Redd Site Selection and Spawning Habitat Use by Fall Chinook Salmon: The Importance of Geomorphic Features in Large Rivers

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ABSTRACT / Knowledge of the three-dimensional connectivity between rivers and groundwater within the hyporheic zone can be used to improve the definition of fall chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat. Information exists on the microhabitat characteristics that define suitable salmon spawning habitat. However, traditional spawning habitat models that use these characteristics to predict available spawning habitat are restricted because they can not account for the heterogeneous nature of rivers. We present a conceptual spawning habitat model for fall chinook salmon that describes how geomorphic features of river channels create hydraulic processes, including hyporheic flows, that influence where salmon spawn in unconstrained reaches of large mainstem alluvial rivers. Two case studies based on empirical data from fall chinook salmon spawning areas in the Hanford Reach of the Columbia River are presented to illustrate important aspects of our conceptual model. We suggest that traditional habitat models and our conceptual model be combined to predict the limits of suitable fall chinook salmon spawning habitat. This approach can incorporate quantitative measures of river channel morphology, including general descriptors of geomorphic features at different spatial scales, in order to understand the processes influencing redd site selection and spawning habitat use. This information is needed in order to protect existing salmon spawning habitat in large rivers, as well as to recover habitat already lost.

The protection and restoration of spawning habitat within large mainstem rivers is included in most recovery plans for Pacific salmon (NPPC 1994; USFWS, 1991, 1996a,b). Realistic predictions of available spawning habitat must be used to define salmon recovery goals (ISG 1996). However, we have little knowledge of spawning site use by salmon beyond our understanding of the physical constraints imposed on site selection, redd construction, and embryo survival. One widely used traditional spawning habitat model, the Physical Habitat Simulation model (PHABSIM) (Milhous 1979, Stalnaker 1979) of the Instream Flow Incremental Methodology (IFIM) (Bovee 1982) uses estimates of water depth, water velocity, and substrate size to predict available spawning habitat. The pros and cons of using IFIM and PHABSIM to model fish habitat have been debated in the literature (Mathur and others 1985, 1986, Orth and Maughan 1986). The IFIM approach has been useful for defining the limits of salmon spawning habitat, but in some situations where PHABSIM has been used, estimates of available spawning habitat were questionably high (Shirvell 1989, Arnsberg and others 1992) suggesting some other variables are involved. More realistic estimates of salmon spawning (i.e., relative to known escapement) have been made with PHABSIM when river channel slope and scour potential were added as model parameters (Connor and others 1994a,b) suggesting that predictions of available spawning habitat for salmon by traditional models such as PHABSIM are improved by including characteristics that consider river channel hydraulics.

In our studies of fall chinook salmon (*Oncorhynchus tshawytscha*) spawning in the Hanford Reach of the Columbia River, we have noted that fall chinook salmon redds are usually aggregated in definite clusters even though it appears suitable spawning areas are widely distributed (Dauble and Watson 1990). These clusters tend to occur in areas with a complex channel pattern,

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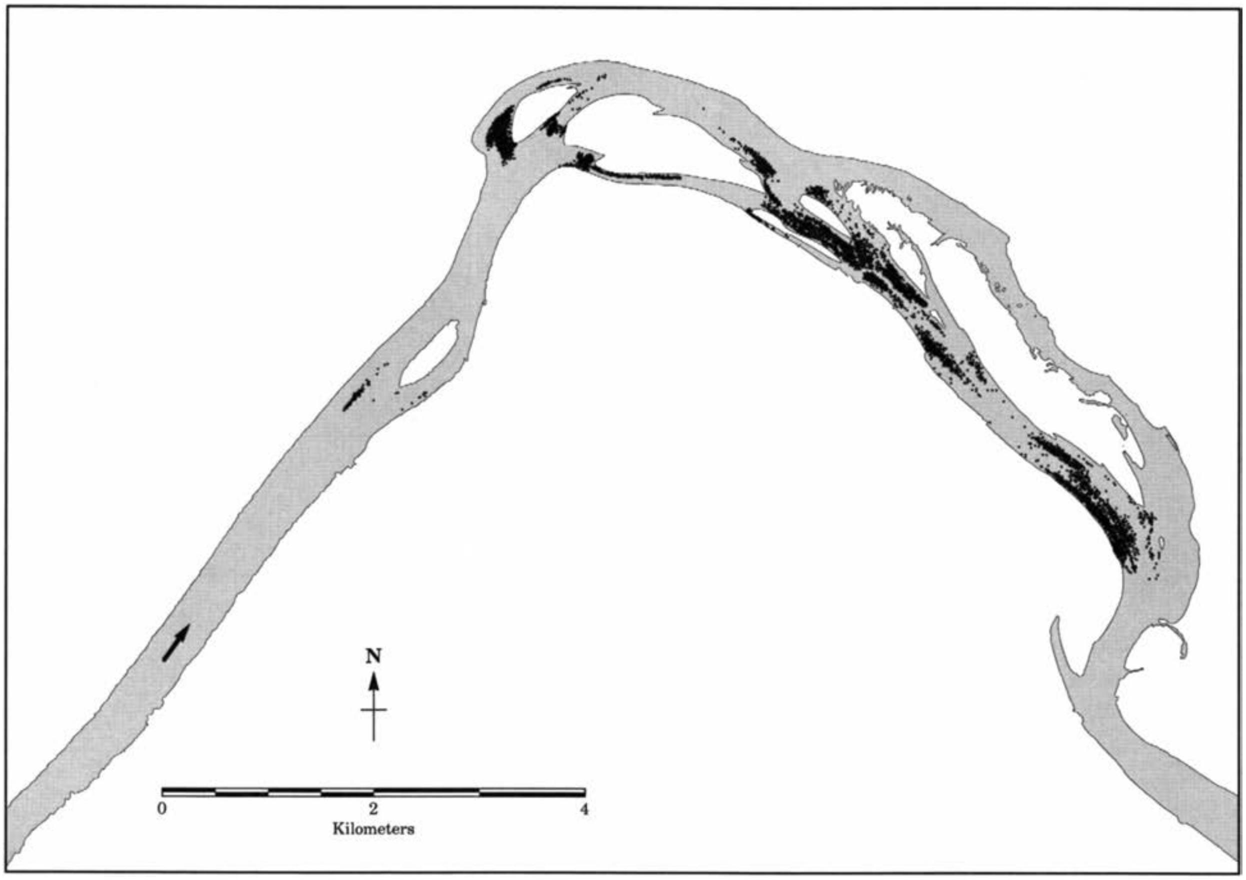

Figure 1. A section of the Hanford Reach of the Columbia River showing several typical fall chinook salmon (*Oncorhynchus tshawytscha*) spawning clusters. Each dot represents an individual salmon nest (redd) that was digitized into a geographic information system from aerial photographs taken during 1994 and 1995 at peak spawning (mid-November). The arrow indicates flow direction.

rather than where the channel is straight and simple (Figure 1). Measurements of water velocity, substrate size, and water depth made at the microhabitat scale (10^0 m) were not related to the distribution of these spawning clusters (D. R. Geist, unpublished data). The patchy distribution of fall chinook salmon redds in relation to available depth, substrate, and velocity suggested that fall chinook salmon have relatively specific spawning habitat requirements that were only partially explained by microhabitat characteristics used in PHABSIM. We believe that these complex channel patterns create geomorphic bed forms at the sediment–water interface that promote the development of interstitial flow pathways between surface water and groundwater.

