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COMPARISON OF MAINSTEM SPAWNING HABITATS FOR TWO POPULATIONS OF FALL CHINOOK SALMON IN THE COLUMBIA RIVER BASIN

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ABSTRACT

Extensive hydroelectric development in the Columbia River system has eliminated most mainstem riverine habitat available for spawning by fall chinook salmon (*Oncorhynchus tshawytscha*). The two remaining populations, Hanford Reach, Columbia River and Hells Canyon Reach, Snake River, are separated geographically and their status is markedly different. Annual escapements to Hanford Reach have averaged approximately 80000 adults, while the Snake River run size has declined to <1500 adults over the past 10 years. We compared their spawning habitat characteristics over a range of measurement scales, as a means to identify strategies for rebuilding the weak Snake River population. Physical habitat characteristics of redds were similar for both study areas. Redd locations were correlated with channel characteristics, such as braiding and sinuosity. Several differences between the two spawning areas were identified at the watershed scale: the Hells Canyon Reach had a much steeper longitudinal gradient, was largely confined by bedrock, and had a more variable flow regime. These features are controlling variables that operate at the reach-scale to limit the availability and size of substrate and other conditions that influence egg deposition and incubation survival. Geomorphological characteristics of the two study sites are sufficiently different to indicate that the production potential of the Hells Canyon Reach population is markedly lower than that of the Hanford Reach population. Copyright © 2000 John Wiley & Sons, Ltd.

KEY WORDS: salmon; spawning habitat

INTRODUCTION

Historic spawning areas for fall chinook salmon (*Oncorhynchus tshawytscha*) in the Columbia River basin once ranged from the mainstem Columbia River, near The Dalles, Oregon, upstream to the confluence of the Pend Oreille and Kootenai Rivers in British Columbia (Fulton, 1968; Dauble and Watson, 1997). Snake River populations occurred from the mouth upstream to Shoshone Falls, Idaho (Gilbert and Evermann, 1892; Fulton, 1968). Overall, their combined mainstem spawning and rearing habitats covered a distance of almost 2500 km. Construction of an extensive network of hydroelectric dams between 1939 and 1975 blocked access to, or inundated more than 75% of their habitats, in both the Columbia and Snake Rivers (Van Hyning, 1969; Horner and Bjornn, 1979; Dauble and Watson, 1997). Thus, current mainstem production areas for upriver fall chinook salmon are largely restricted to two remaining lotic habitats, i.e. the Hanford Reach of the Columbia River (river km (Rkm) 549–639) and the Hells Canyon Reach of the Snake River (Rkm 240–398; Figure 1). Both populations of chinook salmon are considered 'ocean type' (after sea-type, in Gilbert, 1913) because they migrate to the Pacific Ocean during their first year of life, normally within 3 months of emergence from spawning substrate. Adults enter the mouth of the Columbia River in the early fall and spawn during October and November (Rondorf and Miller, 1993; Dauble and Watson, 1997).

The relative success of fall chinook salmon returning to these two mainstem areas differs dramatically. For example, the Hanford Reach population was recently designated as one of 99 'healthy native stocks' of salmon and steelhead in the Pacific Northwest and California and one of 20 stocks considered to be at least two-thirds as abundant as would be expected in the absence of human impacts (Huntington *et al.*,

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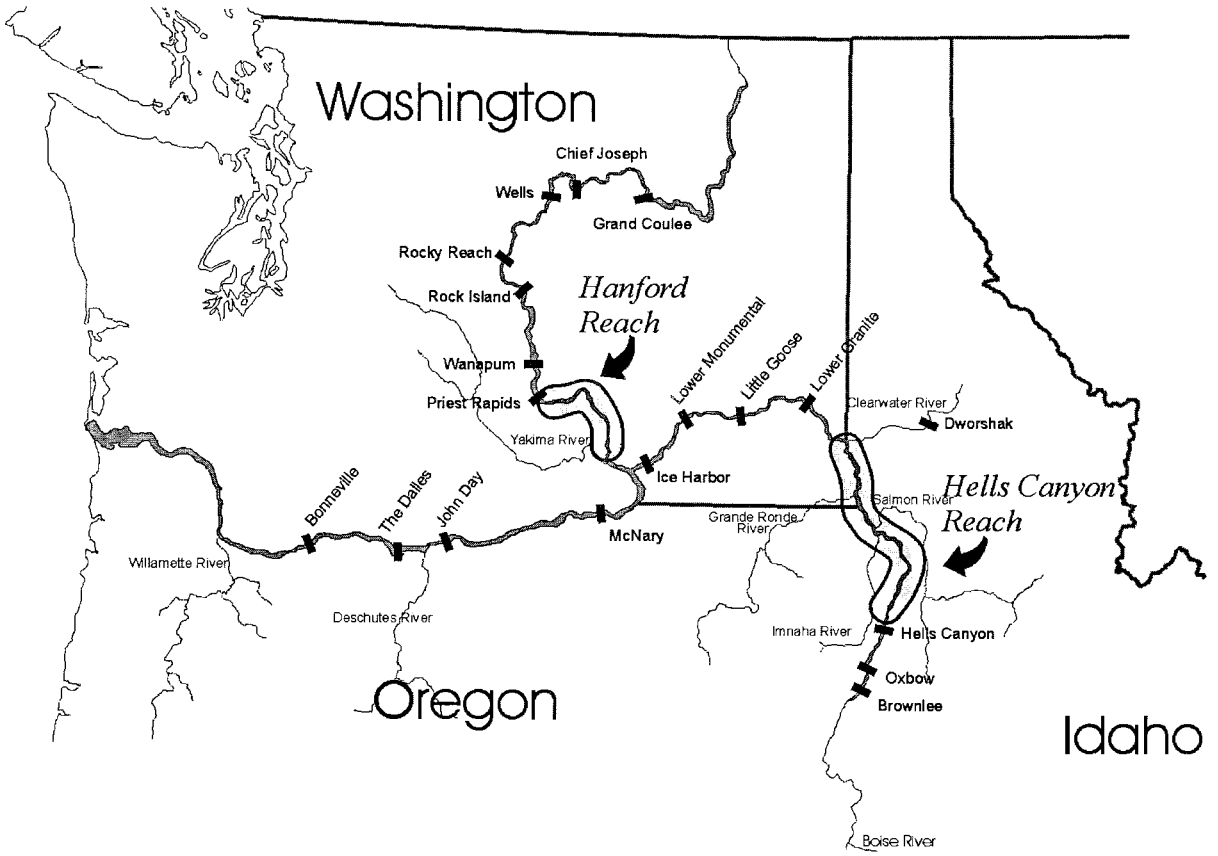

Figure 1. Location of the Hanford Reach and Hells Canyon Reach study areas within the Columbia and Snake River watersheds

1996). This designation was consistent with annual escapements that have remained relatively stable over the past 10 years at about 80000 adults (Dauble and Watson, 1997). In contrast, Snake River populations have steadily declined during the past 25 years. Escapement of fall chinook salmon to present spawning areas upstream of Lower Granite Dam (includes numbers returning to both the Hells Canyon Reach and tributaries) has averaged less than 1500 adults/year since 1975 (Oregon Department of Fisheries and Wildlife/Washington Department of Fisheries and Wildlife, 1996). Concern over the status of Snake River stocks led to their being listed as endangered under the Endangered Species Act in 1994 and planning for the rebuilding of these stocks is currently underway (National Marine Fisheries Service, 1995).

