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ASSESSING JUVENILE SALMON REARING HABITAT AND ASSOCIATED PREDATION RISK IN A LOWER SNAKE RIVER RESERVOIR

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ABSTRACT

Subyearling fall Chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River basin exhibit a transient rearing strategy and depend on connected shoreline habitats during freshwater rearing. Impoundment has greatly reduced the amount of shallow-water rearing habitat that is exacerbated by the steep topography of reservoirs. Periodic dredging creates opportunities to strategically place spoils to increase the amount of shallow-water habitat for subyearlings while at the same time reducing the amount of unsuitable area that is often preferred by predators. We assessed the amount and spatial arrangement of subyearling rearing habitat in Lower Granite Reservoir on the Snake River to guide future habitat improvement efforts. A spatially explicit habitat assessment was conducted using physical habitat data, two-dimensional hydrodynamic modelling and a statistical habitat model in a geographic information system framework. We used field collections of subyearlings and a common predator [smallmouth bass (*Micropterus dolomieu*)] to draw inferences about predation risk within specific habitat types. Most of the high-probability rearing habitat was located in the upper half of the reservoir where gently sloping landforms created low lateral bed slopes and shallow-water habitats. Only 29% of shorelines were predicted to be suitable (probability >0.5) for subyearlings, and the occurrence of these shorelines decreased in a downstream direction. The remaining, less suitable areas were composed of low-probability habitats in unmodified (25%) and riprapped shorelines (46%). As expected, most subyearlings were found in high-probability habitat, while most smallmouth bass were found in low-probability locations. However, some subyearlings were found in low-probability habitats, such as riprap, where predation risk could be high. Given their transient rearing strategy and dependence on shoreline habitats, subyearlings could benefit from habitat creation efforts in the lower reservoir where high-probability habitat is generally lacking. Published 2015. This article is a U.S. Government work and is in the public domain in the USA.

KEY WORDS: habitat; fall Chinook salmon; smallmouth bass; Snake River; modelling; predation; riprap; Lower Granite Reservoir

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INTRODUCTION

Impoundment of rivers has altered or reduced the habitat of many fish species (Baxter, 1977; Williams, 2006). Direct effects include loss of riverine habitat and a shift from a lotic to a lentic fish community (Martinez *et al*., 1994; Gehrke *et al*., 2002), altered food webs (Naiman *et al*., 2012) and reduced water velocities for migratory species (Raymond, 1968). Indirect effects include reduced survival and abundance of lotic species (Taylor *et al*., 2001; Smith *et al*., 2003), and invasive species proliferation (Johnson *et al*., 2008). Within the Columbia River basin, 85% of main-stem, riverine habitats have been altered by impoundment (Dauble *et al*., 2003). This has particularly affected fall Chinook salmon (*Oncorhynchus tshawytscha*), which spend the entire freshwater portion of their life cycle in main-stem habitats, by eliminating or reducing spawning and rearing habitats (Dauble *et al*., 2003). Snake River subyearling fall Chinook salmon (hereafter, subyearlings) are dependent on shoreline habitats during post-emergence rearing from April through June. Shallow-water habitats offer ideal growing conditions (warmer water and more food) and protection from piscivorous predators (Tiffan *et al*., 2014). As temperatures continue to warm seasonally, subyearlings move offshore and begin their seaward migration during summer as smolts (Connor *et al*., 2003; Tiffan *et al*., 2006).

Before impoundment, much of the shoreline habitat in the Snake and Columbia Rivers comprised shallow-water areas characterized by alluvial substrates that supported high invertebrate production and afforded protection from predators (Stanford *et al*., 2006). Long stretches of highly connected habitats supported the subyearling rearing strategy of continually moving downstream through shallow, shoreline habitats until they dispersed offshore and became more pelagic and migratory (Connor *et al*., 2003; Coutant and Whitney, 2006; Tiffan *et al*., 2006). Impoundment eliminated much of the shallow-water habitat that existed and resulted in deeper shoreline habitats characterized by riprap

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and large natural substrates. These areas are generally not suitable for subyearlings (Curet, 1993; Garland *et al*., 2002; Tiffan *et al*., 2006) and are preferred by smallmouth bass (*Micropterus dolomieu*), which have become abundant in the reservoirs and are effective predators of subyearlings (Tabor *et al*., 1993; Anglea, 1997; Naughton *et al*., 2004). The current structure of subyearling rearing habitat in most reservoirs is composed of fragmented patches of habitat interspersed with unsuitable shoreline reaches that are often home to predatory fishes. However, the relative reduction in growth opportunity or predation risk to subyearlings in unsuitable locations is unknown.