Although we believe that salmon respond to physical features of habitat at the microhabitat scale, the form and structure of the physical features at this scale are constrained by geomorphic features of river channels occurring at larger scales. Thus, we argue that traditional salmon spawning habitat models need to incorporate additional characteristics of channel features that are measured at spatial scales reflective of the geomorphic processes that formed them and that these additional characteristics represent geomorphic features of river channels that promote the horizontal and vertical flow pathways between surface water and groundwater. It is possible that estimates of available salmon spawning habitat in large mainstem rivers may be improved by incorporating geomorphic features that influence interstitial flow pathways between surface water and groundwater.

The objective of this paper is to present a conceptual spawning habitat model for fall chinook salmon that describes how geomorphic features of river channels affect hydraulic processes, including hyporheic flows, and in turn, how these hydraulic processes influence where salmon spawn in unconstrained reaches of large mainstem alluvial rivers. The distinction between large and small rivers is arbitrary since the geometry and hydraulic aspects of rivers are often similar in small shallow streams and large deep rivers (Stalnaker and others 1989). Two case studies are presented to illustrate important aspects of our conceptual model. The first case study presents evidence that the hyporheic zone within a fall chinook salmon spawning area was comprised of varying proportions of groundwater and surface water that were interactive with one another. The second case study demonstrates the limitations of using microhabitat characteristics (in this case substrate) for predicting usable fall chinook salmon spawning habitat. Although much of the empirical data discussed in the case studies were collected in the Hanford Reach, we believe this information is applicable to protection and restoration of endangered fall chinook salmon in the Snake River and that this model provides insight into new ways of quantifying spawning habitat for other species of salmonids in other freshwater systems.

Influences of Geomorphic Features on Salmon Spawning Habitat

River systems are best viewed as hierarchically organized geomorphic features arranged predictably within a watershed (Frissell and others 1986, Schlosser and Angermeier 1995). At progressively higher levels of organization, large rivers incorporate microhabitat (10^0 m), pools and riffles (10^1 m), river reaches (10^2–10^3 m), segments of watersheds (10^4–10^5 m), and entire watersheds ($\geq 10^6$ m). The hierarchy is spatially nested, i.e., a geomorphic feature at one level affects the form and function of the geomorphic features at a lower level (Frissell and others 1986, Grant and others 1990, Gregory and others 1991). For example, geomorphic features at the section or segment scale (i.e., regional landforms that reflect different landscape formations) affect channel features at the reach scale (i.e., defined by the degree of lateral constraint and usually consisting of integrated geomorphic units). Examples of reach features in large, alluvial rivers include gravel bars and islands that are longer than one channel width in length. The location and morphology of these features in turn affect specific hydraulic features of the spawning habitat at the channel unit scale or pool–riffle system (i.e., distinct hydraulic and geomorphic structures with characteristic bed topography, water surface slope, depth, and velocity patterns) and those at the subunit or microhabitat scale (i.e., transitory hydraulic features within a channel unit that have homogenous substrate type, water depth, and velocity).

One important and often overlooked hydraulic process that occurs within unconstrained reaches of large, alluvial rivers is the interaction of groundwater and surface water within the hyporheic zone. The hyporheic zone has been described in various ways [see reviews by White (1993) and Brunke and Gonser (1997)], but is generally considered to be the subsurface region of streams and rivers that contains a mix of groundwater and surface water (Valett and others 1993). The characteristics of the hyporheic zone vary widely in space (Brunke and Gonser 1997) and consequently there are many interstitial flow pathways that occur between rivers and the hyporheic zone. For example, localized upwelling and downwelling is largely a function of the riverbed topography and the permeability and depth of alluvium, whereas large-scale exchange processes are determined mainly by geomorphic features of river channels [i.e., gravel bar location and morphology, meander pattern, channel roughness, hydraulic conductivity, and hydraulic gradient (Vaux 1962, Vervier and others 1992, Harvey and Bencala 1993, Brunke and Gonser 1997)] (Figure 2). In general, the change in riverbed topography relative to water depth in areas of aggraded sediments (e.g., upstream end of an alluvial floodplain, crossing or inflection point of a channel meander, or the upstream end of a riffle or gravel bar) creates a high-pressure zone where surface water downwells into the sediments, displacing interstitial water (Brunke and Gonser 1997). The interstitial water then flows through the aquifer and upwells to the channel where the hydraulic gradient of the subsurface water equals that of the channel bed and a low-pressure zone is created (Vaux 1962, 1968, White 1993). Upwelling areas represent hyporheic flow entering the surface water and include both groundwater and surface water that has passed through a permeable substrate (White 1993).

Geomorphic bed forms of the river set up sites for localized upwelling and downwelling, but the relative mix of groundwater and surface water in the hyporheic zone is also a function of the water level of the river and the quantity of regional groundwater discharge to the river. For example, during spring runoff, the higher river level forces water into the bed forms of the river and dilutes the regional groundwater discharge. Consequently, the hyporheic zone may be comprised of mostly river water. The opposite is true during periods of low river flow where regional groundwater in the hyporheic zone is more predominant. In regulated rivers this alteration between high and low river stage (i.e., discharge) occurs much more frequently and, consequently, affects the relative mix of groundwater and surface water in the hyporheic zone more often.