Enhancement of mainstem populations of fall chinook salmon will rely on the protection and restoration of mainstem habitats (Northwest Power Planning Council, 1994; National Marine Fisheries Service, 1995). This action will most likely require major alternations to existing hydrosystem operations, such as reservoir drawdown, or even dam breaching. However, accurate assessments of what constitutes suitable spawning habitat are necessary before protection and restoration steps can be taken (Rondorf and Miller, 1993). Traditional methods to characterize salmon spawning habitat in large river systems include measurements of depth, substrate and velocity at the spatial scale of a redd (e.g. Burner, 1951; Swan, 1989; Groves and Chandler, 1999). While these methods provide useful information, their predictive power is often limited (Shirvell, 1989). Recent reviews suggest that salmonid spawning habitat in river systems is linked to the geomorphic characteristics of river channels that occur at various spatial scales (Frissell *et al.*, 1986; Imhof *et al.*, 1996; Kondolf *et al.*, 1996; Stanford *et al.*, 1996; Geist and Dauble, 1998). Thus, more accurate predictions of what constitutes suitable spawning habitat require an understanding of key relationships between geomorphic features of the river environment and spawning habitat.

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The purpose of this paper is to contrast production constraints on fall chinook salmon populations from two major river segments in the Columbia River ecosystem, specifically in relation to spawning habitat features. This comparison is important because long-term trends in the population status of fall chinook salmon from the Hanford Reach and the Hells Canyon Reach are markedly different. We argue that extensive hydroelectric development and associated changes in available lotic habitat have reduced the production potential of the Columbia River watershed for fall chinook salmon because it has altered the lateral and longitudinal dimensions of the riverine ecosystem (after Ward and Stanford, 1989). Therefore, future rebuilding strategies need to consider the characteristics required for spawning and production within the context of geomorphological features and human activities.

We first compared spawning habitat characteristics of the Hanford Reach and Hells Canyon Reach populations of fall chinook salmon at different measurement scales (largely after Imhof *et al.*, 1996). This allowed us to look for causal linkages between physical habitat characteristics and spawning locations of fall chinook salmon. We used this information to assess how hydroelectric development has influenced availability of fall chinook salmon spawning habitat in mainstem areas of the Columbia River basin. Our approach provides fisheries and water resource managers with another view of the way strategies for rebuilding populations of fall chinook salmon may be affected by human development activities.

BASIS FOR PHYSICAL HABITAT COMPARISON

Rivers can be thought of as hierarchical geomorphic features arranged predictably within a watershed (Frissell *et al.*, 1986; Schlosser and Angermeier, 1995; Imhof *et al.*, 1996). At progressively higher levels of organization, habitat features of large rivers incorporate a range of spatial scales. While most habitat assessments focus on channel or site characteristics, it is well known that habitat hierarchies are spatially nested, i.e. a geomorphic feature at one level affects the form and function of features at a lower level (Frissell *et al.*, 1986; Grant *et al.*, 1990; Gregory *et al.*, 1991). For this reason, we selected three spatial scales for our comparison of physical habitat features between the two study reaches: watershed, reach and redd (Figure 2). These scales encompass a range of measurements from 10^0 to 10^5 m, and operate across different physical, temporal and biological boundaries.

The three spatial scales used to compare spawning habitats include physical features with quantitative dimensions. We recognize that these features have been isolated within the contextual framework of the reach-systems being compared. Nonetheless, the features in Figure 2 provide an analytical basis for determining the availability of physical habitat to fall chinook salmon in the two study areas. To discuss these differences within the context of salmon spawning and production, we first review key watershed characteristics for the two regulated river segments. We then compare physical habitat features at the reach and redd scale, focusing on attributes that currently influence availability of fall chinook salmon spawning habitat.

WATERSHED CHARACTERISTICS

Flow regimes, geology of surrounding landscapes and longitudinal slope are important controlling variables in salmon habitats and operate at both the watershed and reach-scale (Imhof *et al.*, 1996). We describe the general setting for both study areas in this section, including upstream flow regulation practices, general geological features of the watershed and longitudinal profiles.

Flow regimes

Flow regimes in both the Columbia and Snake River drainages are highly regulated by the hydroelectric complex, and seasonal discharge is influenced by water storage and water use practices (Ebel *et al.*, 1989). In addition, fall chinook salmon habitats are affected by daily variation in flow as a result of power-peaking at upstream hydroelectric dams. Adult salmon must pass four lower Snake River dams, as

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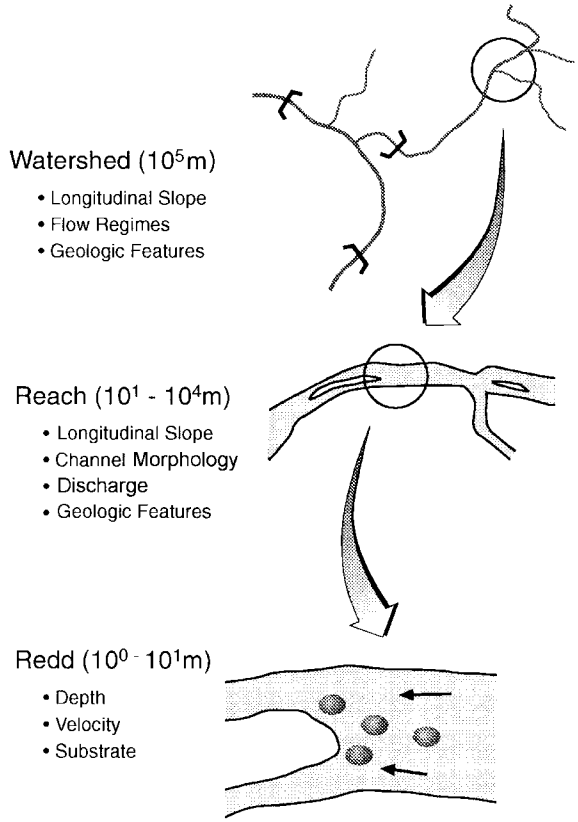

Figure 2. Spatial hierarchy of habitat features used to compare spawning habitat in the Hanford Reach and Hells Canyon Reach

well as four lower Columbia River dams, before reaching spawning grounds in the Hells Canyon Reach (see Figure 1). There is no anadromous fish passage at Hells Canyon Dam, effectively blocking salmon passage further upstream. Adult salmon returning to the Hanford Reach must pass the four lower Columbia River dams, and some may migrate upstream of Priest Rapids Dam.

