Suitability criteria analyzed at the spatial scale of redd clusters improved estimates of fall chinook salmon (Oncorhynchus tshawytscha) spawning habitat use in the Hanford Reach, Columbia River

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Abstract: We improved our predictions of fall chinook salmon (Oncorhynchus tshawytscha) habitat use by analyzing spawning habitat at the spatial scale of redd clusters. Spatial point pattern analyses indicated that redd clusters in the Hanford Reach, Columbia River, were consistent in their location from 1994 to 1995. Redd densities were 16.1 and 8.9 redds·ha–1 in 1994 and 1995, respectively, and individual redds within clusters were usually less than 30 m apart. Pattern analysis also showed strong evidence that redds were uniformly distributed within the clusters where interredd distances ranged from 2 to 5 m. Redd clusters were found to occur predominantly where water velocity was between 1.4 and 2 m·s–1, water depth was 2–4 m, and lateral slope of the riverbed was less than 4%. This habitat use represented a narrower range of use than previously reported for adult fall chinook salmon. Logistic regression analysis determined that water velocity and lateral slope were the most significant predictors of redd cluster location over a range of river discharges. Overestimates of available spawning habitat lead to nonachievable goals for protecting and restoring critical salmonid habitat. Better predictions of spawning habitat may be possible if cluster-specific characteristics are used.

Résumé : Nous avons amélioré nos prédicteurs de l'utilisation de l'habitat par le quinquant (Oncorhynchus tshawytscha) d'automne en analysant l'habitat de fraye à l'échelle spatiale des grappes de nids. Les analyses de voisinage ont indiqué que les grappes de nids dans le tronçon Hanford du fleuve Columbia étaient localisées de façon uniforme de 1994 à 1995. Les densités étaient respectivement de 16,1 et 8,9 nids à l'hectare en 1994 et 1995, et, à l'intérieur des groupements, les nids étaient généralement distants de moins de 30 m. L'analyse de voisinage a aussi montré nettement que les nids étaient distribués de façon uniforme à l'intérieur des grappes, les distances entre les nids allant de 2 à 5 m. Les grappes de nids se retrouvaient principalement aux endroits où la vitesse de l'eau se situait entre 1,4 et 2 m·s–1, la profondeur de l’eau était de 2 à 4 m, et la pente latérale du lit de moins de 4%. Cette utilisation de l'habitat représentait une plage plus étroite que ce qui avait été signalé antérieurement pour le quinquant d’automne adulte. L'analyse de régression logistique a fait ressortir que la vitesse de l’eau et la pente latérale étaient les prédicteurs les plus significatifs de l'emplacement d’une grappe de nids pour une série de débits du cours d’eau. Si l’habitat de fraye disponible est surestimé, les buts fixés pour la protection et la restauration de l’habitat critique des salmonidés ne pourront pas être atteints. Il serait possible d’avoir de meilleures prédicteurs pour l’habitat de fraye si on s’appuie sur les caractéristiques particulières aux grappes de nids.

[Traduit par la Rédaction]

Introduction

Physical habitat simulation models (PHABSIM; Milhous 1979; Stalnaker 1979) are used in instream flow assessment studies to evaluate how spawning habitat of salmon changes with varying stream flow (Shirvell 1989; Connor et al. 1990). PHABSIM combines physical characteristics of the river channel (e.g., substrate and channel dimensions) into a hydraulic model that simulates how water surface elevation, depth, and velocity will change over a range of river discharges (Bovee and Bartholow 1995). A “map” of the river channel can be generated that provides a picture of what the physical characteristics of the river would look like at each simulated river discharge. To translate this picture into an estimate of salmon spawning habitat, spawning habitat suitability criteria are used to define the ranges of depths, velocities, and substrates that are utilized by spawning salmon. The physical attributes of the river are compared against the habitat suitability criteria to determine the relative value of physical characteristics for spawning habitat.