Opportunities to mitigate the negative effects of habitat alteration in large, main-stem impoundments in the Columbia River basin are limited. However, in-water disposal of dredged material has been used to successfully create shallow-water habitats in Lower Granite Reservoir on the Snake River (e.g. Centennial Island, Chipps *et al*., 1997; Knoxway Bench, USACE, 2005; Figure 1), which are heavily used by subyearlings (Bennett *et al*., 1995; Tiffan and Connor, 2012). Continual deposition of sediments at the head of Lower Granite Reservoir requires periodic dredging to maintain the navigation channel and provide access to ports. The US Army Corps of Engineers plans to dredge during the winter of 2014–2015 and has interest in disposing dredged material within the reservoir to create shallow-water habitat for juvenile salmon while at the same time reducing the amount of habitat for predators. However, information on the quantity and distribution of subyearling rearing habitat and relative risk associated with habitats more suited to predators currently does not exist to guide such efforts.

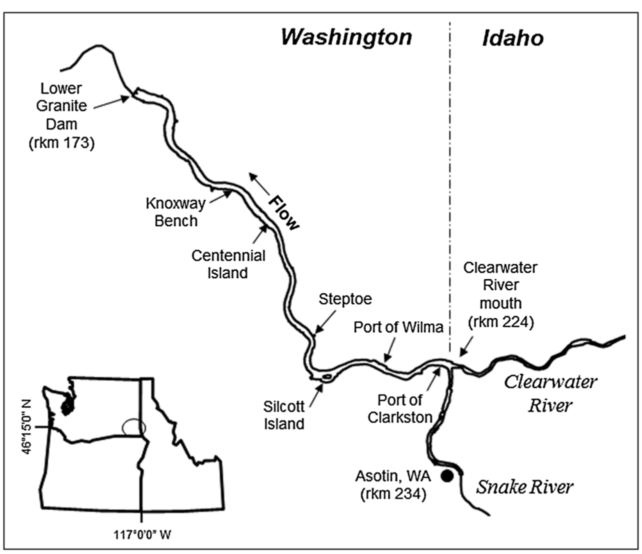

Figure 1. Map of Lower Granite Reservoir on the Snake River and selected landmarks

We initiated a study to (1) quantify the amount and distribution of subyearling rearing habitat in Lower Granite Reservoir and (2) increase our understanding of the relative risk that unsuitable locations pose to subyearlings. Given the differences in habitat preferences between subyearlings and smallmouth bass (e.g. Todd and Rabeni, 1989; Tiffan *et al*., 2006), we hypothesize that subyearlings should be more abundant and exposed to less predation risk along suitable shorelines and less abundant and exposed to higher predation risk in unsuitable areas (i.e. habitats more suited to smallmouth bass). The latter would also depend on how and when subyearlings move through unsuitable areas. For example, subyearlings moving through unsuitable areas during the day or offshore may be exposed to less predation risk if predators occupy deeper, offshore water during the day but move into shallow water nearshore at night to feed. Such information would be beneficial to effectively plan future main-stem improvement projects.

STUDY AREA

Lower Granite Reservoir is located on the lower Snake River in southeastern Washington and is the first of eight impoundments that juvenile fall Chinook salmon encounter as they migrate seaward (Figure 1). It is impounded by Lower Granite Dam, which is located 173 river kilometres (rkm) upstream of the confluence of the Snake and Columbia Rivers. The reservoir extends 61 km upstream to Asotin, Washington. At rkm 224, the Clearwater River enters the reservoir at Lewiston, Idaho. Lower Granite Reservoir is a run-of-the-river reservoir and is operated primarily for hydropower and navigation. Flows can range from above 4248 m^3 s in the spring to 453 m^3 s during winter. The reservoir has an average channel width of 634 m. Water depth averages 17 m and ranges from less than 1 m in shallow shoreline areas to a maximum of 42 m. The normal pool elevation only fluctuates about 1.5 m. To protect roads and railways, much of the shoreline has been lined with riprap. In the lower two-thirds of the reservoir, natural shorelines are generally steep and often characterized by cliffs and talus substrate. There is little riparian vegetation along the shorelines of the reservoir.

METHODS

We used a geographic information system (GIS) (ArcGIS®, Redlands, CA, USA) to conduct spatially explicit, grid-based analyses (ESRI, 1992) of subyearling rearing habitat. A number of GIS layers were required for our analyses. The first was riverbed bathymetry, which was necessary for calculating lateral bank slopes and for hydrodynamic modelling of river flows. The hydrodynamic modelling resulted

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in layers for water velocity and depth for each modelled flow. We divided the study area into a grid of cells with each cell containing values from the different habitat layers. We used these values in a subyearling rearing habitat model that we modified from the work of Tiffan *et al*. (2002). Using the habitat values of each cell, this model predicted the probability of fish presence in each cell that could then be used as a measure of habitat suitability. This probability layer was then used to quantify (i.e. predict) the total amount of available rearing habitat as well as to examine its spatial distribution within the reservoir.