Major floods are not frequent in the central Columbia and lower Snake Rivers because of generally high banks, large channel capacity, and upstream flood-control projects constructed since the 1940s. With the exception of extremely high flow events, the Columbia River basin has no lowlands classed as flood plains (US Army, 1952). Columbia River flows are largely controlled by three major upstream storage reservoirs: Grand Coulee (Rkm 960), Mica (Rkm 1263), and Keenleyside (Rkm 1633) Dams. Flows through the Snake River are mainly influenced by inflows from large tributaries (e.g. Clearwater and Salmon Rivers) and less by upstream storage reservoir (i.e. Hells Canyon Dam complex).

Geological features

Major geological features of the Columbia and Snake Rivers, within the limits of former fall chinook salmon production, can be generally separated into Quaternary (i.e. alluvial), other unconsolidated sediments, and bedrock. Quaternary sediments were deposited in four major areas: lower Columbia River downstream of the present Bonneville Dam site; near the Snake–Columbia River confluence; upstream of Hells Canyon; in the Marsing area upstream of the Boise River (see Figure 1). Much of the remaining stream channel is confined by bedrock, with small deposits of Quaternary and other unconsolidated sediments present.

Both study areas lie within the Columbia Intermontane Province, a product of Miocene flood basalt volcanism and regional deformation that occurred over the past 17 million years. The Columbia River

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flows mostly west and south for about 1000 km from its origin in British Columbia, before turning east at the upper end of the Hanford Reach. The surface topography in this area has been modified by several geomorphic processes, including Pleistocene cataclysmic flooding, Holocene eolian activity, and landsliding. The Snake River flows mostly westward through the Snake River Plain for about 600 km, then turns north before entering Hells Canyon near Rkm 400. Its present course and character have been mostly influenced by its complex geologic setting and extreme flood events, e.g. Bonneville and Missoula floods (O'Conner, 1993). High-gradient narrow canyons have formed where the river was forced to cut through volcanic rocks. At locations where the river was diverted to locations of erodible sediment, wide valleys with low gradients formed.

Longitudinal slope

In general, and within the range of historic fall chinook salmon spawning areas, the longitudinal slope of the Columbia River is not as steep as the Snake River (Figure 3). However, the longitudinal slope of both river systems varies according to their location within the larger watershed. For example, the Columbia River has a relatively uniform slope of about 0.25 m/km from its confluence with the Deschutes River, Oregon to Priest Rapids Dam; the slope then increases to about 0.45 m/km from Priest Rapids

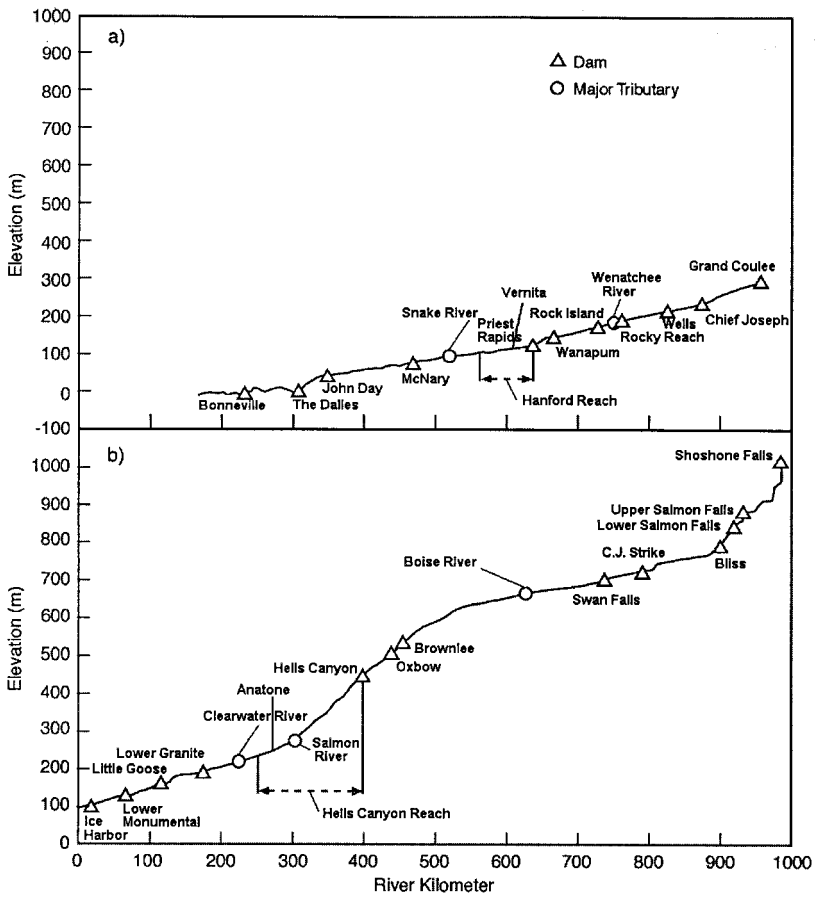

Figure 3. Longitudinal gradient of the (a) Columbia River, and (b) Snake River watersheds. Thalweg elevation data acquired from US Geological Survey (USGS) maps for the Columbia River from Grand Coulee Dam to Bonneville Dam and the Snake River from its confluence to Rkm 383, were used to estimate the gradient. River midlines and all river miles and points at which elevation contours crossed the river midlines were digitized from USGS 7.5 min quadrangles into Geographic Information Systems (GIS; ARC/Info) format. The river midlines were then calibrated against elevation contour points using dynamic segmentation commands and elevations determined for every 0.8 km along section midlines

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Dam to Chief Joseph Dam (Figure 3(a)). Prior to dam construction, there were a succession of rapids and one waterfall in mid-Columbia River, between Wenatchee and Pasco, Washington. The greatest drop in elevation was at Priest Rapids, or 22 m in about 18 km (1.2 m/km; US Army, 1952).