The hyporheic zone is the primary connection between groundwater and surface water within unconstrained reaches of large, alluvial rivers (Stanford and

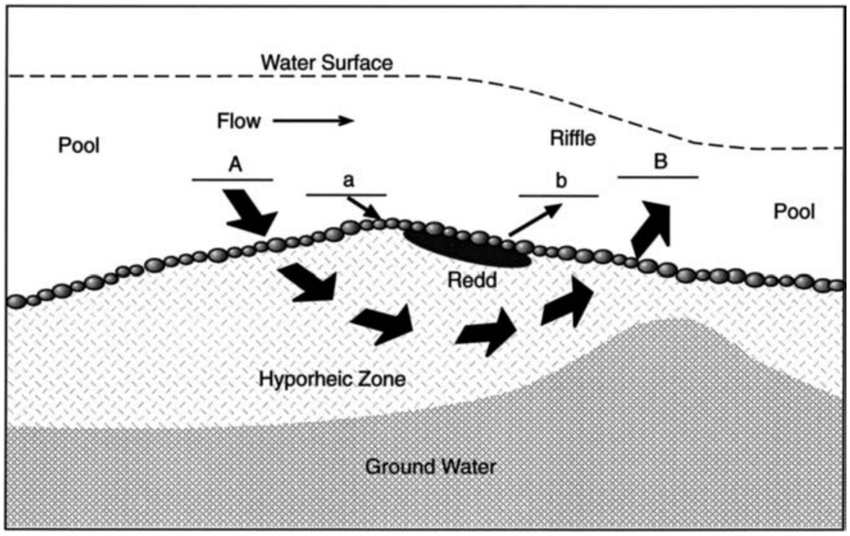

Figure 2. Conceptual model of the hyporheic zone using a longitudinal profile of a hypothetical river channel (after White 1993). Flow into and out of the hyporheic zone is a result of higher hydraulic pressure on the pool side versus riffle side and occurs at more than one spatial scale. For example, a and b depict areas of localized downwelling and upwelling, respectively, at the microhabitat or subunit (i.e., redd) scale. A and B depict areas of downwelling and upwelling, respectively, at the channel unit (i.e., pool-riffle) scale (scale is exaggerated).

others 1996). Unconfined flow is vertically and laterally dynamic with the surface water, and the convergence of the surface water and groundwater may be critically important in the formation of river channel morphology (Hynes 1983, Stanford and Ward 1993, Hakenkamp and others 1993). The alluvial nature of rivers results in riverbeds and their floodplains being networks of interconnected surface water and groundwater flow pathways lateral to the river channel that occur within the hyporheic zone at both large and small spatial scales (Figure 3). Conceptualizing the hyporheic zone as a corridor (Stanford and Ward 1993) that extends laterally within the floodplain and longitudinally along the river profile provides a working model that integrates the geomorphic features of river channels across the hierarchy of spatial scales (Ward 1989).

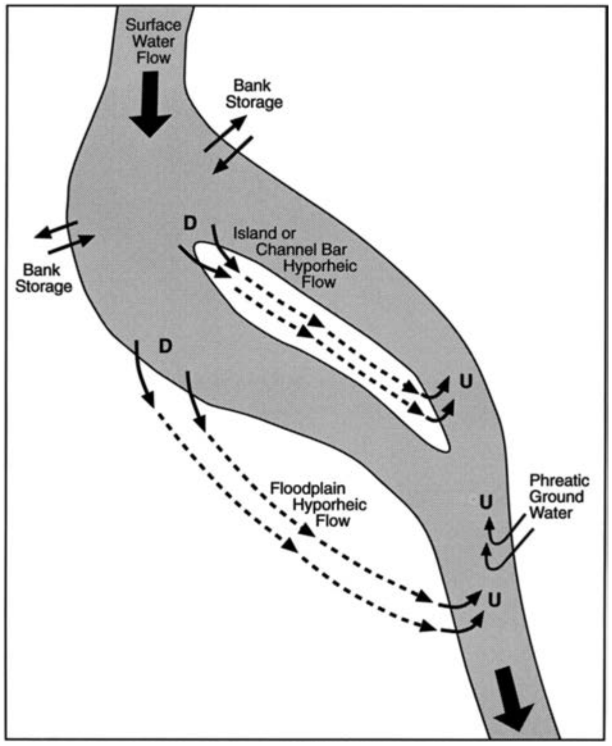

Figure 3. Conceptual model of hyporheic flow within an unconstrained alluvial floodplain reach of a large river (plan view). Hyporheic flow within the river bank, islands, and floodplain is a function of channel pattern, morphology, and hydraulic connectivity of the alluvial material and can occur at more than one spatial scale (i.e., island, channel bar, and floodplain). U and D depict areas of upwelling and downwelling.

Conceptual Spawning Habitat Model

We propose that salmon redd distribution within large alluvial rivers may be a function of the interaction of surface water and groundwater via the hyporheic zone. Traditional spawning habitat models can not represent the heterogeneous features of river channels associated with interstitial flow pathways. Thus, our conceptual spawning habitat model includes additional characteristics that we suggest represent geomorphic features of river channels promoting the horizontal and vertical flow pathways within the hyporheic zone (Table 1). These features are related across a range of spatial scales. For example, the longitudinal profile of a river reach (reach scale) reflects its long-term geological development (segment or section scale) (Frissell and others 1986). Under conditions of uniform discharge, a direct relationship exists between slope and bed material particle sizes (Richards 1982). Thus, longitudinal slope will largely determine substrate available for spawning (channel unit or microhabitat scales) unless substrate size is influenced by inputs from tributaries or bank erosion. In unconstrained reaches of large gravel-

Table 1. List of typical physical habitat parameters used in previous studies to describe fall chinook salmon (*Oncorhynchus tshawytscha*) spawning habitat (empirically derived) and additional characteristics we suggest be included[a]

Traditional characteristics	Additional characteristics
Water depth	Longitudinal and transverse slope
Water velocity	Channel morphology (channel pattern, channel islands, bedforms, and lateral activity)
Substrate size	Hyporheic temperature, dissolved oxygen, pH, and electrical conductivity
	Near-bed velocity gradient
	Vertical hydraulic gradient (upwelling and downwelling)
	Substrate depth, stability, permeability, and porosity
	Hydraulic conductivity and transmissivity
	Presence or absence of natural bedforms (e.g., dunes and / or ripples) and their type, shape, amplitude, frequency, etc.
	Rate of bedform migration
	Presence of groundwater springs

[a] Traditional characteristics are usually measured at the microhabitat scale (10^0 m) in large rivers. Additional characteristics could be measured at various spatial scales.

and cobble-bed rivers, the longitudinal slope is reduced and alluvium is deposited (Stanford and others 1996). This alluvium is highly porous, allowing river water to penetrate into the bed material, and creating interstitial flow pathways that link surface water and groundwater within the hyporheic zone (Stanford and Ward 1993). These conditions result in heterogeneous salmon spawning habitat (microhabitat scale).