Bathymetry

High-resolution bathymetry was acquired with a 250-KHz Geoswath multi-beam echo sounder in Lower Granite Reservoir from the dam (rkm 173) upstream to rkm 227 on the Snake River (Southway Bridge) and to rkm 3 on the Clearwater River (Memorial Bridge). All bathymetric positions were geo-referenced with a real-time kinematic global positioning system (GPS) (±2 cm horizontal accuracy). The vertical resolution of bathymetric elevations was ±3 cm, and bathymetry point data were processed to a resolution of 0.6 m (USACE, 2014).

Because multi-beam bathymetry was not collected in very shallow areas where juvenile fall Chinook salmon potentially rear, we collected additional bathymetry in shallow nearshore areas with an acoustic Doppler current profiler (ADCP). A boat equipped with a Rio Grande (Teledyne RDI Inc., Poway, CA, USA) 1200 kHz ADCP was used to collect bottom track data in water less than 4 m deep. The position of the ADCP was geo-referenced with a Trimble GeoXT GPS. The bottom was tracked along transects oriented perpendicular to the shoreline spaced at roughly 30-m intervals. The elevation of the bottom was later determined by subtracting the water depth from the water surface elevation.

The multi-beam and ADCP shallow-water bathymetry data were merged to create a final bathymetry layer. Position and elevation data were then used to create a triangulated irregular network (TIN, three-dimensional mesh) of points (ESRI, 2000), or nodes, for use in the hydrodynamic model. The resolution of the mesh was 30 m.

Hydrodynamic modelling

Steady-state water depths and velocities were estimated with the two-dimensional River2D model (Ghanem *et al*., 1996). River2D is a transient finite element model that can be set to obtain a steady state based upon the two-dimensional, depth-averaged St. Venant equations. Developed for use in streams and rivers, River2D has been verified through a number of comparisons with theoretical, experimental, and field results (Ghanem *et al*., 1995; Waddle *et al*., 1996; Hatten and Batt, 2010). We modelled five flows (1388, 3342, 4050, 4361 and 5664 m^3 s) but only a report results for the 3342-m^3 s flow for simplicity and because there was little variation in habitat results between flows. The 3342-m^3 s flow modelled was the median probability flow-duration (i.e. exceedance) discharge for 30-d, which is close to the average flow (3030 m^3 s, calculated for the years 2009–2013) during May and June when most subyearlings rear in the reservoir (Tiffan and Connor, 2012). Model inputs included bathymetry with geographic position, elevation and hydraulic roughness information, as well as the inflow discharge and the water-surface elevation (224.6 m, NAVD88) at the downstream end (forebay) of the modelled area. Using the constraints of inflow discharge and downstream water-surface elevation, the hydrodynamic model produced a simulated water depth, water-surface elevation and depth-averaged velocity for each mesh node.

Following hydrodynamic modelling, we created depth, velocity and lateral bed slope grids for spatial analyses of subyearling rearing habitat. For the simulated discharge, we imported depth and velocity data into ArcGIS as geo-referenced point data to produce TINs and grids of depths and velocities. We used a grid resolution of 3 m when we converted the TINs to grids. Finally, a bed-slope grid was produced from the bathymetry data using Environmental Systems Research Institute Spatial Analyst.

Habitat model

We modified an existing logistic regression rearing habitat model for juvenile fall Chinook salmon developed by Tiffan *et al*. (2002) to estimate rearing habitat in Lower Granite Reservoir. The original model included water velocity and lateral bed slope (i.e. gradient), which were each modelled as dummy variables with four levels. A reanalysis of the Tiffan *et al*. (2002) data suggested that it was more appropriate to model water velocity as a two-level dummy variable and gradient as a continuous variable. This was performed to satisfy the assumption that the relation between a predictor variable and the logit would be linear (Hosmer and Lemeshow, 1989; Demaris, 1992; Hardy, 1993).

The habitat model was used to predict the probability, P_i, of subyearling presence in i shoreline habitats. P_i can be expressed as a logit function as follows:

$$P_i = \frac{e^{g(x)}}{1 + e^{g(x)}}$$

where $g(x)$ is the linear combination of parameter estimates of the predictor variables. Our multivariate logistic regression model was expressed as follows:

$$g(x) = 0.4279 - 0.0588G + 2.5633V_1 + 1.7035V_2$$

where G represents gradient (measured in percent) and V_1 and V_2 represent water velocity (measured in centimetres per second, Table I). Because velocity was modelled as a dummy variable, an individual variable assumed a value of 1 when its category contained a measure for a given habitat cell; otherwise, its value was 0. Velocities >45 cm s represented the reference category. The model had an overall correct prediction rate of 81% using a jackknife classification at a probability cut-point of 0.5. When applied to an independent data set (i.e. one-third of the data withheld from model development), the overall correct prediction rate was 73%. The error of commission rate (i.e. predicting fish to occur where none were observed) was 28%, and the error of omission rate (i.e. predicting fish to be absent where fish were present) was 21% from classifications of the independent data.

