study area. Determining stream-groundwater exchange via the vertical hydraulic gradient has been demonstrated to be a critical variable for spawning habitat choice for salmon (Stanford and Ward, 1993; Geist and Dauble, 1998); however, the risk of redd disruption with piezometer installations was too great in this system, and these measurements could unfortunately not be made.

Image acquisition and processing

High-resolution three-band (red, green, blue) digital images (pixel size = 20 cm) were acquired at baseflow conditions for floodplain areas of Big Creek on 25 July 2008, using a Kodak Professional DCS Pro SLR/n digital camera flown onboard a light aircraft (Figure 2A). These analyses were part of a larger study (the Salmonid Rivers Observatory Network, or SaRON, of the Flathead Lake Biological Station, Whited *et al.*, 2012) focused on understanding the ecological processes occurring in functional salmon rivers across the Pacific Rim. Research efforts were focused on complex floodplain reaches with the conceptual understanding

that river floodplains are centres of ecological organization and key drivers of salmon life history diversity and productivity (Stanford and Ward, 1993). Further, data collected over the past several decades by tribal, state and federal agencies show that floodplain reaches are used most heavily by spawning salmon to build redds. Discharge at Taylor Wilderness Research Station (~8 km upstream of the confluence of the MFSR) at the time of acquisition was 14.5 m³/s. ERDAS IMAGINE 9.2 (ERDAS, Inc., Atlanta, Georgia, USA) was used to geo-reference the images with QuickBird satellite imagery (DigitalGlobe, Longmont, Colorado, USA) acquired in 2008 (2.4 m multispectral band resolution, 0.6 m panchromatic band resolution) and National Agriculture Imagery Program imagery from 2004 (1 m resolution). A root mean square error of less than 0.5 m was attained for all images, and from the individual images, a continuous image mosaic was created for upper (UBC), middle (MBC) and lower (LBC) Big Creek.

Definiens Developer software (Definiens AG, Munchen, Germany) was used to isolate water and remove surrounding landscape features (riparian vegetation, tree cover, gravel bars, etc.) from the image mosaic. Definiens Developer software is an object-oriented image analysis programme that uses segmentation algorithms to group pixels into polygons on the basis of a suite of user-defined variables (pixel values, texture, neighbourhood associations, etc.). We used fine scale (~20) segmentation and established a threshold value using the hue, saturation and intensity value to create a classification rule set to extract water from the three-band high-resolution imagery. This procedure generally produced an over-classification of water within the imagery; therefore, to improve the water delineation, we performed an unsupervised classification using ERDAS

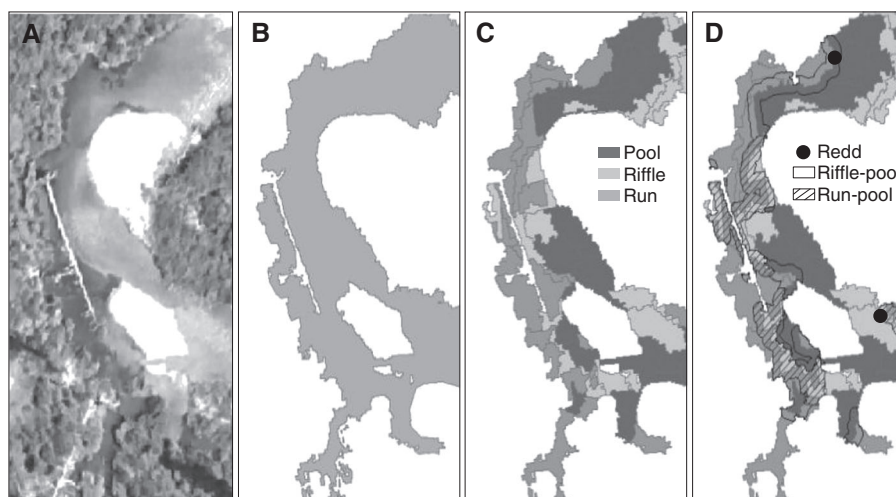


Figure 2. Habitat classification process using object-oriented methods. (A) From the aerial image mosaic (colour image converted to greyscale here), (B) water is extracted, and (C) classified into run, riffle and pool habitat types. (D) Transitional areas are identified as places where either runs or riffles meet pool habitats, and redd positions are overlaid

IMAGINE 9.2 followed by heads-up digitizing in ArcGIS 9.3 (ESRI, Redlands, California, USA) to refine the water boundary. The resulting image contained only the visible water (Figure 2B).