The standard procedure when using PHABSIM to predict available spawning habitat is to collect or use spawning habitat criteria that originate within the river of interest (Bovee 1995). River-specific suitability criteria were used in a previous application of PHABSIM to fall chinook salmon (Oncorhynchus tshawytscha) spawning habitat in the Hanford Reach, Columbia River (Bovee and Bartholow 1995). River-specific suitability criteria were used in a previous application of PHABSIM to fall chinook salmon (Oncorhynchus tshawytscha) spawning habitat in the Hanford Reach, Columbia River.
Oncorhynchus tshawytscha spawning habitat in the Hanford Reach of the Columbia River (Geist et al. 1997). In that study, approximately 200 redds were randomly sampled from spawning areas located throughout the entire length (~80 km) of the Hanford Reach. Fall chinook salmon redds were found to occur in water velocities that ranged from 0.5 to 2.0 m·s⁻¹, water depths of 0.5–7.0 m, and substrate particles that were 2.5–15.2 cm in diameter (Geist et al. 1997). This was consistent with habitat use by adult fall chinook salmon in other parts of the Columbia River Basin (reviewed by Geist and Dauble 1998), including the Snake River where fall chinook salmon are listed under the Endangered Species Act (Groves and Chandler 1999). Using these criteria, PHABSIM predicted that approximately 50% of the river bottom at each of two spawning areas in the Hanford Reach could have been utilized for spawning. In contrast, even though fall chinook salmon escapements during the study were sufficient to completely seed the two areas (D.R. Geist, unpublished data), actual use was 0% at one area and 20% at the second area.

We believe that the disparity between PHABSIM predictions and actual use occurred because the suitability criteria did not consider that fall chinook salmon redds are typically aggregated in patches or “clusters” within the Hanford Reach (Geist and Dauble 1998). The patchy redd distribution provides strong evidence that clusters may contain specific features that fall chinook salmon use when selecting spawning locations. We hypothesized that the PHABSIM estimates from Geist et al. (1997) would have been improved had they incorporated habitat suitability criteria from redd clusters rather than from individual redds that were sampled throughout the reach.

The objective of this paper was to determine if an analysis of suitability criteria based on cluster-scale measurements would result in better predictions of habitat use from two spawning areas where PHABSIM previously overestimated spawning habitat (Geist et al. 1997). We applied spatial point pattern analysis to demonstrate that spawning was clustered and logistic regression analysis to identify important factors influencing redd distribution. Our intent is to apply the improved predictions of habitat use by adult fall chinook salmon to develop recovery plans for fall chinook salmon from the Columbia River Basin.

Materials and methods

Study area

The Hanford Reach of the Columbia River is approximately 80 km long, unimpounded, and bounded by Priest Rapids Dam on the upstream end and McNary Reservoir on the downstream end (Fig. 1a). The largest population of fall chinook salmon in the Columbia River Basin returns each year to spawn in the Hanford Reach (Dauble and Watson 1997). Peak fall chinook salmon spawning habitat Olsen Northwest of the United States with the Hanford Reach of the Columbia River highlighted. Mainstem hydroelectric dams (triangles) and major tributaries are also shown. (b) Enlargement of the Hanford Reach showing the Locke Island and Wooded Island study sites. Arrows indicate the flow direction of the river.
spawning occurs from approximately the last week in October through the third week in November (Dauble and Watson 1990). Physical habitat data were collected at two sites in the Hanford Reach (Fig. 1b): Locke Island (river kilometres 596–600) and Wooded Island (river kilometres 560–563). Each study site was approximately 3.5 km in length and 300–400 m wide and occurred in a braided channel. These sites have similar channel characteristics but very different redd densities. The average annual redd count from 1990 to 1995 was 513 redds (range 340–855 redds) and 10 redds (range 0–32 redds) for the Locke Island and Wooded Island study sites, respectively (Dauble and Watson 1997; D.D. Dauble, unpublished data).

Although the Hanford Reach is unimpounded, upstream hydropower dams control flow through the study sites. During the fall chinook salmon spawning period, flows at Priest Rapids Dam are operated according to the Vernita Bar Settlement Agreement (Federal Energy Regulatory Commission 1988). The primary objective of the Agreement is to minimize spawning in areas where flow cannot be maintained throughout the egg incubation period. This is accomplished through reverse load factoring, i.e., influencing the location of fall chinook salmon redds by intentionally reducing power generation during the daylight hours (approximately 06:00–17:00) and then increasing generation during hours of darkness. Implicit in the Agreement is that fall chinook salmon are capable of completing spawning within a 24-h period between two successive nighttime flows (Chapman et al. 1986).