Quantifying habitat

We predicted the quantity of subyearling rearing habitat in Lower Granite Reservoir by analysing the GIS data with the logistic regression model. GIS grids were created for water velocity and gradient. Based on these habitat attributes, we then used our model to predict the probability of fish presence in each GIS cell. We created a probability grid in GIS and considered habitat cells with probabilities greater than or equal to 0.5 (i.e. high-probability) to be suitable for rearing subyearlings. We applied a depth mask to eliminate all potential habitats if depths were greater than 1.8 m based on the work of Tiffan and Connor (2012) who collected 97% of rearing subyearlings in habitats shallower than 1.8 m. We also eliminated (masked) shorelines lined with riprap (digitized from aerial photos and field surveys) as rearing habitat because subyearlings avoid this type of substrate (Garland *et al*., 2002). Finally, we summed the areas of all cells with probabilities greater than or equal to 0.5 to determine the total amount of potential rearing area in the reservoir. We selected this binary habitat classification approach to more easily examine the spatial distribution of subyearling habitat, which would have been difficult had we used a continuous probability distribution, as well as to select field validation sampling sites (described in the succeeding texts). Given that most rearing subyearlings are shoreline oriented (Connor *et al*., 2003; Tiffan *et al*., 2006), we measured the linear extent of high-probability, low probability and riprap shorelines in GIS. We summarized results on habitat area and distance between habitat patches by river kilometre to examine longitudinal changes in habitat distribution within the reservoir.

Field validation

We sampled shorelines in the reservoir for subyearlings and smallmouth bass presence to validate model predictions. Low-probability habitats (<50% probability) were divided into natural (i.e. unaltered) and riprap reaches. In addition, we divided the reservoir into 4-km segments that each contained four sampling sites, two high-probabilities and two low-probabilities (one natural and one riprap). Within each 4-km segment, each sampling site was chosen by randomly selecting a river kilometre (delineated to the 0.1 km) and side of the river and then choosing the nearest habitat patch of interest. Our goal was to select 24 high-probability sites and 24 low-probability sites (12 natural and 12 riprap sites). To determine diel differences in habitat use, we randomly selected one-third of sites for night sampling and two-thirds for day sampling.

At each site, we sampled 200 m of shoreline with boat electrofishing during May and June 2014. The electroshocker was set to output 2 amps of pulsed direct current. Sampling distances were measured with a GPS, and shocking times were recorded. All smallmouth bass >150 mm [the minimum size considered to be a predation risk (Naughton *et al*., 2004)] were collected as well as natural-origin subyearlings. Most sampling was conducted before the release of hatchery subyearlings, and at the few sites where hatchery subyearlings were present, they could be easily distinguished from natural fish based on their larger size and morphology (Tiffan and Connor, 2011). All smallmouth bass were measured to the nearest millimetre total length, but only a subsample of the subyearlings was measured to minimize handling of this federally listed species. The number of each species collected at each site was standardized to 100 m of shoreline.

Table I. Summary of the logistic regression model used to predict juvenile fall Chinook salmon rearing habitat in Lower Granite Reservoir

Variable	Regression coefficients (95% Wald confidence interval)	SE[a]	Odds ratio
Intercept	0.4279 (−0.7960 to 1.6519)	0.6245	
Gradient (%)	−0.0588 (−0.0847 to −0.0329)	0.0132	0.943
V_1 (<5 cm s)	2.5633 (1.2573 to 3.8693)	0.6663	12.979
V_2 (5–45 cm s)	1.7035 (0.5753 to 2.8317)	0.5756	5.493

[a]SE refers to standard error.

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We initially examined the effects of habitat probability (i.e. high or low) and diel period (i.e. day or night) on subyearling and smallmouth bass abundance in separate two-way analyses of variance (ANOVAs). In both analyses, neither diel period (subyearling, $p > 0.09$; smallmouth bass, $p > 0.89$) nor the interaction between habitat probability and diel period (subyearling, $p > 0.29$; smallmouth bass, $p > 0.28$) was significant. Therefore, we dropped the diel term from the model and conducted separate one-way ANOVAs to examine the effects of habitat probability on subyearling and smallmouth bass abundance. We also examined the relation between smallmouth bass size and habitat probability in a one-way ANOVA. Pairwise comparisons of least-square means were made using Fisher's test for least-significant difference. Finally, we examined the relationship between subyearling abundance and the habitat probability at each site. Habitat probability at each site was calculated as the mean of 10 shoreline cell probabilities determined at systematic intervals based on site length.