To classify the water raster into habitat types, we again employed Definiens Developer software. Using an iterative approach to the segmentation process, we came up with meaningful run, riffle and pool polygons within the imagery that incorporated elements of texture, size and tone on the basis of visual inspection (Bisson *et al.*, 1982; Figure 2C). Specifically, pool polygons had smooth surfaces, no turbulence and were dark blue or dark grey. Riffles had a speckled surface texture, were visually turbulent and appeared blue or brown. Finally, like pools, runs had smooth surfaces but had minimal surface turbulence and were blue or brown. Polygons were visually inspected for assignment accuracy on the basis of field observations and familiarity with the study stream, and misclassified polygons were manually reclassified in ArcGIS 9.3. Because of the relationship between redd building and transitional bedforms, we used ArcGIS 9.3 to locate all areas of the imagery where pools were adjacent to either riffles or runs. Because redds were sampled during baseflow conditions, we rationalized that run/pool transitions would function similarly to riffle/pool transitions. In subsequent analyses, these two types of transitional areas were combined with the overlapping areas removed. We created a 1-m buffer around these areas to more adequately represent the transitional area and allow for error in GPS point locations that would be associated with these zones. These areas were classified jointly as transitional habitat (Figure 2D).

Spatially explicit measures of water depth and vertical profile measurements of flow velocity were collected in order to ground truth habitat classification results using methodology modified from Whited *et al.*, 2002. A SonTek RS3000 Acoustic Doppler velocity-Profiler (ADP, Sontek/YSI, San Diego, California, USA) linked with a GPS receiver was deployed in front of a cataraft and manoeuvred throughout specified study reaches to obtain data for the full array of aquatic habitat types in Big Creek. Shallow depths and low flows limited ADP functionality in this system, however, and the satellite imagery was too coarse to adequately represent the variability in habitat types that existed in a stream of this size. For these reasons, habitat classification was limited to the object-oriented segmentation algorithms and field observations.

Using the habitat classification results, we hypothesized that redds would occur more frequently in transitional zones than in other locations within the stream. To test this, we created 500 random points within the UBC study reach and measured their proximity to transitional areas to determine if redds occurred more frequently in these areas than would happen by chance. A 2-m buffer was added to

all actual redds and randomly generated points to reflect the mean size of redds measured in 2009 and alleviate potential error in GPS accuracy. Similar analysis in MBC and LBC was not possible because of low sample size and lack of historical redd data from this area of the drainage.

Statistical analyses

Redds were grouped into one of three primary spawning aggregations (LBC, MBC or LBC) on the basis of relative distance from the confluence of the MFSR (Figure 1). To evaluate spawning habitat availability versus use independent of the relative abundance of each habitat type, we used Jacobs's electivity analysis (Jacobs, 1974; Manly *et al.*, 1993). Jacobs's index was determined using the following formula

$$D = (r-p)/(r+p-2rp)$$

where 'r' is the proportion of habitat used, 'p' is the proportion of habitat available and 'D' varies from -1 (indicating strong avoidance) to +1 (strong preference). Values near 0 indicate that a habitat was used in proportion to its availability in the environment (Kauhala and Auttila, 2010). Redds obscured by shadows were not included in this analysis.

Analysis of variance ($\alpha \leq 0.05$) was used to determine if differences in measured physical habitat attributes existed between the three spawning aggregations, namely water depth, velocity, substrate composition, floodplain width, channel wetted width and distance to pools. Tukey's honestly significant difference was then used to determine where significant comparisons existed between sites ($\alpha \leq 0.05$).

Principal components analysis was used to reduce dimensionality and determine which stream habitat variables accounted for the most total variation among all redd sites throughout the basin regardless of group assignment. We standardized the data and limited analysis to six physical stream attributes associated with each redd (same as in the previous discussion).