Spatial pattern analysis

Fall chinook salmon redds were photographed at each site from a fixed-wing airplane flying approximately 600 m above the water surface (photographic scale of ~1:2400). Flights occurred during the peak spawning interval with one flight per week made in 1994 (Locke Island site only) and 1995 (both sites). Each redd was digitized into an Arc-Info® geographic information system. Cumulative distributions for week 4 of the spawning period are presented here (Fig. 2). Aerial photographs were limited by water depth. However, additional redd surveys, conducted in 1995 using an underwater video camera, showed that no additional redds were present outside the area of photographic record.

Refined nearest-neighbor analysis (Boots and Getis 1988) was used on the digitized redds to determine whether fall chinook salmon redds were randomly distributed or if they followed a uniform (i.e., regular) and (or) clustered pattern. The spatial pattern analysis was also used to determine the distance between redds within any given pattern type. The nearest-neighbor analysis required the use of a rectangular boundary for the study area. For
that reason, a reasonably straight section of the river within the Locke Island study site was chosen, and the location coordinates of the redds were transformed by rotation so that the long axis of the spatial study area was parallel to the longitudinal axis of the river (Fig. 2). This provided a rectangular boundary 425 m wide and 2,850 m long. A contingency table and $X^2$ test were also used in that study area to test the hypothesis that occupation of a 20 x 20 m cell by a chinook salmon redd in 1995 was independent of occupancy in 1994.

Refined nearest-neighbor analysis (Boots and Getis 1988) uses the cumulative distribution function $F(d)$ to describe the probability that the nearest neighbor to a redd is within a given distance $d$. For a random spatial distribution generated by a Poisson process, the expected cumulative distribution function is

$$F(d) = 1 - e^{-\lambda \pi d^2}, \quad d \geq 0$$

where $\lambda$ is the intensity of the points within the area, estimated by $\lambda = n/A$ for $n$ points in area $A$. The empirical cumulative distribution of distances can be calculated from the data set for each distance $d$ and compared with the expected value for that distance.

The software used to conduct the spatial pattern analyses (Moer 1993) generates a Monte Carlo confidence envelope around the expected value for each distance $d$. The empirical cumulative distribution determined from the data is compared with the confidence envelope for each $d$; if the proportion of the nearest neighbors less than distance $d$ is outside the confidence envelope, then the hypothesis that the spatial pattern of the data points resulted from a random process is rejected at the 95% confidence level. The direction of the deviation above or below the confidence envelope indicates whether the nonuniform pattern tended toward a clustered or uniform distribution, respectively.

**Hydraulic habitat data**

Hydraulic data were collected following the procedures of the instream flow incremental methodology (Bovee 1982). Eight transects were set perpendicular to the flow, approximately 450 to 550 m apart, at each study site. River stage and river discharges were measured on three separate occasions (October 1995, June 1996, and July 1997) to establish stage–discharge relationships. Elevations were measured using a laser transit (Leitz/Sokkisha S02 Electronic Total Station®). Discharge was measured using an acoustic Doppler current profiler (ADCP model 600®). River discharge during the surveys ranged from 2,206 to 7,061 m$^3$·s$^{-1}$.

During hydraulic calibration surveys conducted in October 1995, mean water column velocities, channel elevations, and substrate sizes were measured at locations along each transect, which we refer to as “habitat cells” (Payne and Lapointe 1997). Habitat cells were assumed to represent depth and velocity conditions of a hydraulically uniform area of river. An ADCP was used to measure water velocity and depth along each transect when water depth was greater than 1 m. At water depths less than 1 m, channel elevation and water velocity (0.6 of the water depth) were measured using a standard top-set wading rod and a Marsh McBirney® flowmeter. Lateral slope of the river bottom at each habitat cell was determined using cross-section elevations of the transects and water depths measured with the ADCP. Average river discharge at the Locke Island and Wooded Island study sites during these surveys was 1,250 and 2,462 m$^3$·s$^{-1}$, respectively.