Channel morphology (channel pattern, channel islands, bedforms, and lateral activity) (Kellerhals and Church 1989) is another component of our conceptual spawning habitat model (Table 1). Channels that are capable of carrying sediment result in the development of lateral and point bars (Church and Jones 1982). Salmonid spawning usually occurs at the transition between pools and riffles (Bjornn and Reiser 1991) (Figure 2), which are areas often associated with a lateral bar deposition area (Church and Jones 1982). Downwelling and upwelling of hyporheic flow occurs at the upstream and downstream portions of a channel bar or island (reach or channel unit scale, depending on size) creating interstitial flow pathways through the bed material (Brunke and Gonser 1997). Additionally, the inside edge of a channel bend may have strong flow divergence and nonlaminar velocity patterns would be more prevalent in areas of channel bifurcation (Leopold and others 1964). A quantitative measure of channel pattern can be made by plotting segment azimuth versus channel distance, allowing an investigator to determine thalwag configuration (Brice 1973 from Richards 1982). The more complex the channel pattern, the more likely are downwelling and upwelling zones (Brunke and Gonser 1997), which will result in increased habitat heterogeneity (Stanford and others 1996) and may ultimately affect the specific locations salmon spawn (microhabitat scale).

Traditional salmon spawning habitat models such as PHABSIM are useful in predicting usable habitat because they use traditional characteristics that define the limits to where salmon can successfully spawn (Table 1). However, the input parameters for PHABSIM are very specific, and incorporating our additional characteristics into it may be difficult. An alternative approach would be to combine PHABSIM with our conceptual model using geographic information systems (GIS). A hypothetical example of this approach is illustrated in Figure 4. A spawning habitat polygon (SHP) is quite large when traditional characteristics are used to define suitable spawning habitat. Consequently, most of the redds within the spawning area are included within the SHP, but much of the river reach not used for spawning is also included. When additional characteristics (i.e., key hydraulic and hydrologic characteristics proposed here; Table 1) are incorporated into the model, the single large SHP is reduced to two smaller SHPs and more closely approximates the area actually used for spawning (Figure 4). Because this approach may result in more definitive predictions, we propose that researchers include general characteristics of hydrologic and bed processes in PHABSIM and future salmon spawning habitat models.

The characteristics proposed in our conceptual model are present in spawning habitat, yet are difficult to measure and quantify, and thus, typically are ignored. We argue that this information can be empirically derived using recent tools developed for monitoring and modeling groundwater and surface-water interactions in large rivers. For example, groundwater monitoring wells have been used to monitor the large-scale movement of subsurface flow and ecological connectivity within large river basins (Stanford and Gaufin 1974, Stanford and Ward 1988, Obrdlik and others 1992). Piezometers have been used to monitor the intragravel flow within salmon spawning areas of small streams and rivers where installation costs and / or access for drill rigs prohibited the use of monitoring wells (Wickett 1954, Terhune 1958, Vaux 1962, Sheridan 1962, Hansen 1975), but their application to large rivers is limited (Geist and others 1998). Estimates of hyporheic flux in large rivers may now be possible using recently developed remotely operated seepage meters (Cherkauer and McBride 1988, Taniguchi and Fukuo 1993). Rapid

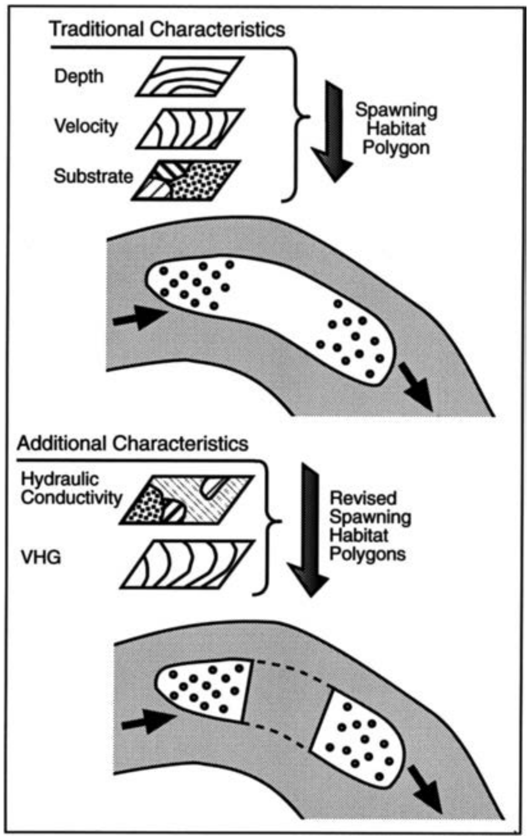

Figure 4. Spawning habitat polygons (SHPs) within a hypothetical salmon spawning area. Salmon redds are depicted by small circles. A large SHP is generated using data layers comprised of traditional characteristics (i.e., substrate, depth, and water velocity). The single SHP is refined into two smaller SHPs using data layers comprised of additional characteristics; in this example we have used hydraulic conductivity of the riverbed sediment and the vertical hydraulic gradient (VHG) between the hyporheic zone and the river.

reconnaissance methods have also been developed to detect groundwater upwelling (Lee 1985), including areas in the Hanford Reach used for spawning by fall chinook salmon (Lee and others 1997).

Improved predictions of usable fall chinook salmon spawning habitat can only be made if resource managers begin to consider the hyporheic zone in their studies of salmon spawning habitat. By measuring the difference in hydraulic head at various locations and combining this information with the hydraulic properties of the hyporheic zone (i.e., horizontal and vertical conductivity, substrate porosity and permeability, transmissivity, and aquifer depth), general hyporheic gradients and flow rates can be modeled. Perhaps the simplest way to make these hydraulic measurements is with the use of piezometers installed into the riverbed within salmon spawning areas. The following case study demonstrates one approach using piezometers that has been used to characterize the hyporheic zone within a salmon spawning area in a large river.

Case Study: Preliminary Characterization of Hyporheic Zone Within Fall Chinook Salmon Spawning Areas

Water depth, substrate size, lateral slope, and water velocity were not significantly related to fall chinook salmon spawning sites in the Hanford Reach (D. R. Geist, unpublished data). It was hypothesized that fall chinook salmon were spawning near areas of hyporheic upwelling. Thus, piezometers (Geist and others 1998) were installed into riverbed sediments (particle size = 2.5 to >30 cm diameter) in the river channel within a major fall chinook salmon spawning area during 1995 and 1996 (Figure 5). The piezometers allowed us to determine the relative mix of groundwater and surface water in the hyporheic zone based on differences in electrical conductivity; Columbia River water at Hanford is normally around 125–150 μS/cm compared to undiluted groundwater, which is normally around 300–500 μS/cm (Peterson and Johnson 1992, Dresel and others 1995). The piezometers also allowed us to determine the relative magnitude of upwelling and downwelling within the spawning area based on the vertical hydraulic gradient (VHG) between the river and the piezometers:

$$VHG = \frac{\Delta h}{L}$$

where Δh is the water surface elevation inside the piezometer minus the water surface elevation of the river and L is the distance below the riverbed to the top of the piezometer perforations. A positive VHG indicates potential upwelling of hyporheic water into the river, while negative values indicate a potential for river water to downwell into the bed sediments (Dahm and Valett 1996).