RESULTS

Use of transitional zones

Overall, 32% of redds measured in Big Creek in 2009 were built in transitional zones. Riffles were used most frequently (42%), whereas runs (15%) and run/riffle transitions (11%) contributed smaller proportions. Redds obscured by shadows in the imagery were removed from this analysis.

When looking at each section separately, UBC redds ($n=27$) were located in transitional zones 41% of the time. On the basis of the random point analysis, this would occur by chance 33% of the time. Chinook salmon in Big Creek built redds in multiple habitat types, but transitional zones were chosen most frequently only in UBC. In MBC and LBC, riffle areas were chosen most often for redd construction (Figure 3).

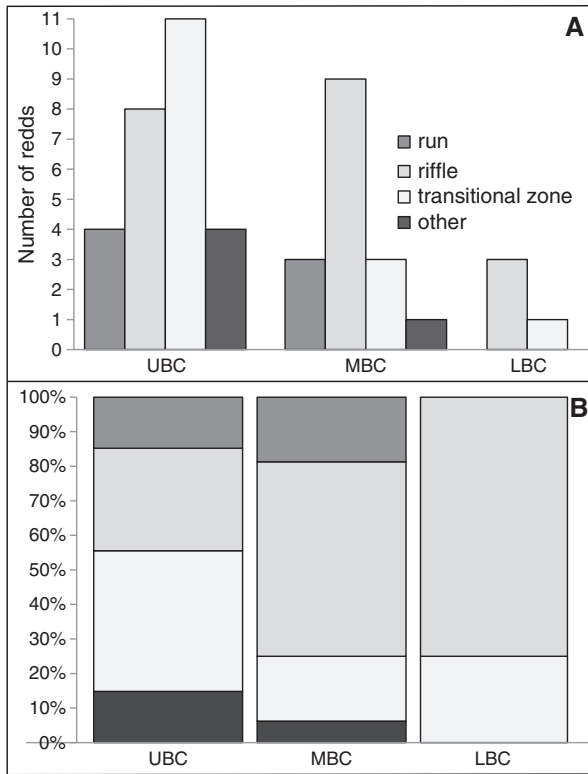


Figure 3. Number and cumulative proportion of redds found in each habitat type at each site [upper Big Creek ($n=27$); middle Big Creek ($n=16$); and lower Big Creek ($n=4$)] ‘Other’ is riffle/run transitional area

On the basis of the electivity analysis, UBC spawners avoided pool and riffles and preferred transitional zones for redd building, whereas runs were used in proportion to their availability. Likewise, LBC spawners preferred transitional

zones but avoided pools and runs; riffles were a neutral spawning choice. Imagery for MBC was not available for this analysis (Table 1).

Habitat variables at multiple spatial scales

Stream reach scale. The amount of transitional habitat in LBC was almost double the amount in UBC (Figure 4A). Run, riffle and pool habitat types contributed similar proportions to the total area in both UBC and LBC. However, the combination of riffle/pool and run/pool transitional areas accounted for 16% of the total area in UBC and only 4% in LBC (Figure 4B).

Redd scale. Depth at the upstream edge of redds was not significantly different between the three spawning locations ($F=2.13$, $P=0.1315$). However, UBC redds were constructed in significantly slower-moving water than both MBC and LBC redds ($F=31.34$, $P<0.0001$), and substrate particle sizes in MBC were significantly larger than in both UBC and LBC ($F=9.8$, $P=0.0003$). Floodplains were significantly wider in UBC than in MBC ($F=4.94$, $P=0.0119$), and stream wetted width varied significantly between all basin groups ($UBC < MBC < LBC$; $F=50.09$, $P<0.0001$). Distance to pool was significantly farther in LBC compared in UBC ($F=6.4$, $P=0.0039$; See Table 2 for site-specific descriptive statistics; Table 3).

Using Kaiser’s rule, three principal components were retained that accounted for 77% of the variation in the data. Velocity, substrate and stream wetted width loaded heavily on PC1, depth highly influenced PC2 and floodplain width and distance to pool loaded heavily in the opposite direction on PC3 (Table 4).