There are four major changes in slope within the Snake River system (Figure 3(b)). The lower Snake River, from the Columbia River confluence near Pasco, Washington to the Salmon River, Idaho, has a slope of about 0.6 m/km. The middle portion of the drainage, containing the Hells Canyon Reach, has a higher slope of about 1.4 m/km. The slope decreases again from Burnt River upriver to Bliss, averaging about 0.5 m/km. Finally, the slope increases sharply to >2.0 m/km for the next 100 km upstream of Bliss.

REACH CHARACTERISTICS

Measurements at the reach or channel unit scale (Table I) are interdependent with those at the watershed scale because channel form is largely related to the discharge of water and sediment from upstream catchments, and on valley characteristics such as gradient and sedimentology of valley fill deposits (Richards, 1982). Thus, discharge, geology and longitudinal slope can also be considered as reach-scale characteristics. Other important physical features that affect the spawning habitats of fall chinook salmon at this scale include channel morphology, especially channel pattern and width, and associated hydraulic features.

Discharge

The Hanford Reach is bounded by Priest Rapids and McNary Dams on the upstream and downstream portion, respectively. The Federal Energy Regulatory Commission has established minimum licensed flows of 1086 m^3/s through the project and these flows are regulated by releases at Priest Rapids Dam. The Hanford Reach contains no major tributary streams. At this scale, daily fluctuations in water surface elevation, as a result of power-peaking operations, can be significant (e.g. up to 2 m/day).

Average annual discharge through the Hanford Reach has not changed appreciably during the 20th century. For example, mean annual discharge for the Columbia River at Trinidad, Washington (Rkm 710) was 3270 m^3/s between 1912–1946 (US Army, 1952), which is within 5% of the 1959–1996 average after dam construction. Annual average discharge for the Hanford Reach during 1959–1996 ranged from 2600 m^3/s in 1973 to 4410 m^3/s in 1996 (Figure 4a). Annual flow magnitudes (mean monthly maximum discharge/mean monthly minimum discharge) through the Hanford Reach during this interval ranged from 1.5 to 7.1, with a median of 2.5.

Hells Canyon (Rkm 398), Oxbow (Rkm 440), and Brownlee (Rkm 459) Dams control most of the flow through the middle Snake River, although three major unregulated tributaries enter the lower Hells Canyon Reach. In recent years, flows through the upper section have been held stable at about 250 m^3/s

Table I. Comparison of general typology and channel morphology of the Hanford Reach, Columbia River and the Hells Canyon Reach, Snake River

Characteristic	Hanford Reach	Hells Canyon Reach
Stream order	7	6
Number of tributaries	0	3
Reach length (km)	90	160
Mean annual discharge (m^3/s)	3500	1100
Maximum flood (m^3/s)	21 000	11 600
Longitudinal slope (m/km)	0.2	1.3
Thalweg shifts	1 per 3.6 km	1 per 3.2 km
Mean channel width (m)	400	50
Dominant substrates	Cobbles	Gravels, cobbles, bedrock

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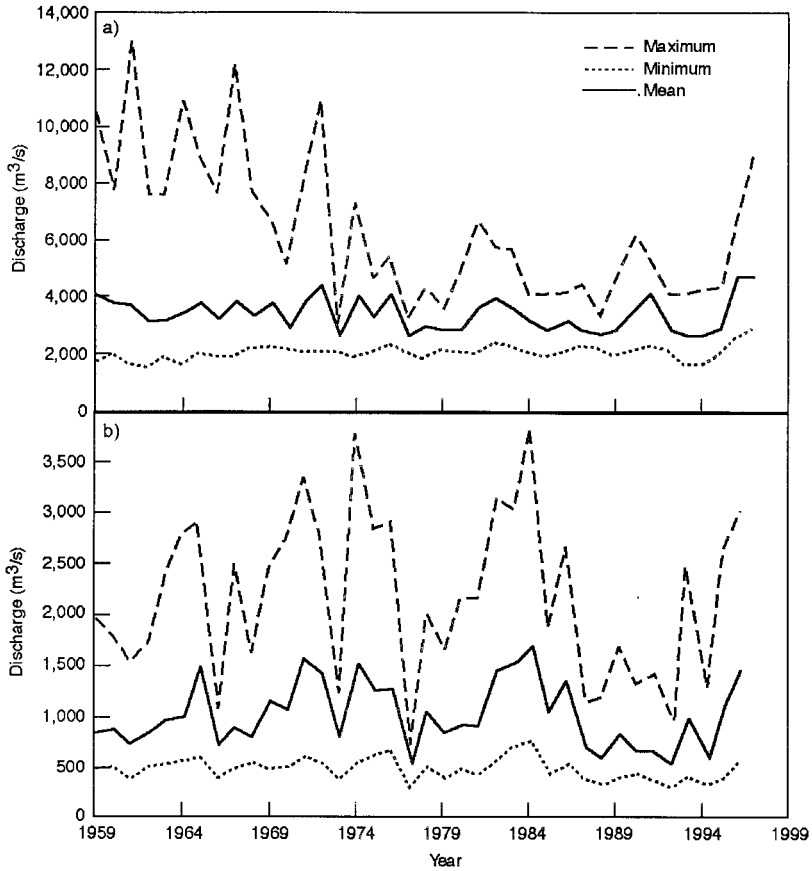

Figure 4. Discharge profiles for (a) the Columbia River downstream of Priest Rapids Dam, and (b) Snake River at Anatone, 1959–1994. Continuous discharge records for the Columbia River at Vernita (Rkm 637) and the Snake River at Anatone (Rkm 270) were obtained from the USGS files in Pasco, Washington, and Boise, Idaho, respectively. Vernita data were available for water years 1918–1996, while the Anatone data were available from only 1959 to 1996. Thus, only the last 38 years of record were used to determine monthly average and range in flows through each reach

by releases from Hells Canyon Dam during the October–early December spawning period. Flows in the lower section are heavily influenced by the unregulated Salmon River and, as a result, more variable.