Data collected from the piezometers clearly showed the hyporheic zone was comprised of varying proportions of groundwater and surface water, as evidenced by the measurable differences in electrical conductivity within some of the piezometers (Figure 6A). Furthermore, the data revealed that a vertical hydraulic gradient existed between the hyporheic zone and the river (Figure 6B). The relative magnitude of the hyporheic discharge appeared to be a function of the river stage (Figure 6C), which fluctuates cyclically on a daily basis in response to discharge at a hydropower project (Priest Rapids Dam) located 39 km upstream.

These data suggest that the riverbanks, bars, and islands become saturated with river water as the river

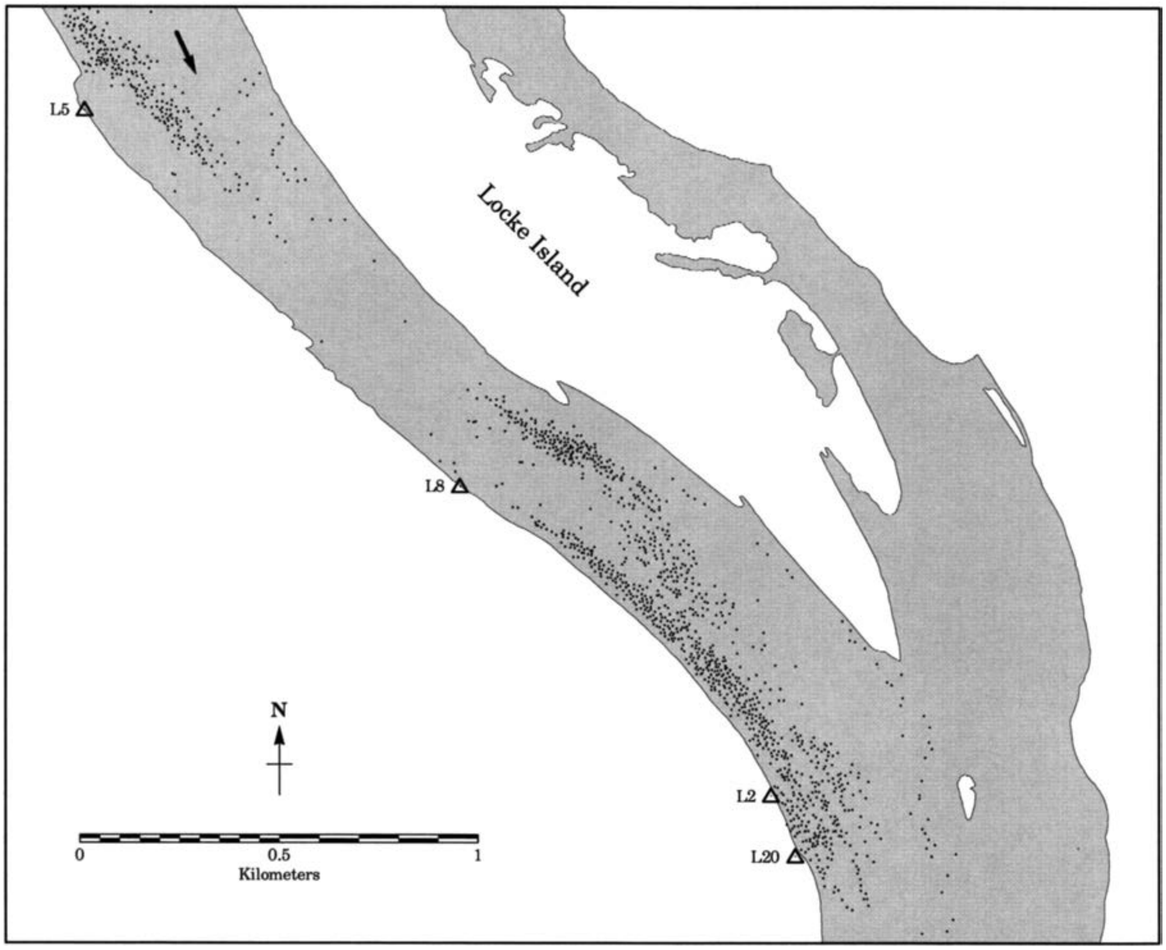

Figure 5. The location of four piezometers (L2, L5, L8, and L20) installed during 1995 and 1996 within the river channel within a major fall chinook salmon (*Oncorhynchus tshawytscha*) spawning area in the Hanford Reach of the Columbia River. Each dot represents an individual salmon nest (redd) that was digitized into a geographic information system from aerial photographs taken during 1995 at peak spawning (mid-November). Triangles depict piezometer location and the arrow indicates direction of river flow.

discharge and stage increase. Depending on substrate permeability, bed morphometry, channel configuration, and the relative rise in river level, river water downwells into the hyporheic zone due to high pressure created from increased water depth (negative VHGs; Figure 6C). Eventually the river and hyporheic zone come to a dynamic equilibrium; if the river discharge is reduced and the stage decreases, the pressure is released and water flows back into the river in the form of surface seeps or off-shore upwelling (positive VHGs; Figure 6C). Within the Hanford Reach, this alteration between upwelling and downwelling can occur several times per day, depending on the discharge pattern at Priest Rapids Dam. In unregulated rivers this phenomenon still occurs but is protracted over a longer time period (days to months). Overall, the piezometer data provide evidence that the river at Hanford is connected to the groundwater within the hyporheic zone.