Table I. Jacobs’s electivity index was used to assess the relationship between habitat use and availability in Big Creek

	Habitat proportion	Redd count	Used sample proportion	Jacobs’s electivity index (D)	Interpretation
Upper Big Creek					
Run	0.235	6	0.32	0.20	Neutral
Riffle	0.597	6	0.32	-0.52	Avoid
Pool	0.168	0	0.00	-1.00	Avoid
Transitional zone	0.158	7	0.37	0.51	Prefer
Total	1.158	19	1.00		
Lower Big Creek					
Run	0.208	0	0.00	-1.00	Avoid
Riffle	0.717	3	0.75	0.08	Neutral
Pool	0.074	0	0.00	-1.00	Avoid
Transitional zone	0.041	1	0.25	0.77	Prefer
Total	1.040	4	1.00		

In both upper Big Creek and lower Big Creek, transitional zones were preferred for redd building, whereas other habitat types were avoided or used in proportion to what was available in the environment. Redds were removed from this analysis if their location could not be determined because of the presence of shadows in the imagery if they were not located in habitat types described herein. The total habitat proportion in both upper Big Creek and lower Big Creek exceeds 1 because transitional habitat incorporates run, riffle and pool habitat types. The total amount of available habitat could not be determined from the middle Big Creek imagery, and it was excluded from this analysis.

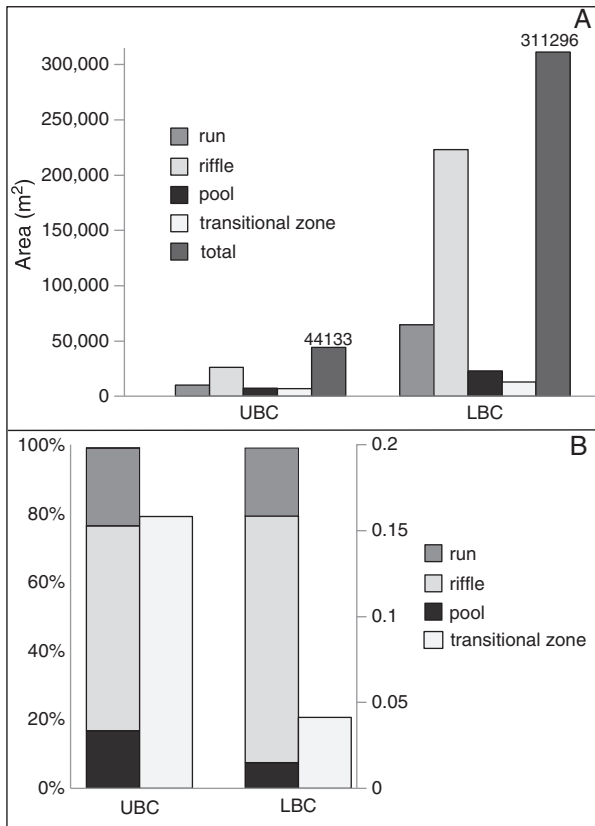


Figure 4. (A) Total area contributed by each habitat type in upper and lower Big Creek. ‘Transitional zones’ include run/pool and riffle/pool transitions with overlap removed. (B) Cumulative percentage of habitat types and proportion of total area by site that is run/pool or riffle/pool transition

DISCUSSION

Contrary to our expectations, the location of transitional areas did not serve as a clear indicator of redd occurrence in Big Creek. Instead, spawning habitat choice is complex and variable, even at the scale described here. The habitat parameters chosen by female Chinook salmon exhibit a tremendous range of potential habitat values (Healey, 1991), and that variability was evident across the entire system (albeit within a smaller range; see Table 2).

Adult Chinook salmon returns to Big Creek are at a fraction of historical levels (Nehlsen *et al.*, 1991), and it is consequently unlikely that the available spawning habitat in this system is saturated. In 2009, for example, the total number of spawners returning to Big Creek was estimated at 243, likely less than 10% of average historic values (Thurrow, unpublished data), and therefore, it is possible that suitable locations in the stream were not used simply because of the lack of spawners (McHugh and Budy, 2004). Because of low escapement and the lack of density-dependent factors on spawning site selection, it is likely that salmon chose the

best available habitat for redd construction in this study and that these reflect a subset of the sites that would have been chosen even at higher spawner densities. Because salmon prefer to spawn in areas of high intergravel flow, aggregations of fish tend to occur in these locations (Vronskii and Leman, 1991), and redd superimposition and clumping at spawning sites is common (Witzel and Maccrimmon, 1983). This occurs even when habitat does not appear to be limiting (Essington *et al.*, 1998) and helps explain why salmon choose to cluster redds rather than colonize new sites. Redd distributions remain clustered even at high escapements, and these high-density spawning areas are likely most important at low spawner densities (Isaak and Thurrow, 2006).