Substrate measurements were made on the hydraulic transects and on four additional transects that overlapped and bounded the spawning areas. Images of the substrate on the surface of the riverbed were collected using an underwater camera suspended about 40 cm above the riverbed (Garcia et al. 1994; Groves and Garcia 1998). Up to 20 substrate images were collected on each transect, or approximately 250 images at each study site. The location of substrate images was recorded using a global positioning system (Trimble Pro-Excel®). All individual substrate clasts within each image were measured (long-axis diameter and surface area) and stored using a computer program (Optimus®). Each substrate image was assigned a dominant and subdominant size-class (Bruvven 1977; Groves and Chandler 1999) based on long-axis diameter. The percentage of fine-grained material ($d < 2$ mm) visible within interstitial spaces was also recorded.

We used IFG-4 (Milhous et al. 1984) to simulate depth and velocity at each habitat cell. Simulation flows were selected to represent the range of flows under which fall chinook salmon spawn. We excluded nighttime flows from our analysis because they were intentionally high due to reverse load factoring and artificially raised the average flows above levels that we believed would be representative of potential spawning flows. Flow fluctuations at Priest Rapids Dam are attenuated with increasing distance downstream and not representative of the minimum or maximum hourly flows that occurred at the study sites. This has been verified by comparing hourly discharge at Priest Rapids Dam with continuous stage measurements of the river recorded at hourly increments (Walters et al. 1994). Therefore, hourly flows from Priest Rapids Dam were input to a one-dimensional hydraulic simulation model in order to estimate the minimum ($Q_{min}$), average ($Q_{ave}$), and maximum ($Q_{max}$) hourly flows during the daylight hours (06:00–17:00) within the peak spawning period at the Locke Island (1994 and 1995) and Wooded Island (1995 only) study sites (Fig. 3). The $Q_{min}$, $Q_{ave}$, and $Q_{max}$ flows at the Locke Island site were 1,453, 2,034, and 3,034 m$^3$·s$^{-1}$, respectively, in 1994 and 1896, 2,474, and 3,481 m$^3$·s$^{-1}$, respectively, in 1995. The $Q_{min}$, $Q_{ave}$, and $Q_{max}$ flows at the Wooded Island site in 1995 were 2,285, 2,974, and 3,420 m$^3$·s$^{-1}$, respectively. Based on the close agreement between simulated river stage and actual river stage (less than ±10 cm), flow simulations were estimated to be within less than ±5% of the actual values (G. Guensch, Pacific Northwest National Laboratory, Richland, Wash., personal communication).

Velocity adjustment factors were calculated by dividing the simulated velocity by the measured velocity (Bovee and Bartholow 1995). Simulations were rejected if the velocity adjustment factor was less than 0.1 or greater than 5.0; none of our simulations exceeded these criteria. We used measured values for substrate and lateral slope, as we assumed that these values would not change between the simulated flows and measured flows. Following hydraulic simulations, each habitat cell contained a value for depth, substrate class (dominant and subdominant), mean water column velocity, and lateral slope.

**Logistic regression model**

Logistic regression, based on negative log likelihood (Hosmer and Lemeshow 1989), was used to determine which explanatory variables were important in spawning habitat selection. The specific form of the logistic regression model was

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

where $\pi(x)$ was the probability that a habitat cell would be suitable for spawning and $g(x)$, the logit transformation of $\pi/l - \pi$, is the linear combination of parameter estimates from the logistic regression

$$g(x) = B_0 + B_1X_1 + \ldots + B_nX_n.$$
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Hydraulic habitat data

Hydraulic habitat data were collected at 403 habitat cells at the Locke Island study site in 1994. The pattern analysis showed
that 84 of these cells fell within redd clusters and were defined as suitable spawning habitat. The remaining cells (319) fell outside redd clusters and were defined as unsuitable spawning habitat. Habitat cells within redd clusters had significantly lower lateral slope, shallower depths, and significantly higher velocities than habitat outside redd clusters (Fig. 6). Spawning habitat inside redd clusters also contained significantly more dominant substrate between 5.1 and 15.2 cm and subdominant substrate between 2.5 and 7.6 cm than habitat outside redd clusters (Fig. 6). Approximately 80% of the habitat within redd clusters contained water velocity between 1.4 and 2.0 m·s⁻¹, lateral slope less than 4%, and water depth of 2.0–4.0 m. Less than 2.5% of the habitat cells inside redd clusters contained water velocities less than 1.0 m·s⁻¹. In contrast, approximately 40% of the habitat cells outside redd clusters were characterized by water velocities less than 1.0 m·s⁻¹.