RESULTS

Most (91%) subyearling rearing habitat (probability >50%) was located in the upper portion of Lower Granite Reservoir upstream from Steptoe (Figures 1 and 2). At a flow of 3342 m^3 s, we estimated that a total of 89 ha of subyearling rearing habitat existed in the reservoir. This represents about 3% of the total reservoir surface area. Habitat areas ranged from less than 1 ha to over 14 ha when expressed in increments of one river kilometre. The largest habitat areas were associated with known shallow-water locations. The most habitat occurred at Silcott Island (31.3 ha or 35% of all habitat) followed by Port of Wilma [13.1 ha (15%)], the area above Steptoe on the east side of the river [11.7 ha (13%)] and at Steptoe [10.8 ha (12%), Figures 1 and 2]. Other important locations included the Port of Clarkston (7.9 ha) and Centennial Island (2 ha, Figures 1 and 2). In the Clearwater River arm of the reservoir, no shoreline areas were predicted to be suitable because all shorelines were lined with riprap and depths were greater than 1.8 m.

Only 29% of the shoreline in Lower Granite Reservoir contained high-probability subyearling rearing habitat, and its distribution varied longitudinally within the reservoir and by reservoir side (i.e. north or south). The linear distances of suitable shorelines generally decreased in a downstream direction (Figure 3). There was two and one-half times more shoreline that was predicted to be suitable in the upper half of the reservoir than in the lower half, and there was almost three times more shoreline that was predicted to be suitable on the south side of the reservoir than on the north side (Figure 4). Similarly, the south side of the reservoir contained seven times more natural low-probability shoreline distance than the north side (Figure 4). Over 46% of the shoreline in Lower Granite Reservoir was lined with riprap, and the north shoreline contained three and one-half times more than the south shoreline (Figure 4).

In field collections of fish, subyearlings averaged 55 mm fork length ($N = 93$, SD = 10.7 mm, range 34–88 mm). Subyearlings were present in most habitats sampled, but their abundance varied significantly by habitat type ($F = 14.79$, $p < 0.0001$). Subyearling abundance in high-probability habitat was four times higher than in low-probability natural habitat and 14 times higher than in low-probability riprap

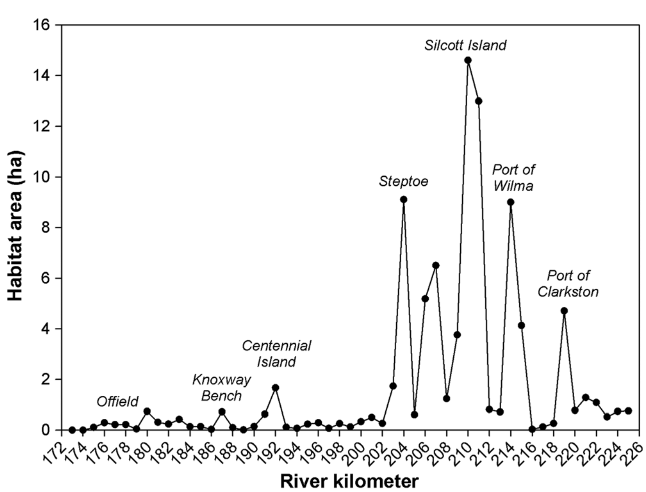

Figure 2. Estimates of subyearling fall Chinook salmon rearing habitat area by river kilometre in Lower Granite Reservoir on the Snake River. Habitat was predicted at a flow of 3342 m3 s and for depths ≤1.8 m

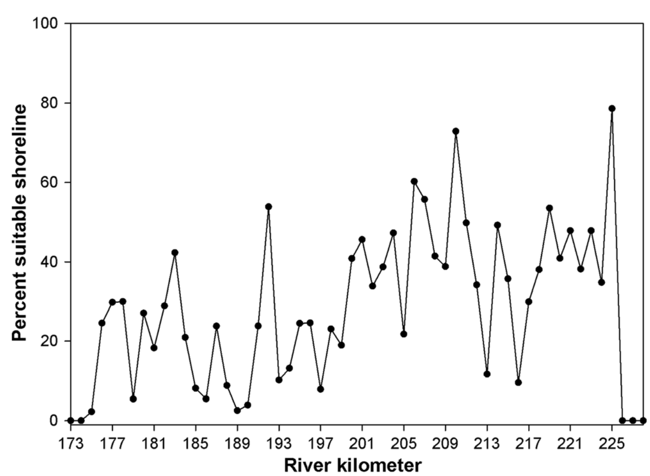

Figure 3. Percentage of shoreline within 1-km intervals in Lower Granite Reservoir that contains suitable (probability >50%) subyearling fall Chinook salmon rearing habitat. The last three points on the right side of the plot are from the Clearwater River arm of the reservoir