The average annual discharge through the Hells Canyon Reach was much lower than those through the Hanford Reach from 1959 to 1996 (Figure 4(b)), ranging from 515 m^3/s to 1650 m^3/s at Anatone (Rkm 270). The relative magnitude of annual flows through the Hells Canyon Reach during this interval was 4.2, with monthly values ranging from 2.4 to 6.4. Thus, flows through the Hells Canyon Reach are more variable than those through the Hanford Reach.

Geological features

The Hanford Reach is located in the Columbia Plateau. The river channel is mostly unconfined, and much of the river bed consists of a relatively uniform layer of fluvial sediments (Reidel *et al.*, 1994). Gravel bars in the Hanford Reach (Figure 5) represent the youngest portion of the more extensive and older alluvial flood plain that overlies both a basalt layer, and former lake bed deposits of Ringold formation (Jenkins, 1922). Thus, most bed material is coarse and ground water passes through it readily. The Hanford Reach appears to have had no major changes in river platform and channel cross-sectional characteristics over the past century. Only small differences in bank migration, river bar shifting and channel aggredation or degradation have been observed. River bed materials in the Hanford Reach are

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Figure 5. Alluvial characteristics of the Hanford Reach, Columbia River near Rkm 586 (photo by D.D. Dauble)

thought to be sufficiently coarse to resist movement by flows as high as the regulated 100-year frequency discharge (i.e. 12500 m^3/s). Lack of bed material mobility here has resulted in an extremely stable channel thalweg with little lateral migration (Hall, 1988). Geologic materials adjacent to the Hanford Reach consist mainly of Quaternary and other unconsolidated sediments (Figure 6(a)).

Three major tributaries join the middle Snake River as it flows through Hells Canyon, a 1800 m deep v-shaped gorge with a narrow valley bottom. The upper canyon segment is mostly bedrock (Figure 6(b)) and the river remains confined (Figure 7). This feature reduces channel bed stability, availability of

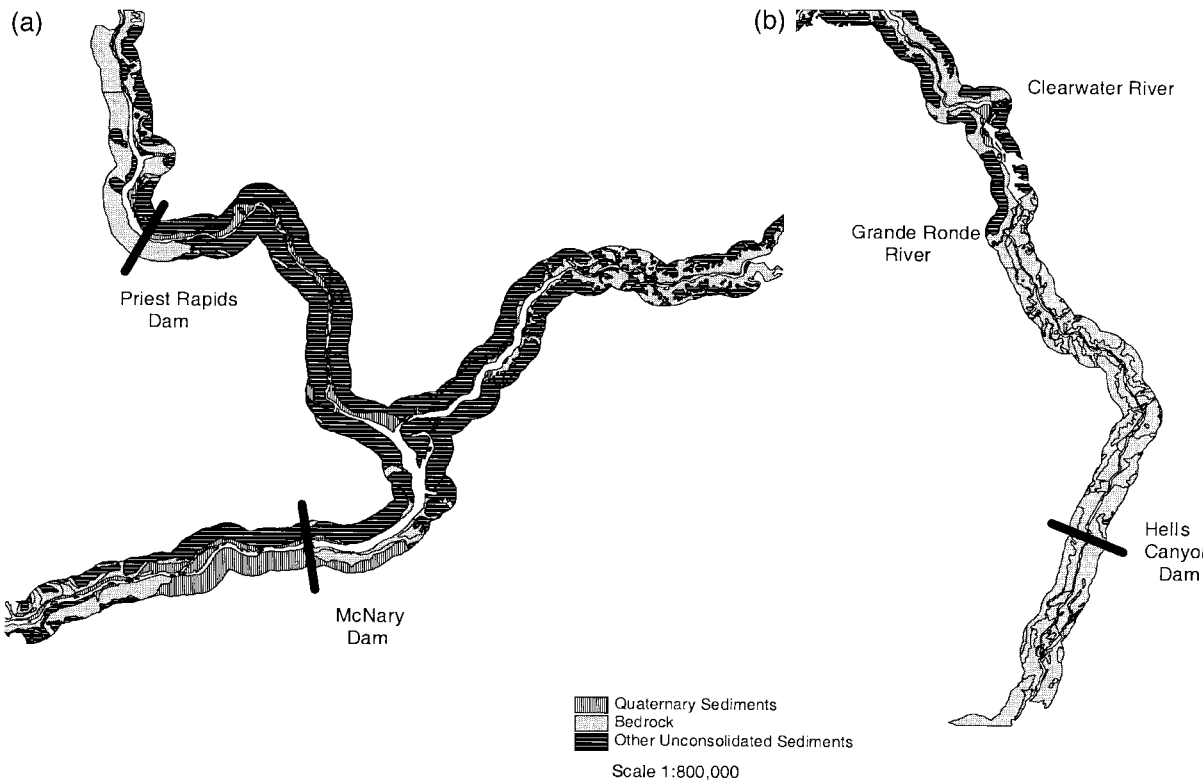

Figure 6. Principal geological features of the (a) Hanford Reach, and (b) Hells Canyon Reach spawning areas

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Figure 7. Upper section of the Hells Canyon, Snake River, near Rkm 386 (photo by A. Garcia)

smaller substrate typically used for spawning, and intragravel flow, where gravel is limited in depth. Thus, in contrast to the Hanford Reach, saturated alluvium is limited, being confined mainly to gravel bars. The lower canyon begins to widen downstream of Rkm 180, with less defined pool-rapid sequences.

Longitudinal slope

During its 90-km distance, the Hanford Reach of the Columbia River has a fairly uniform slope of about 0.2 m/km. In contrast, the much steeper Hells Canyon Reach of the Snake River has two major segments with a distinctly different gradient. The lower segment, extending from Rkm 241 to 306, has a slope of about 0.8 m/km, while the remaining 90 km upstream to Hells Canyon Dam has a slope of about 1.9 m/km. Thus, the gradient in the Hells Canyon Reach of the Snake River is 4–10 times steeper than the Hanford Reach of the Columbia River.

Channel morphology

We used thalweg deflection as a measure of channel sinuosity or change in channel morphology (e.g. pattern) over distance within the two reaches. For example, the Columbia River changes course 25 times within the Hanford Reach, while the Snake River changes course 46 times within the Hells Canyon Reach (Table I). The Hells Canyon Reach has about twice the number of changes in thalweg bearing $\geq 30°$ and nearly three times the number of changes $\geq 40°$, relative to distance, than the Hanford Reach. Most major changes in thalweg bearing occur in the lower part of the Hells Canyon Reach (about 1 per 4 km for Rkm 241–308) versus the upper part (1 per 9 km for Rkm 308–410). The only major change in thalweg bearing for the Hanford Reach occurs between Rkm 586 and 605.