Prediction of Salmon Spawning Based on Microhabitat Characteristics

The predictive power of PHABSIM is restricted because it includes characteristics that are only measured at the microhabitat scale. Often these characteristics differ considerably both between and within major spawning areas of similar stocks or races of chinook salmon (Table 2). For example, water depth over fall chinook salmon redds in the Hanford Reach has been reported to be from 0.3 to 9.0 m (Chapman and others 1986, Swan 1989); substrate particle size ranges from 5 to 30.5 cm (Swan 1989); and near-bed velocity ranges

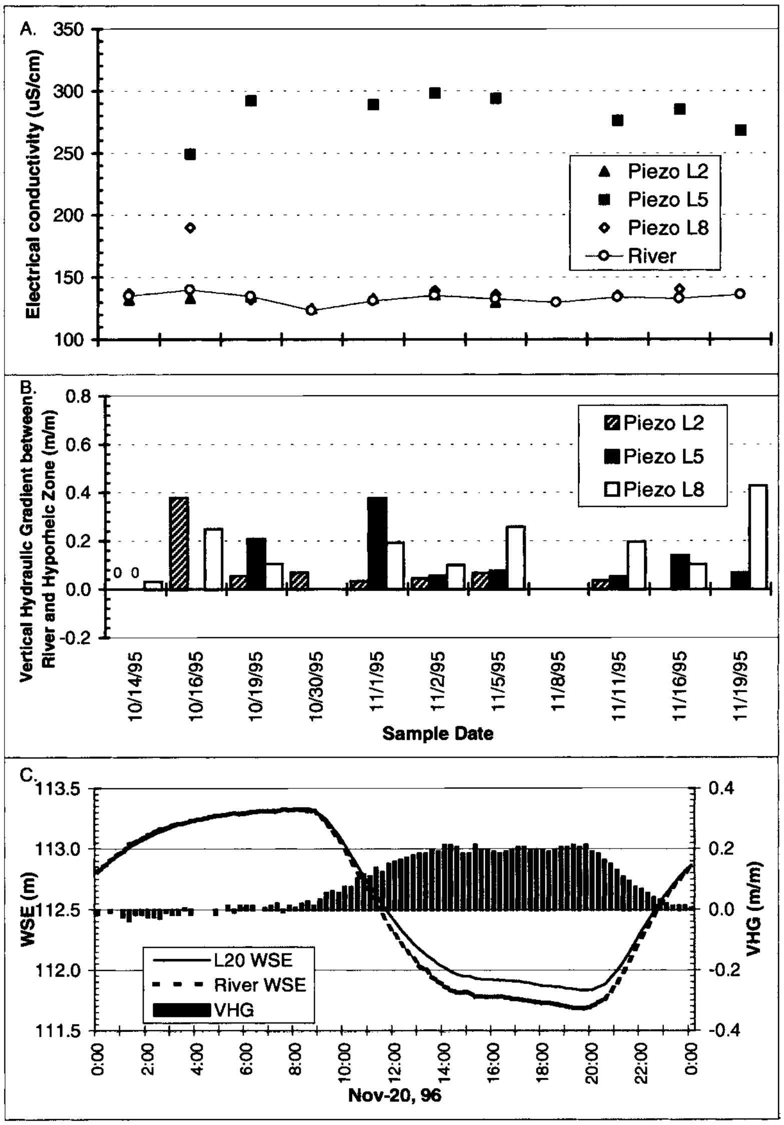

Figure 6. Data collected from piezometers placed in the hyporheic zone of the Hanford Reach of the Columbia River (see Figure 5 for salmon redd locations). (**A**) Measurements of electrical conductivity, and (**B**) vertical hydraulic gradient (VHG) from the river and three piezometers (L2, L5, and L8) during October and November, 1995, in the Hanford Reach of the Columbia River. VHGs of 0.0 (indicated by zeros) were recorded in piezometers L2 and L5 on 14 November; the absence of a vertical bar on subsequent dates indicates no measurements of elevation were made. The *x* axis scale is the same for **A** and **B.** (**C**) Continuous measurements of water surface elevation (WSE) of the river and within piezometer L20 over a 24-h period on 20 November 1996. WSEs were used to calculate VHGs over the same time period. Measurements of electrical conductivity in L20 during November 1996 were similar to electrical conductivity measurements taken in the river.

from 0.4 to 2 m/sec (Chapman and others 1986). Similar variability in physical habitat characteristics has been noted for chinook salmon spawning sites in the Snake River, Idaho (Groves 1993, Connor and others 1994c, Groves and Chandler in press), Kalama and Toutle rivers, Washington (Burner 1951), Nechako River, British Columbia, Canada (Neilson and Banford 1983; Shirvell 1989), and Kamchatka River, Russia (Vronskiy 1972; Vronskiy and Leman 1991).

Spawning habitat characteristics for chinook salmon in small rivers encompass a smaller range of possible conditions than those in the Columbia and Snake rivers because of differences in scale, i.e., the upper limits for depth and velocity are related to discharge (volume). For example, Smith (1973) recommended velocity criteria of 0.3–0.8 m/sec for spawning fall chinook salmon. Additionally, Bovee (1978) generated probability of use curves for substrate, depth, and velocity characteristics that ranged from 12 to 15 cm, 0.1 to 1.4 m, and 0.2 to 1.3 m/sec, respectively. These values are less than the upper limits reported in the Columbia and Snake rivers for fall chinook salmon redds.

It is apparent that water depth, velocity, and substrate constrain where fall chinook salmon can successfully spawn. These limits are defined both by the size of the fish and the geomorphic characteristics of the river system. For example, chinook salmon will typically not spawn if their backs are out of the water (Bjornn and Reiser 1991). Thus, 30 cm is probably the minimum depth limit for successful spawning of an average-sized

Table 2. Summary of fall chinook salmon (*Oncorhynchus tshawytscha*) spawning characteristics in mainstem Columbia River, major tributaries, and other streams in Pacific Northwest

Location	Substrate size (cm)	Depth (m)	Velocity (m/sec)	Reference
Columbia River				
Upper	—	0.6–4.5	—	Chapman (1943)
Near Wells Dam	—	range 1.6–9.6 most 5.3–7.2	range 0.4–1.2 average 0.9	Giorgi (1992)
Hanford Reach	—	range 1.2–2.6 average 1.4	0.4–1.9 at 2,000 m^3/sec 0.4–2.0 at 3,400 m^3/sec	Chapman and others (1983)
Hanford Reach	range 5–30 average 10–20	range 0.3–9.0 average 1.8–7.6	—	Swan and others (1988), Swan (1989)
Not specified	—	0.2–2.0	0.8–1.1	Chambers (1955)
Columbia River tributaries				
Snake River	2.5–15	~1–2	~0.5–1.2	Connor and others (1993)
Snake River	2.5–15.0	0.2–6.5 average 2.8	0.4–2.1 average 1.1	Groves and Chandler (in press)
Snake River	—	4.6–7.9	0.3–0.7	Dauble and others (1995)
Kalama River	—	average 0.4	average 0.6	Burner (1951)
Toutle River	—	average 0.3	average 0.4	Burner (1951)
Other river systems				
Campbell River, British Columbia	—	range 0.3–0.8 average 0.6	range 0.4–0.8 average 0.6	Hamilton and Buell (1976)
Nechako River, British Columbia	—	—	0.15–1.0	Neilson and Banford (1983)
Oregon streams	—	average 0.4	average 0.5	Smith (1973)
Unspecified streams	1.3–10.2	—	—	Bell (1986)

(i.e., 5 kg) fall chinook salmon female. Maximum spawning depth is limited by river channel dimensions and is also likely affected by water clarity. Visual cues related to mate recognition and substrate differentiation in the Hanford Reach would be reduced at depths greater than 4 m because this is the maximum depth of light penetration during the spawning period (Swan 1989).