**Logistic regression model**

Multivariate logistic regression analysis of the hydraulic data collected at the Locke Island site in 1994 revealed that substrate was not a significant predictor of spawning habitat suitability. This was in contrast with the univariate analysis that showed that substrate was significantly different inside and outside redd clusters (Fig. 6). However, the multivariate analysis was consistent with the results from the univariate analysis for the other hydraulic variables. Stepwise logistic regression selected lateral slope and depth, velocity, and the velocity-squared term at the $Q_{ave}$ flow as significant variables explaining the spawning site selection by fall chinook salmon at Locke Island (Table 1). The highest odds ratios were associated with velocity, suggesting that this variable was most important in predicting spawning habitat suitability. Both lateral slope and depth were negatively associated with spawning habitat suitability. The odds ratios showed that a decrease of approximately 1% in slope resulted in a 25% increase in the probability of the site being utilized for spawning, while a decrease in depth of 0.5 m resulted in an increase in the probability that the site would be utilized for spawning of approximately 60%.

At Locke Island in 1995, the logistic regression model explained a significant proportion of the variance in habitat cell designation, with approximately 78–87% of the habitat cells correctly predicted as either suitable (ps,as) or unsuitable (pu,au) spawning habitat (Fig. 7). Even though the percentage of correct predictions was relatively high at Locke Island, 29–56% (Fig. 7, ps,au/ps) of the sites predicted to be utilized for spawning were not (i.e., errors of commission). Sites where errors of commission occurred contained similar physical features as those sites where spawning occurred, i.e., mean lateral slope, depth, and velocity of 2.4%, 2.5 m, and 1.6 m·s⁻¹, respectively. Approximately 9–19% of spawning at Locke Island (Fig. 7, pu,as/pu) occurred in areas that the model predicted as unusable habitat (i.e., errors of omission). Sites where errors of omission occurred had a mean lateral slope of 3.5%, a water depth of 3.9 m, and a velocity of 1.8 m·s⁻¹.

Although fall chinook salmon appeared to spawn within a specific area at Wooded Island (Fig. 2), there were an insufficient number of redds within 30 m of one another to be considered clustered. Thus, none of the habitat cells at Wooded Island were coded as suitable spawning habitat. At Wooded Island, the logistic regression model correctly predicted habitat cell designation (pu,au) 79–91% of the time, with approximately 9–21% of the habitat cells predicted to be suitable spawning habitat (Fig. 7). The actual number of habitat cells that were suitable for spawning at Wooded Island was zero; thus, none of the sites predicted to have redds had redds. The predicted spawning sites at Wooded Island contained similar physical features as found within spawning areas at Locke Island, i.e., mean lateral slope 3%, water depth 2.9 m, and velocity 1.7 m·s⁻¹.

**Discussion**

Spatial pattern analysis confirmed that fall chinook salmon redds at the Locke Island site occurred in clusters. Even though the number of redds varied almost twofold in 1994 and 1995, the locations of these clusters were similar. In both years, the majority of redds occurred in clusters and were within 30 m of each other. In 1994 when redd densities
were higher, there was strong evidence of a uniform distribution of redds within the clusters at distances of 2–5 m. The crossover distance (i.e., 2–5 m) where patterns switched from uniform to clustered was approximately the distance between the centers of two adjacent redds. In other words, at the spatial scale of a spawning area, redds exhibited high fidelity and occurred in clusters, but within each cluster, redds were uniformly spaced.

Uniformity in the spatial patterns of redds within clusters at Locke Island in 1994 likely resulted from interactions between individuals competing for space (Ludwig and Reynolds 1988). Interactions between neighboring chinook salmon females influenced redd site selection within a cluster of redds in the Nechako River, British Columbia (Neilson and Banford 1983). That the redd densities within clusters were high in 1994 suggests that the available space was exhaustively partitioned among redds. Competition for spawning locations within clusters of redds apparently occurred in the Locke Island study site despite the fact that escapements of fall chinook salmon to the Hanford Reach in
If sites suitable for spawning were patchily distributed, as the nonrandom distribution of redds suggested, they could have a unique set of attributes that were not found throughout the entire study area. An alternative interpretation might be that spawning salmon do not have strong habitat-specific fidelity but choose to spawn adjacent to sites chosen by the earliest arriving individuals in a season (Duker 1981). For example, brook trout (Salvelinus fontinalis) and brown trout (Salmo trutta) were found to selectively spawn in areas of the streambed that had been disturbed by earlier spawners (Essington et al. 1998). However, the high rates of reoccupation of redd clusters between years suggest that cluster location is not random and support the site-specific fidelity interpretation. Specific habitat utilization and clustering of salmon spawning has been observed in other populations. For example, chinook salmon in the Kamchatka River, Russia, spawned in distinct patches, even though apparently similar habitat was available nearby (Vronskiy 1972). Chapman (1943) noted concentrated chinook salmon spawning in the mainstem Columbia River below Kettle Falls, Washington, where “the greater part of the river was not in use.” Clusters of chinook salmon spawning in the