Site selection is tightly linked with philopatry in salmon, as they characteristically home to natal rearing locations (Healey, 1991; Quinn *et al.*, 1999; Quinn, 2005). Although previous work has quantified the spatial extent and frequency of straying in this system (Hamann and Kennedy, 2012), it is likely that homing mechanisms place constraints on redd positioning at scales exceeding 5 km (i.e. between rather than within our study sections). Within this watershed, results suggest that straying away from natal origins is far more likely at scales of 1–3 km than at spatial scales exceeding 5 km (Hamann and Kennedy, 2012). These findings support the contention that habitat variables drive spawning habitat selection. At these smaller spatial scales, olfactory recognition gives way to selection for appropriate habitat variables, as increasingly sites would become more difficult to differentiate (Dittman and Quinn, 1996).

Differences in habitat choice for Chinook salmon reflect differences in fish size, as bigger salmon tend to choose habitats that are deeper and have faster flows (Bjornn and Reiser, 1991). Greater depths and increased velocities presumably provide a greater opportunity for the spawning site to remain within suitable conditions for developing embryos (Keeley and Slaney, 1996). In Big Creek, depth at redd locations was not significantly different across sites, but velocities in middle and lower sections of the watershed were significantly faster. However, based upon fork lengths of female salmon carcasses collected at each site (UBC $n=48$, MBC $n=5$, LBC $n=3$), no significant size difference was observed (analysis of variance, $\alpha \leq 0.05$; $F=0.35$, $P=0.71$).

Some simplifications must be made in order to classify a complex stream network into a limited number of habitat types, which could have potentially impacted the results of this study. Clearly, more complex designations could have been assigned, but for the sake of data interpretability, we limited the aquatic habitat designations to runs, riffles and pools. These habitat classifications ideally would have been validated using depth and velocity ground data obtained from the ADP and Flowtracker measures. Because of shallow depths and low flows, ADP functionality was limited

Table II. Descriptive statistics for Chinook salmon redd locations in Big Creek measured in 2009

	Depth (m)	Velocity (m/s)	Substrate (cm)	Floodplain width (m)	Wetted width (m)	Distance to pool (m)
Upper Big Creek; $n = 31$						
Minimum	0.183	0.008	4.0	21.78	3.78	0.00
Maximum	0.671	0.674	9.7	790.20	19.42	29.30
Mean	0.353	0.302	6.3	378.35	10.98	7.94
Standard deviation	0.133	0.153	1.6	244.52	4.64	8.01
Middle Big Creek; $n = 9$						
Minimum	0.300	0.401	6.9	105.37	13.74	0.00
Maximum	0.550	1.037	11.2	159.01	28.32	142.73
Mean	0.432	0.742	9.1	135.77	20.71	34.77
Standard deviation	0.089	0.214	1.6	17.37	5.09	58.04
Lower Big Creek; $n = 4$						
Minimum	0.396	0.642	4.3	313.15	31.42	0.00
Maximum	0.564	0.741	9.1	514.80	39.02	134.02
Mean	0.446	0.686	6.5	417.47	33.61	67.51
Standard deviation	0.080	0.045	2.0	112.48	3.62	76.46

in this system, however, and habitat classification was based on object-oriented segmentation algorithms/manual interpretations and field observations. Definiens Developer software proved to be quite successful in identifying discrete polygons of aquatic habitats (riffles, pools, etc.), and we believe that with sufficient ADP coverage, accurate depth and velocity values could be achieved. The object-oriented classification scheme is well suited for riverine habitats, as the shift from pixel-by-pixel habitat classifications to object-oriented classification will likely enhance stream habitat classifications by identifying discrete habitat patches, which are inherently intuitive for river ecologist to understand. Aquatic habitat types are usually defined by multiple, adjacent pixel values in high-resolution imagery, and object-based methods allow for the classification of groups rather than individual pixel values (Thompson and Gergel, 2008).