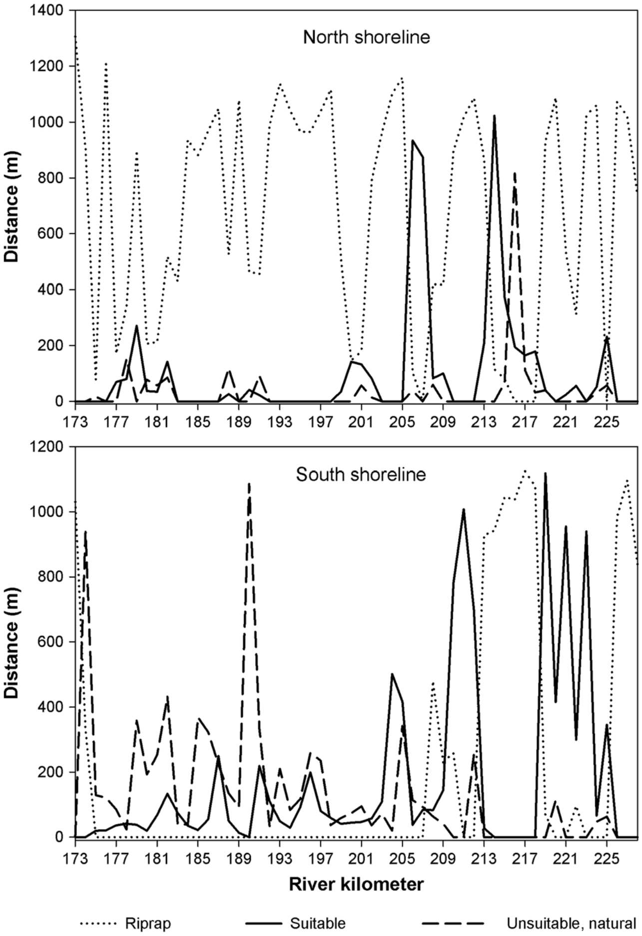

Figure 4. Linear shoreline distances of riprap, suitable (>50% probability) and unsuitable (<50% probability) natural habitats along the north (top panel) and south (bottom panel) shores of Lower Granite Reservoir. The last three points on the right side of the plots are from the Clearwater River arm of the reservoir

(Table II). Comparison of least-square means showed that subyearling abundance in high-probability habitat was significantly greater than in either low-probability natural habitat or riprap locations, with the latter two not being significantly different from each other. Eighty-three percent of high-probability habitats we sampled contained more subyearlings than smallmouth bass. Subyearling abundance generally increased with increasing habitat probability, but the relationship encompassed a large amount of variability resulting in an R^2 of 0.25 (Figure 5).

Smallmouth bass were found in most sampled habitats (low-probability and high-probability), but their abundance varied significantly by habitat type ($F = 7.25$, $p < 0.0019$). Smallmouth bass were three times more abundant in low-probability riprap than in high-probability habitat, but slightly less abundant in low-probability natural habitat (Table II). Comparison of least-square means showed that smallmouth bass abundance in low-probability riprap was significantly greater than in either of the other habitats, which were not significantly different from each other. Seventy-two percent of low-probability sites we sampled contained more smallmouth bass than subyearlings (Table II). Smallmouth bass lengths also varied significantly by habitat type ($F = 57.56$, $p < 0.0001$). Fish were similar in size in both high-probability and low-probability natural habitat but were significantly smaller in low-probability riprap (Table II).

DISCUSSION

Our modelling approach was useful for understanding the distribution of subyearling rearing within an entire reservoir. To accomplish this, we relied on a 0.5 probability cut-point in our habitat model to define habitat suitability. This simplified the spatial quantification of habitat in the reservoir as well as the selection of sampling sites for field validation of the model. A sensitivity analysis using 0.3, 0.5 and 0.7 cut-points did not appreciably change the pattern or magnitude of our habitat estimates. There was only a 4.4% difference between the total amount of suitable area predicted at a cut-point of 0.3 compared to 0.7. While the rearing model predicts fish presence, we assumed that increasing probability should be associated with increasing subyearling abundance, which was supported by our field validation (Figure 5). The variability in this relationship was influenced by variation in fish abundance, often due to schooling, and errors of commission and omission. The relatively high commission and omission error rates of our model are not too surprising considering the rearing model only contained two variables, and must be put in the context of subyearling rearing strategies. The presence of subyearlings in low-probability habitat (omission error) may not indicate preference for such habitat but may result from their movement through it because of their transient rearing. Similarly, the absence of subyearlings in high-probability habitat (commission error) may result from fish movement or from the fact that not all available habitat was occupied. We recognize that our results should be interpreted in light of these assumptions and limitations.