The Hanford Reach is much wider than the Hells Canyon Reach, ranging from about 240 to 1200 m (Figure 8(a)). Mean widths of the Snake River within the Hells Canyon Reach range from about 46 to 400 m (Figure 8(b)). Both the Hanford and Hells Canyon Reaches widen with distance downstream, providing room for increased channel complexity or braiding. For example, the mean width of the Hells Canyon Reach downsteam of Rkm 290 is over twice the width for Rkm 290–386. Several areas of major channel braiding are evident in the middle portion of the Hanford Reach. In contrast, channel braiding through the Hells Canyon Reach is largely limited to the section downstream of the Salmon River confluence.

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REDD CHARACTERISTICS

A key question is whether differences in redd densities can be explained by physical habitat differences at the redd or site measurement scale. The relative abundance and distribution of fall chinook redds has been monitored in both study areas for several years. Frequency of use for known spawning areas in the Hells Canyon Reach is highly variable from year-to-year and redd density is generally low (< 2 redds/km; Groves and Chandler, 1996). In contrast, temporal use patterns for known spawning areas in the Hanford Reach are more consistent and redd densities are much higher (i.e. up to 2000 redds/km; Dauble and Watson, 1997).

Standard habitat characteristics used to describe mainstem spawning habitat of fall chinook salmon include water depth, substrate size and instream velocity (Chapman *et al.*, 1986; Swan, 1989; Groves and Chandler, 1999). The depth and dominant substrate size for fall chinook salmon redds in the Hanford Reach displayed a wider range of values than those in the Hells Canyon Reach (Table II). Average water

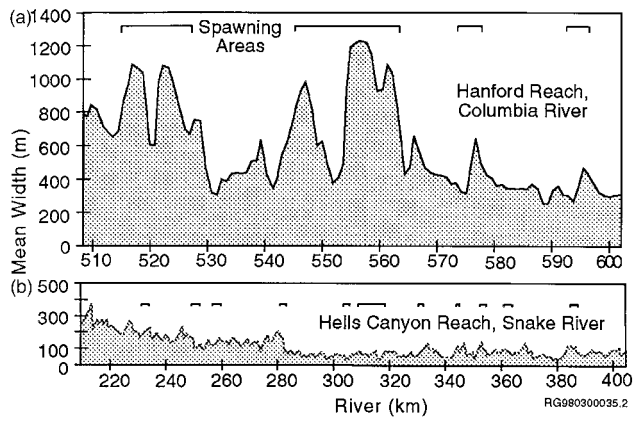

Figure 8. Mean channel widths of the (a) Hanford Reach, and (b) Hells Canyon Reach. Shoreline elevation and channel cross-sections (i.e. bank-to-bank) for both the Hanford and Hells Canyon Reaches were taken from USGS 7.5° quadrangles at 1.6 km (1-mile) intervals to estimate channel size

Table II. Summary of physical characteristics[a] for fall chinook salmon redds from the Hanford Reach, Columbia River in 1994 (D.D. Dauble, unpublished data) and the Hells Canyon Reach, Snake River, 1993–1994 (from Groves and Chandler, 1999)

	Hanford Reach	Hells Canyon Reach
Depth		
n	239	162
Range (m)	0.6–8.4	0.2–6.5
Mean ± S.D. (m)	3.2 ± 1.5	2.5 ± 0.2
Instream velocity		
n	222	124
Range (m/s)	0.2–1.7	0.1–2.0
Mean ± S.D. (m/s)	0.9 ± 0.3	0.9 ± 0.1
Substrate		
n	222	112
Dominant (cm)	7.5–15	5.0–7.5
Subdominant (cm)	2.5–7.5	7.5–15

[a] Redd measurements in the Hanford Reach were taken under variable flow regimes that ranged from 1130 to 1750 m^3/s. All depths were adjusted to flows of 2200 m^3/s using a stage–discharge relationship (Walters *et al.*, 1994). Redd characteristics in the Hells Canyon Reach were measured under a stable discharge of about 280 m^3/s.

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depths for redds in the Hanford Reach were about 30% higher than those found in the Hells Canyon Reach. Water depths of 2–3 m and 1–2 m were most frequently selected in the Hanford Reach and Hells Canyon Reach, respectively. Average instream velocities for redds in the Hanford Reach were similar to those in the Hells Canyon Reach, i.e. about 70% of the redds from both areas occurred at velocities ranging from 60 to 120 cm/s. Substrate size of redds within the Hanford Reach was generally larger than those within the Hells Canyon Reach and encompassed a wider range of values. For example, 65% of the redds in the Hanford Reach had a dominant substrate of 7.6–15.2 cm, compared with 15% of Hells Canyon Reach redds. However, subdominant substrate associated with redd sites was typically larger in the Hells Canyon Reach. Because physical habitats have not been fully inventoried in either study area, it is not possible to know whether differences in redd characteristics are a result of differential habitat selection or are a nonselective response to available habitat.

REVIEW OF SPATIAL LINKAGES

Our review of spawning habitat characteristics showed that the alluvial river attributes used for comparison between the two study areas operated at different scales. There was a high degree of correspondence between spawning sites for fall chinook salmon and their geological profiles at the watershed scale. Historic spawning populations were most abundant adjacent to well-developed floodplains and gravel bars (DeVoto, 1953; Fulton, 1968). These locations typically had a lower gradient than other parts of the Columbia River watershed. At one time, important mid-Columbia spawning sites were adjacent to the Snake–Columbia confluence (Fulton, 1968) and included the Hanford Reach. For the Snake River, areas upstream of Hells Canyon Dam near Marsing, Idaho (Rkm 685) had more extensive alluvium and lower gradient than the Hells Canyon Reach, and were thought to be particularly important for fall chinook salmon production (Haas, 1965; Irving and Bjornn, 1981). There is no evidence that significant numbers of fall chinook salmon ever spawned in the Hells Canyon Reach.

Large-scale geomorphic variables, such as channel slope, have been shown to influence distribution and abundance of other salmonids (Kruse *et al.*, 1997). The relative magnitude and frequency of high flow events also acts to modify channel form, but only within the constraints of existing geological features. Consequently, geologic formations at the watershed scale affect longitudinal gradient, which along with flow regime and bedload, affects the quality and quantity of spawning habitat available at the reach and redd scale.