Table 1. Stepwise model selection results from multiple logistic regression of hydraulic simulation data explaining the distribution of fall chinook salmon spawning at Locke Island in 1994.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Estimated regression coefficient</th>
<th>Wald $\chi^2$</th>
<th>$P$</th>
<th>Lower 95% CI</th>
<th>Upper 95% CI</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lateral slope</td>
<td>$-27.1\pm8.47$</td>
<td>10.2</td>
<td>0.0014</td>
<td>0.65</td>
<td>0.90</td>
</tr>
<tr>
<td>$Q_{ave}$ depth</td>
<td>$-1.8\pm0.27$</td>
<td>44.7</td>
<td>&lt;0.0001</td>
<td>0.32</td>
<td>0.54</td>
</tr>
<tr>
<td>$Q_{ave}$ velocity</td>
<td>$31.0\pm6.69$</td>
<td>21.5</td>
<td>&lt;0.0001</td>
<td>5.98</td>
<td>82.29</td>
</tr>
<tr>
<td>$Q_{ave}$ velocity$^2$</td>
<td>$-8.6\pm2.17$</td>
<td>15.9</td>
<td>&lt;0.0001</td>
<td>0.28</td>
<td>0.64</td>
</tr>
<tr>
<td>Intercept</td>
<td>$-20.9\pm5.0$</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

Note: Regression statistics for the spawning habitat model (4 df) were log likelihood = 200.73 (intercept only) and 101.97 (intercept and covariates). Regression coefficients are depicted as estimate $\pm$ 1 SE. The significance level for stepwise selection was 0.05. $Q_{ave}$ depth, $Q_{ave}$ velocity, and $Q_{ave}$ velocity$^2$ are the simulated depths and velocities at the 12-h average discharge (2034 m$^3$/s$^{-1}$).

Fig. 7. A logistic regression model was used to predict fall chinook salmon spawning habitat suitability in 1995 at Locke Island and Wooded Island at $Q_{min}$, $Q_{ave}$, and $Q_{max}$ hourly discharges. (a) Locke Island at $Q_{min}$ (1896 m$^3$/s$^{-1}$); (b) Locke Island at $Q_{ave}$ (2474 m$^3$/s$^{-1}$); (c) Locke Island at $Q_{max}$ (3481 m$^3$/s$^{-1}$); (d) Wooded Island at $Q_{min}$ (2285 m$^3$/s$^{-1}$); (e) Wooded Island at $Q_{ave}$ (2974 m$^3$/s$^{-1}$); (f) Wooded Island at $Q_{max}$ (3 420 m$^3$/s$^{-1}$). p, predicted; a, actual; s, spawning habitat suitable; u, spawning habitat unsuitable.
Nechako River corresponded to river bottom topography and substrate, with fish preferentially spawning along the lateral gravel ridges (Neilson and Banford 1983).

PHABSIM estimates spawning habitat using criteria based on published or measured redd selection data (Bovee 1995). The use of river-specific suitability criteria is currently believed to be the best method for predicting spawning habitat for salmonids within rivers and streams (Shirvell 1989; Bovee 1995). Our logistic regression model used characteristics of spawning habitat measured within a local spawning area and represented the suitability criteria over a finer spatial scale than river-specific criteria. The analysis suggested that 9–22% of the riverbed at Locke Island and 9–21% of the riverbed at Wooded Island were suitable as spawning habitat for fall chinook salmon. These estimates were closer to the actual amount (~20% at Locke Island and 0% at Wooded Island) than the results from the previous study where river-specific criteria were used (estimates of 50%; Geist et al. 1997). Better predictions were possible because our approach removed much of the variation between spawning areas that are widely separated and resulted in a narrower range of suitable spawning habitat. That the logistic regression analysis, based on spawning habitat characteristics measured at Locke Island, predicted higher spawning utilization than actually occurred at Wooded Island showed that chinook salmon did not respond to habitat in a similar manner at each site. Additional evaluations of the logistic regression model at other high-use spawning areas are needed and may show that each individual spawning area contains a unique combination of physical habitat.