Underlying geomorphology was the primary determinant of subyearling rearing habitat quantity and distribution in Lower Granite Reservoir. The lateral bed slope variable in our rearing habitat model varied more than water velocity in the reservoir and thus had a greater effect on habitat estimates. The land adjacent to the reservoir upstream of Steptoe is gently sloping, particularly along the south shoreline. As such, the lateral bed slopes are lower that explains why the most subyearling rearing habitat was predicted there. Downstream of Steptoe, the reservoir is

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Table II. Mean ± SD (range) subyearling and smallmouth bass abundance and smallmouth bass size in high (>0.5) and low (<0.5) probability natural and riprap habitats in Lower Granite Reservoir, 2014

Habitat probability	Subyearling abundance (fish/100 m)	Smallmouth bass abundance (fish/100 m)	*N*	Smallmouth bass total length (mm)
High, natural	18.9 ± 14.1 (0–46.8)	4.3 ± 4.6 (0–17.6)	170	237 ± 56 (151–463)
Low, natural	4.5 ± 4.6 (0–13.7)	3.9 ± 2.8 (0.5–14.1)	69	244 ± 58 (150–416)
Low, riprap	1.3 ± 1.3 (0–4.3)	13.8 ± 13.6 (3.5–53.2)	216	189 ± 42 (150–370)

N refers to the sample sizes of bass that were measured.

predominantly confined by steep hillsides and basalt cliffs. The steep lateral bed slopes provide little shallow water habitat that subyearlings prefer (Tiffan *et al*., 2006) except at Centennial Island, Knoxway and in areas where small alluvial fans exist at the mouths of draws and at the toes of more gentle hillslopes. But even at these areas, large substrates often dominate, which subyearlings tend to avoid (Garland *et al*., 2002). Given that large substrates were present within many of the locations where our model identified high-probability habitat, our model likely overestimated the amount of habitat that is truly usable for subyearlings.

Riprap substrate also had a large effect on subyearling rearing habitat estimates. We determined that over 46% of the shoreline of Lower Granite Reservoir was lined with riprap, which we excluded as habitat based on subyearling avoidance of this substrate (Knudsen and Dilley, 1987; Curet, 1993; Garland *et al*., 2002). Indeed, our lowest catch of subyearlings occurred in low-probability reaches lined with riprap. Most riprap was located on the north side of the reservoir and the Clearwater River arm to protect levies, highways and a railway. Long, contiguous sections of riprapped shoreline often extend for many kilometres on this side of the reservoir making it more suited to smallmouth bass than to subyearlings. Riprap shorelines were also characterized by steep lateral

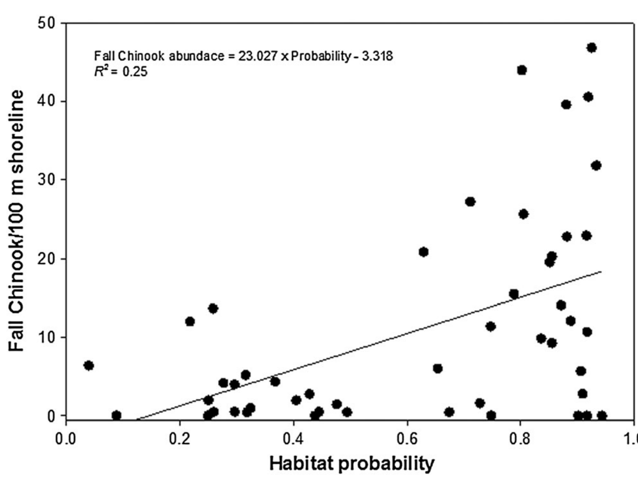

Figure 5. Relationship between subyearling fall Chinook salmon abundance and habitat probability at 48 field validation sampling sites in Lower Granite Reservoir on the Snake River

bed slopes, and the large substrate provided interstices that smallmouth bass often use as cover (Munther, 1970).