Egg incubation success may be reduced at low water velocities, particularly where oxygen exchange is inadequate and metabolic wastes accumulate in the egg pocket (Chapman 1988). Thus, there is a selective disadvantage against fish that spawn in areas of low water velocity. Conversely, prespawning adult fall chinook salmon would be expected to avoid areas of very high water velocity because of costs to their available energy budget (Brett 1964, 1965). Maximum substrate size is limited by both the size of the fish (i.e., physical ability to dislodge substrate) and by water velocity, which may provide a boost to help in the excavation process (Kondolf and Wolman 1993). Minimum substrate size for spawning is critical in the sense that a high percentage of fines may smother eggs during incubation (Chapman 1988). In summary, the range of potential conditions accessible to fall chinook salmon for spawning appears quite broad.

The large database available on the physical characteristics of salmon redds, particularly for water velocity and depth, implies that spawning habitat of chinook salmon is well understood. However, the following example illustrates that major discrepancies exist between the amount and type of substrate thought to be available for spawning by fall chinook salmon and the habitat actually used.

Case Study: Spawning Site Characteristics in Hanford Reach

In 1986, Swan and others (1988) selected eight study sites in the Hanford Reach that were presumed to contain suitable spawning habitat for fall chinook salmon based on substrate, depth, and velocity data. Their objective was to survey these sites and to document redd locations prior to assessing potential impacts of channel dredging on fall chinook salmon spawning habitat. Although data were collected for other purposes, the data set of Swan and others (1988) is the most definitive available on substrate types in major spawning areas of the Hanford Reach.

We capitalized on recent advances in GIS technology to evaluate substrate use and preference relative to available habitat. The study-site boundaries, substrate polygons, and redd locations were digitized from study site maps of Swan and others (1988) into our GIS (ArcInfo). For each study site, the area of each of five substrate types was calculated, and the number of salmon redds within the substrate type was enumerated.

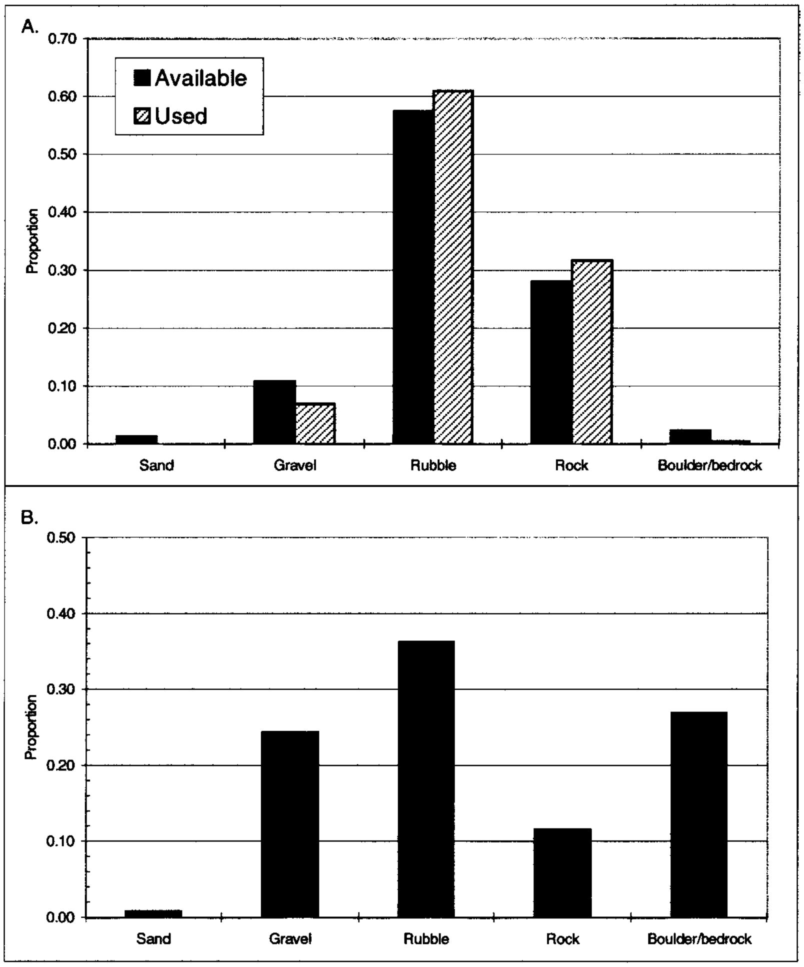

Figure 7. Analysis of substrate data from eight study sites in the Hanford Reach of the Columbia River (Swan and others 1988). (**A**) The proportion of substrate available and substrate used within the five study sites where fall chinook salmon (*Oncorhynchus tshawytscha*) spawned. (**B**) Distribution of substrate size classes within the three study sites without fall chinook salmon redds.

Substrate types included sand (<5 cm), gravel (5–10.2 cm), rubble (10.2–20.3 cm), rock (20.3–30.5 cm), and boulder/bedrock (>30.5 cm) (Swan 1989). Spawning habitat used was defined as the proportion of the total number of redds within a study site found within each substrate type. Available spawning habitat was defined as the relative proportion of the five substrate types (based on area) within each study site. A preference index for a particular substrate was calculated by dividing the proportion of redds found within a substrate type by the proportion of habitat available within the same substrate type (Bovee 1986, Knapp and Vredenburg 1996). We then used linear regression analysis to test the hypothesis that the number of redds were related to the amount of preferred substrate. The dependent variable was the number of redds found within the preferred substrate at each study site, and the independent variable was the area of preferred substrate at each study site.

All study sites were located in areas of the Hanford Reach where fall chinook salmon spawn (Dauble and Watson 1997). We assumed that all the sites were equally available to returning adults. The number of fall chinook salmon that spawned in the Hanford Reach during the study year (1986) was estimated to be 72,560, or approximately 40% higher than the average annual spawning population measured from 1982 to 1992 (Dauble and Watson 1997). Superimposition of redds was noted in some study sites (Swan and others 1988, Swan 1989). Thus, we assumed the returning adult population was sufficient to allow full seeding of each of the eight study sites.

Fall chinook salmon spawned at five of the eight study sites in 1986 (Swan 1989). Sand was the least predominant substrate type at all sites and, with one exception, rubble and rock were the most predominant substrate types. Within the five study sites where spawning occurred, approximately 90% of the redds were found within the rubble and rock substrate types (Figure 7A), and indices suggested a slight preference for these substrates (i.e., preference index values were 1.1 for both substrate types). Within the study sites where no spawning occurred, approximately 45% of the available substrate was classified as rubble and rock, the preferred substrate types (Figure 7B). However, regression analysis showed that the number of redds in the study sites was not related to the amount of available rubble and rock ($r = 0.07$, $df = 7$, $P = 0.870$).