Table III. Analysis of variance results for physical habitat attributes measured at each redd

Variable	F	p -value ($\alpha < 0.05$)	Significant comparisons
Depth	2.13	0.1315	
Velocity	31.34	<0.0001*	UBC-MBC, UBC-LBC
Substrate	9.8	0.0003*	UBC-MBC, MBC-LBC
Floodplain width	4.94	0.0119*	UBC-MBC
Wetted width	50.09	<0.0001*	UBC-MBC, MBC-LBC, UBC-LBC
Distance to pool	6.4	0.0039*	UBC-LBC

All measured variables (with the exception of depth at upstream edge) varied significantly between sites, and significant comparisons are noted. UBC, upper Big Creek; MBC, middle Big Creek; LBC, lower Big Creek.

The presence of shadows in the imagery creates another obstacle for efficient application of this approach (Marcus and Fonstad, 2008). In UBC, 37% of the total aquatic habitat was obscured, whereas in LBC, shadows made 4% of the total area unclassifiable. Additionally, 25% of all redd point locations measured in 2009 fell into shadowed areas. The inability to include one quarter of the sampling points impacted our ability to assess spawning habitat preferences in Big Creek; however, there is no reason to assume that it biased our results as shadowed stream reaches appeared to be a random representation of stream habitat.

Our large-scale analysis of spawning habitat choice for Chinook salmon was based on the underlying assumption that habitat selection remained static throughout the length of the entire stream. However, our data from individual redd sites within Big Creek revealed significantly more differences than expected. As previously mentioned, the types

Table IV. Principal component loadings for habitat variables

Variable	PC1	PC2	PC3
Depth	0.172	0.806	0.308
Velocity	0.807	0.247	0.007
Substrate	0.675	-0.489	0.03
Floodplain width	-0.511	0.479	-0.608
Wetted width	0.749	0.36	0.038
Distance to pool	0.576	-0.058	-0.726
Eigenvalue	2.290	1.311	0.994
% variance explained	38.17	21.86	16.57
Cumulative %	38.17	60.03	76.60

Three principal components were retained that accounted for 77% of the variation in the data. Velocity, substrate and stream wetted width loaded heavily on PC1 (indicated with boldface), depth highly influenced PC2, and floodplain width and distance to pool loaded heavily in the opposite direction on PC3.

of habitat salmon choose for spawning varies between upper, middle and lower sections of the watershed, with transitional zones preferred by spawners in UBC and LBC. By assuming that salmon select for the same attributes across stream segments (i.e. primarily transitional zones), a significant portion of habitat would have been removed from consideration. For example, although a substantial amount of transitional habitat exists in the LBC, it is only used 25% of the time. High variability in habitat choice exists between the three major spawning areas along Big Creek, and if analysis would have been limited merely to the presence of transitional zones in the stream, a substantial amount of habitat would have been missed.

Information regarding the abundance and spatial distribution of critical spawning habitat is a key element in the protection and conservation of these ecosystems, and high-resolution mapping of these areas provides a way to delineate these habitat types (Thompson and Gergel, 2008). Despite the limitations we encountered in habitat analysis for this particular stream, remote sensing and GIS-based analysis provide a way to assess habitat quickly over extensive spatial extents for large-scale salmon habitat preservation, conservation and restoration. Considerable resources have been allocated toward aquatic habitat restoration for wild salmon stocks in the Pacific Northwest, and a GIS-based analysis provides a rapid, cost-effective tool for guiding the prioritization of salmon habitat over large geographic extents (Lunetta *et al.*, 1997; Feist *et al.*, 2003). Ground measures are often costly and logistically difficult to obtain in remote environments. Remotely sensed data can complement field surveys and provide an alternative to costly and time-consuming collection of ground data (Legleiter and Goodchild, 2005; Harvey and Clifford, 2009). By identifying key features that serve as indicators of potential habitat in aerial imagery, the techniques described here could be used to identify critical spawning areas over large or inaccessible areas. Remote sensing of aquatic habitat could be similarly used to establish baseline data for recovery efforts by determining the current state of streams and identifying potential locations for restoration activities (Frissell, 1993; Stanford *et al.*, 1996; Egan, 1999; Nienhuis and Leuven, 2001).

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