The quantity and distribution of different habitats are important metrics because they confer potential benefits and risks for the fish using them. For subyearlings, high-probability habitats characterized by low lateral bed slopes and velocities enable fish to exploit productive littoral prey resources, maximize growth in warmer temperatures and enjoy some level of protection from piscine predators afforded by shallow water (Tiffan *et al*., 2014). This reasoning is supported by the fact that more subyearlings were found in high-probability habitats compared with low-probability reaches of natural or riprap habitat. Assuming the benefits of high-probability habitat are reflected in growth opportunity, the amount of rearing habitat within the reservoir should be manifested in fish growth at the individual and population level. Tiffan *et al*. (2014) found that subyearling growth was lower in Lower Granite Reservoir than in the unimpounded river upstream. It is possible that the limited amount of high-probability habitat (29% of available shoreline) in the reservoir reduces the growth opportunity for subyearlings that could explain this lower growth rate. Thus, efforts to increase the amount of rearing habitat in Lower Granite Reservoir should promote better subyearling growth and survival.

In contrast, we suggest that low-probability habitat in Lower Granite Reservoir is associated with higher subyearling predation risk because that habitat is more preferred by smallmouth bass, as evidenced by their higher abundance in those habitats. We did find smallmouth bass in many of the high-probability habitats, but many were observed on spawning nests or associated with larger substrates that were not captured in our rearing habitat model. Nonetheless, smallmouth bass abundance was higher in lower-probability natural habitats, which should equate to a higher potential for predation. The relative predation risk could be substantially higher in riprap reaches because smallmouth bass were over three times more abundant than in high-probability habitat. This is particularly true for the north side of the reservoir where riprap lines much of the shoreline. Although we did not measure predation risk directly, our contentions are supported by the recent work of Erhardt *et al*. (2014) who estimated higher loss of subyearlings to smallmouth bass predation in

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low-probability riprap habitat than in natural habitat (both low-probability and high-probability) in Lower Granite Reservoir. Additionally, numerous studies have documented that smallmouth bass are effective predators of subyearlings, which supports the notion that subyearling predation risk should increase as their exposure to smallmouth bass increases via movement through the low-probability habitat they occupy (Rieman *et al*., 1991; Curet, 1993; Tabor *et al*., 1993; Fritts and Pearsons, 2004; Naughton *et al*., 2004).

Subyearling predation risk is also a function of prey and predator size. Smallmouth bass were smaller on average in riprap than in low-probability natural habitat. However, per capita consumption of subyearlings has been shown to be higher for smaller smallmouth bass (above 150 mm) than for larger fish (Tabor *et al*., 1993; Fritts and Pearsons, 2006). Fritts and Pearsons (2006) found that smallmouth bass could consume salmonid prey up to 57% of their length. This would make virtually all the subyearlings we collected vulnerable to predation by smallmouth bass as small as 150 mm. Given the higher abundance of smallmouth bass in riprap, subyearling predation risk may be highest there despite smallmouth bass being smaller in that habitat.

Subyearling exposure to predation risk is partly dependent on the duration of movement through low-probability habitats. Our collection of subyearlings from low-probability (natural and riprap) habitats supports the contention of Connor *et al*. (2003) that some fish move continuously downstream along shorelines during rearing regardless of habitat suitability. This rearing behaviour would incur increased predation risk the more fragmented high-probability habitat becomes, and as distances of lower-probability shoreline between habitat-patches increase. Indeed, our results show this to be the case in Lower Granite Reservoir as both the amount and linear extent of high-probability shorelines decrease in a downstream direction. However, the relatively low subyearling abundance in lower-probability habitats may also provide some support for the ‘spiralling’ concept proposed by Coutant and Whitney (2006). They suggest that juvenile salmon predominantly move downstream offshore at night and move inshore to feed during the day, resulting in a daily spiral of movement between offshore and nearshore habitats. Our low catch of subyearlings in low-probability habitats may have been due to fish moving downstream offshore to avoid them. Spiralling movement behaviour could reduce predation risk because smallmouth bass typically are not found in pelagic habitats. However, our results do not completely support the spiralling concept because we found no diel differences in subyearling catches regardless of habitat type.

Currently, we can only speculate on the relative predation risk of low-probability habitat to subyearlings, but our assessment of the quantity and distribution of existing subyearling rearing habitat provides insight for future habitat restoration work in Lower Granite Reservoir. Given that the least amount of high-probability rearing habitat exists in the lower portion of the reservoir, subyearlings would likely benefit most from actions to create shallow-water habitat in this area. Habitat created in areas currently classified as low-probability would have the double benefit of providing habitat for subyearlings while reducing the amount of smallmouth bass habitat. This was effectively accomplished by using dredge spoils to create shallow-water habitat at Centennial Island and Knoxway Bench (Chipps *et al*., 1997; USACE, 2005). Because a large percentage of shoreline is unsuitable in the lower reservoir, maximizing the linear extent of new shallow-water habitat along the shore could provide more benefit than creating a more expansive offshore, shallow-water area, as was carried out at Knoxway Bench.

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