Several reach-scale differences were found between the two study areas relative to their geology, longitudinal gradient and discharge. For example, the Hells Canyon Reach is more geologically confined and contains less alluvium than the Hanford Reach. The Hanford Reach also has a lower gradient, a feature that results in greater bedform stability and greater intragravel flow. A direct relationship exists between slope and bed material particle size under conditions of uniform discharge (Richards, 1982). In unconfined reaches of large gravel and cobble-bed rivers, the longitudinal gradient is reduced and alluvium is deposited (Stanford *et al.*, 1996). Alluvium is highly porous, allowing river water to penetrate into the bed material (hyporheic habitats), creating conditions beneficial to spawning and egg incubation.

The Hanford and Hells Canyon Reaches are both contained within large rivers in which fluvial processes and geological constraints determine their morphology (Church, 1992). Both areas have developed channel bed forms over time relative to discharge and to channel shape/slope. At the reach-scale, we observed that gravel bars formed where changes in thalweg direction occurred as a result of geological obstructions. Gravel bars provide favorable spawning habitat for fall chinook salmon because they promote conditions necessary for redd construction and embryo survival, i.e. suitable substrate size and depth, and intragravel flow. Highest densities of redds in the Hanford Reach occur near areas of major thalweg shifts (Dauble and Watson, 1997). Similarly, many Snake River spawning sites were found near major thalweg shifts and associated substrate deposition zones. We calculated the absolute difference in thalweg bearing for each river mile (1.6 km) of the Hells Canyon Reach of the Snake River and determined whether that river mile supported spawning or not. The difference between

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spawning and non-spawning segments of the river were compared using notched box plots, which provide 95% confidence intervals around the medians of the two groups (McGill *et al.*, 1978; Systat Inc., 1997). There was a significant relationship between spawning sites and the absolute value of changes in thalweg direction for locations downstream of the Salmon River confluence in the Hells Canyon Reach (Figure 9), but not for upstream spawning sites.

Presence of channel bars were useful indicators of spawning sites for both the Hells Canyon Reach and the Hanford Reach (Table III). In the Hanford Reach, 22 out of 27 segments with channel bars had spawning activity, whereas only six out of 25 segments without bars had spawning activity. Channel bar formations and associated high densities of redds also occur in the Hanford Reach where high relief occurs along one shoreline, e.g. Vernita Bar and Locke Island (Dauble and Watson, 1997). These bars contain substrate of suitable size for spawning and have high enough instream velocities to limit deposition of fine sediments in spawning areas. Furthermore, the deposited material is geologically loose and deep, with sufficient permeability to promote intragravel flow.

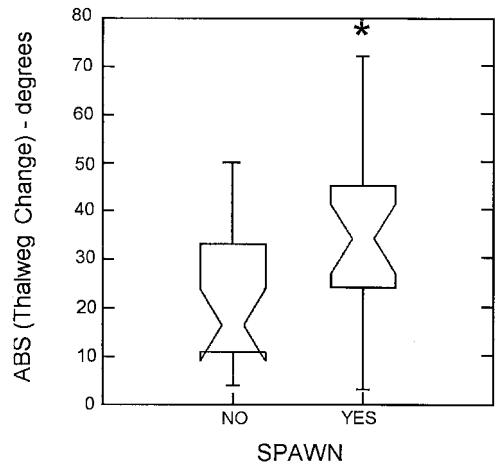

Figure 9. Notched box plots of the absolute value (ABS) of change in thalweg bearing for spawning and non-spawning sections of the Hells Canyon Reach of the Snake River, downstream of the Salmon River confluence ($n = 43$). The notches in the box plots represent 95% confidence intervals around the medians (McGill *et al.*, 1978; Systat Inc., 1997). Therefore, the lack of overlap between the notches on each plot indicates that the median changes in thalweg bearing are significantly different at the 95% level, with greater changes found in segments of the rivers where spawning occurs. Asterisks represent extreme values (Systat Inc., 1997)

Table III. We used chi square analysis to test the hypothesis that there was no relationship between bar formation and distribution of spawning sites[a]

	Bars—spawn	Bars—no spawn	No bars—spawn	No bars—no spawn
Hanford Reach				
Channel bars[b]	22/14.5	5/12.5	6/13.5	19/11.5
Lateral bars	4/2.7	1/2.3	24/25.3	23/21.7
Hells Canyon Reach				
Channel bars[b]	12/8.3	4/7.7	40/43.7	44/40.3
Lateral bars[b]	34/27.6	19/25.4	18/24.4	29/22.6

[a] Use patterns (actual/expected) were analyzed for 1.6 km segments in the Hanford Reach, Columbia River ($n = 52$) and Hells Canyon Reach, Snake River ($n = 100$). Bar identification was based on aerial photographs taken by the US Army Corps of Engineers in 1982, at flows of approximately 400 m^3/s (Hells Canyon Reach) and by the US Department of Energy in 1973, at flows of approximately 1400 m^3/s (Hanford Reach), and classified according to definitions in Church and Jones (1982).
[b] Values significantly different than expected at $p < 0.05$ based on chi-square contingency analysis.

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There was also a strong association between spawning sites and lateral bar formation in the Hells Canyon Reach (Table III). Some lateral bars are deposition zones from the Bonneville flood and somewhat elevated above the main river channel at normal flows (O'Conner, 1993). Other bar formations in the Hells Canyon Reach have formed as alluvial fans from side canyons. Bjornn and Reiser (1991) reported that salmon usually spawn at the transition between pools to riffles, or in areas that are often associated with a lateral bar deposition.

We found most spawning in the Hanford Reach was concentrated in braided sections or wider areas of the river having complex channel formations. There was a significant relationship between channel width and redd distribution for all of the Hanford Reach and for the Hells Canyon Reach upstream of Rkm 290 ($\alpha = 0.05$; Figure 10), near the confluence with the Salmon River. Channel complexity may help establish hydraulic processes within the hyporheic zone that favor selection of redd sites. The more complex the channel pattern, the more likely are downwelling and upwelling zones (Brunke and Gonser, 1997), conditions which may ultimately affect where salmon spawn. The extent of upwelling and downwelling is often a function of channel morphology and flow characteristics (Geist and Dauble, 1998). For example, downwelling and upwelling of hyporheic flow occurs at the upstream and downstream portions of a channel bar or island. This process creates interstitial flow pathways through the bed material (Brunke and Gonser, 1997).