The aerial photographs from Locke Island in 1994 and 1995 did not show fall chinook salmon redds above the 1415 m³·s⁻¹ flow elevation. The minimum hourly discharges in 1994 (1453 m³·s⁻¹) and 1995 (1896 m³·s⁻¹) were above this level, suggesting that redd clustering was not a function of minimum flows. It would appear from our analysis in 1994 when the minimum flows were near the 1415 m³·s⁻¹ flow level that the clustering of redds may have been in response to the rapid change in discharge because fish appeared to select habitat at the highest flow elevation that did not become dewatered in a 24-h period. However, the results in 1995 do not support this, as the minimum flows were substantially higher than in 1994 but the location of spawning was very similar. This would suggest that factors other than flow fluctuations were responsible for redd clustering. That the logistic regression analysis showed that redd locations were more correlated with velocity and depth simulated at the average flow conditions than at the minimum or maximum flows suggests that fish were responding to flow conditions that occurred over a longer time period than represented by minimum or maximum hourly values.

Approximately 29–56% of the sites at Locke Island and all the sites at Wooded Island predicted to have redds using the physical attributes did not have redds (i.e., errors of commission). Some of this error can be explained by the lower number of redds in 1995. The logistic regression model was constructed using redd data from 1994, so not all the sites predicted to be suitable in 1995 could be filled. However, even in 1994 at Locke Island when redd densities were near capacity (D.R. Geist, unpublished data), errors of commission resulted. Most of these errors occurred adjacent to large clusters of redds. This suggested that although the depth, lateral slope, and velocity in these locations were similar to those in the clusters, some other key attribute was different and resulted in fewer fish colonizing these areas. In contrast, some areas of streambed predicted to be unsuitable by our model had redds (i.e., errors of omission). Errors of omission may result from spawners being forced into “suboptimal” habitat located on the fringes of the clusters (Neilson and Banford 1983). Most of these errors occurred near the boundaries of the clusters where the lateral slope increased due to a change in riverbed form.

In either case, there was some unmeasured factor(s) that influenced redd site selection. For example, the long, sinuous, and narrow gaps frequently observed within the redd clusters in the Hanford Reach suggest that spawning is controlled by geomorphic features of the river bottom (i.e., sedimentary structures). The shapes of redd clusters were very similar to those commonly observed in longitudinal bars and channels deposited by gravelly braided rivers (e.g., Rust and Koster 1984). Hydraulic processes that form the longitudinal bars and channels in the river directly influence the topography (depth and slope) and the sediment size exposed on the river bottom. Geist and Dauble (1998) proposed that geomorphic features promote groundwater–surface water interactions within hyporheic habitats and may play a role in spawning site selection by fall chinook salmon. In fact, upwelling from hyporheic habitats into the river in Locke Island spawning areas was greater than upwelling into nonspawning areas at Locke Island and Wooded Island (Geist 2000). Further, the upwelling in spawning areas contained more oxygen and was composed of a higher proportion of river water than upwelling in nonspawning areas. These upwelling characteristics could provide cues that adult fall chinook salmon used to locate preferred spawning habitat.

Fisheries managers use hydraulic models like PHABSIM because they provide a conservative estimate of fish habitat. When river-specific habitat suitability criteria are used, this modeling approach may not help define the relative importance of physical habitat features that control spawner use at the cluster scale. The risk in overestimating suitable spawning habitat is that many recovery goals for anadromous salmonids are not supported by empirical data. Evaluating habitat characteristics at the scale of redd clusters provides an alternative means for describing specific physical features that influence salmon spawning and improves the overall understanding of factors affecting redd site selection. We believe that this will lead to more realistic estimates of spawning habitat capacity, which will result in better recovery goals and a more efficient use of recovery resources.

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