We conclude that available spawning habitat (based only on substrate) at these sites did not provide a useful predictor of fall chinook salmon spawning potential. Swan (1989) concluded that water velocity and depth characteristics at these eight study sites were within the range thought suitable for spawning. More accurate predictions of spawning potential might have been possible if depth and/or velocity data were available for our analysis. However, our analysis demonstrated that superficial measures of spawning habitat quality, as measured at the microhabitat scale, were limited in their ability to predict spawning habitat availability. Thus, we believe that other features of the river channel, such as hyporheic processes, must be considered.

Hyporheic Zone and Salmon Spawning Habitat

Upwelling hyporheic flow is commonly associated with the spawning locations of salmonids, including brook trout (*Salvenlinus fontinalis*) (Latta 1965, Curry and others 1994, Curry and Noakes 1995), sockeye salmon (*O. nerka*) (Lorenz and Eiler 1989), chum salmon (*O. keta*) (Leman 1993), and rainbow trout (*O. mykiss*) (Sowden and Power 1985). Brook trout will preferentially spawn in sites of upwelling (Webster and Eiriksdottir 1976), often in areas with sandy and silty substrate, even when clean, uncompacted gravel containing no upwelling water is available nearby (Witzel and MacCrimmon 1983). Upwelling hyporheic flow was detected in nearly 60% of the sockeye spawning sites sampled in the mainstem areas of a glacial river where spawning habitat was limited because of siltation and substrate compaction (Lorenz and Eiler 1989). However, spawning brown trout (*Salmo trutta*) were shown to avoid areas of groundwater flow (Hansen 1975).

Provided that water quality is good and sufficiently oxygenated, upwelling areas would tend to improve survival of eggs and emergent fry by providing a stable egg incubation environment and increasing the water exchange around the egg pocket, thereby replenishing oxygen and removing waste (Becker and others 1983, Bjornn and Reiser 1991, Curry and others 1995). Owing to the tremendous heat sink of the underlying sediments (Freeze and Cherry 1979), the average temperature of the hyporheic zone during the egg incubation period is often warmer than the river, which could ensure emergence at optimal times (Burger and others 1985, Lorenz and Eiler 1989, Berman and Quinn 1991). Although it is clear that oxygen and temperature content of intragravel flow is important in salmonid egg survival, the importance of hyporheic upwelling to spawning site selection is not known. Gradients created by discharging hyporheic upwelling may provide chemical cues for homing (Hara 1982), changes in flow patterns that fish could sense, and/or temperature aberrations that would attract spawning fish; however, these hypotheses remain largely untested.

There are no definitive assessments of chinook salmon spawning in large rivers near hyporheic upwelling, rather, most information is circumstantial. For example, Chapman (1943) noted chinook salmon spawning in the mainstem Columbia River below Kettle Falls, Washington, and hypothesized that perhaps "seepage outlets [hyporheic upwelling] could explain the concentration of fish on the same spot when the greater part of the river was not in use." Most spring chinook salmon spawning in the Entiat River, Washington, took place on gravel through which there was a flow of water as determined chemically (Burner 1951); however, hyporheic flow was not quantified. Chinook salmon spawned in the mainstem Kenai River, Alaska, at the tips of vegetated islands where loose mounds of clean gravel were available (Burger and others 1985). Although groundwater hydraulics were not examined in the Kenai River study, the vegetated islands were suspected to facilitate gravel mound formation, which presumably increased subsurface flows and the incubation success of eggs. In the Kamchatka River, Russia, chinook salmon spawned in sections of the river that had a descending current of water (i.e., downwelling) in the substrate (Vronskiy and Leman 1991). Although most studies suggest that upwelling areas are more important than downwelling areas for spawning, this finding by Vronskiy and Leman suggests that intragravel flow is critical and whether it is upwelling or downwelling may not be as important.

The preference of salmon to spawn in locations with high intragravel flow may explain their tendency to aggregate in particular locations, while ignoring others that are superficially similar (Chapman 1943, Vronskiy and Leman 1991). These aggregations may explain why superimposition of redds, rather than colonization of new sites, appears to occur within some spawning areas. For example, Dauble and Watson (1990) noted that fall chinook salmon in the Hanford Reach exhibited an apparent high selectivity for certain locations, even though other sites with similar physical habitat characteristics were not used for spawning. This sometimes resulted in extensive overlapping of redds in the heavily used spawning areas. As previously noted, Swan (1989) also found that deep-water redds (i.e., >3 m depth and typically not visible during aerial surveys) (Dauble and Watson 1990) commonly overlapped during the latter part of the spawning season. Superimposition of chinook salmon redds also occurred in the Kamchatka River, where dense aggregations formed in selected locations, while superficially similar areas remain unused (Vronskiy 1972). Although these studies did not confirm that the chinook salmon spawning areas were associated with the local emergence of hyporheic flow, they do suggest that specific, yet currently undescribed, geomorphic features of spawning areas may be critical to salmon reproduction.

The subsurface movement of water in the hyporheic corridor should be given more consideration. We believe that additional information on the location and quantity of hyporheic flow and flux would better describe the connectivity between surface water and groundwater, and provide better predictions of available chinook salmon spawning habitat in large alluvial rivers. Improvements in techniques to sample and monitor the hyporheic zone in large rivers now makes this possible.

Conclusions

Considerable effort currently is underway to rebuild and enhance native salmon populations in the Pacific Northwest (NPPC 1994) and elsewhere on the west coast of the United States (USFWS 1991, 1996a,b). Several salmonid stocks already have been listed under the Endangered Species Act (ESA), and additional petitions currently are being reviewed by federal resource management agencies. The ESA requires that recovery plans be developed for listed species, and most plans include the protection and restoration of spawning habitat. However, appropriate strategies cannot be successfully implemented without an adequate understanding of the critical elements within watersheds that determine where salmon spawn (Rondorf and Miller 1993, ISG 1996, Stanford and others 1996). Although a large amount of information exists on the microhabitat characteristics that define suitable salmon spawning areas, the predictive power of current habitat models is restricted because they are limited in scale. These models could be improved by incorporating additional information that relates the physical characteristics of salmon spawning habitat to hydraulic and geomorphic processes that occur within river systems, especially processes within the hyporheic zone. Improvements in our ability to predict salmon spawning habitat in large river systems will result in more realistic recovery potentials and aid in prioritization of restoration efforts.

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