There were no clear differences in spawning habitat between the two study areas based on redd scale measurements. While dominant substrate size and water depth of fall chinook salmon redd sites in the Hanford Reach exceeded those in the Hells Canyon Reach, instream velocity characteristics were similar. Differences in bed substrate size are reflective of the relative flow regimes of each river, geological features of the surrounding landscape and sediment input from tributaries. Saturated alluvium is often more limited in bedrock-constrained channel segments, which might result in smaller hyporheic zones confined only to gravel bars (Stanford and Ward, 1993). These geologic features may help explain the patchy distribution and low densities of fall chinook salmon redds in the Hells Canyon Reach. Velocity over, and depth of, redd sites were affected by the volume of discharge from upstream storage operations. Upper limits for spawning depth and instream velocity are also defined by available channel depth (Geist and Dauble, 1998). There were sufficient differences in characteristics of the two study areas, at both the watershed and reach-scale, to suggest that direct comparisons of physical habitat use based on redd scale measurements are not useful for estimating production potential.

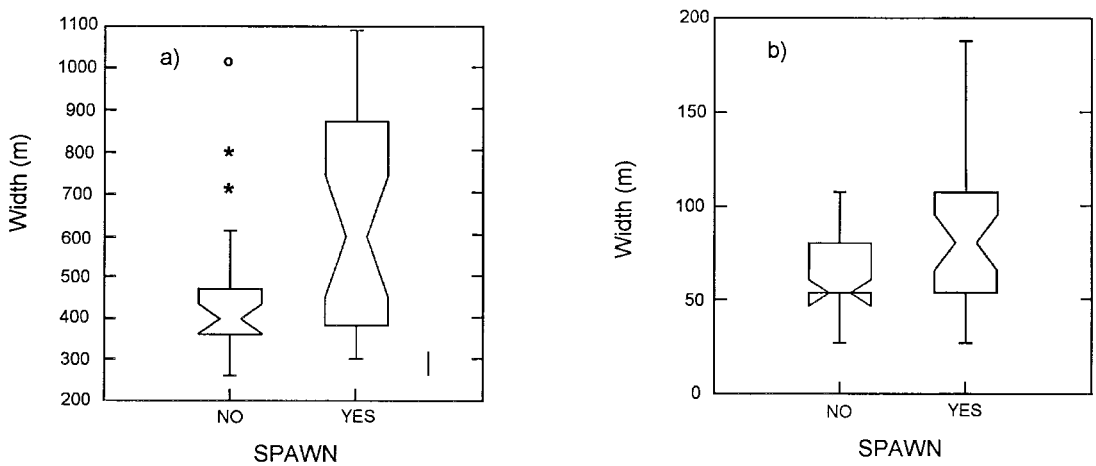

Figure 10. Notched box plots of channel width for spawning and non-spawning sections of (a) Hanford Reach, Columbia River ($n = 52$), and (b) Hells Canyon Reach, Snake River, upstream of Rkm 290 ($n = 67$). The notches in the box plots represent 95% confidence intervals around the medians (McGill *et al.*, 1978; Systat Inc., 1997). Therefore, the lack of overlap between the notches on each plot indicates that the median channel widths are significantly different at the 95% level, with greater channel widths found in segments of the rivers where spawning occurs. Asterisks represent extreme values and open circles represent very extreme values (Systat Inc., 1997)

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The hierarchical-based comparison identified several cause-effect linkages between watershed and reach-level characteristics of the two study areas and spawning sites. Watershed characteristics, such as geology and slope, are invariant over the time scales of our study and effectively limit riverine processes required for the provision of spawning habitat. Flow regimes, geological features, and slope influenced channel morphology and associated bed substrate, controlling variables in redd distribution and abundance. Discharge becomes a controlling factor at both the reach and site scale, as the flow regimes are regulated to meet power-peaking and water storage demands. Indeed, flow regulation practices in the Columbia River have largely eliminated flood peaks and increased daily variability of flows through the Hanford Reach (Stanford *et al.*, 1996).

In summary, our analysis indicated that geomorphological features of river systems, over a range of measurement scales, influence the alluvial characteristics required by fall chinook salmon for spawning. Thus, geomorphological features of the Columbia and Snake Rivers must be carefully considered prior to implementation of any management action, e.g. reservoir drawdown, removal of hydroelectric projects, and the establishment of 'normative' flow scenarios (Independent Scientific Group, 1996; Stanford *et al.*, 1996), designed to enhance the production of fall chinook salmon in mainstem habitats.

EFFECTS OF HYDROELECTRIC DEVELOPMENT ON SPAWNING HABITATS OF FALL CHINOOK SALMON

Construction and operation of early dams (e.g. Bonneville and Grand Coulee) had no apparent effect on production of fall chinook salmon in the mid-Columbia and Snake River systems because most mainstem spawning grounds remained accessible. Subsequent hydroelectric development drastically reduced the amount of mainstem riverine habitat required for spawning by fall chinook salmon. During the post-development period (i.e. after the mid-1940s or when adult salmon return data became available from dam passage or redd counts), the Snake River was the major mainstem production area for fall chinook salmon (according to average returns during 1957–1960), followed by the main Columbia River from John Day to McNary Dams (Fulton, 1968). Brownlee (1958), Oxbow (1961) and Hells Canyon (1967) Dams then blocked upstream access to about 320 km of productive habitat in the Snake River (Haas, 1965). The four lower Snake River dams inundated an additional 220 km of the mainstem Snake River (Irving and Bjornn, 1981). Currently, less than 25% of historic spawning habitat is still available for fall chinook salmon in the mainstem Snake River. Similarly, less than 20% of the former riverine habitat in the Columbia River is not inundated.

Physical habitat over the 'longitudinal dimension' (Ward and Stanford, 1989) has been severely disrupted for both Hanford and Hells Canyon populations during the past 40 years. Extensive fragmentation of spawning has occurred, as the Columbia River watershed was systematically changed from lotic to lentic habitats via contruction and operation of mainstem dams. Fall chinook salmon returning to the Snake River have experienced greater disruption to their spatio-temporal pathways (after Stanford *et al.*, 1996; Ebersole *et al.*, 1997) than those returning to the mid-Columbia River, as a result of their greater migration distance (800 + km versus 600 + km) and of increased numbers of hydroelectric reservoirs (eight versus four). Upstream passage blockage at Hells Canyon Dam has also resulted in loss of connectivity between former upstream and downstream production areas in the Snake River.

The Hanford Reach may be considered the only remaining 'core population' of fall chinook salmon within the Columbia River system (Independent Scientific Group, 1996). Hanford Reach populations have increased during the past 25 years because suitable spawning and rearing habitat remained intact, runs were supplemented by hatcheries, and because the mainstem core population remained viable (Dauble and Watson, 1997). In contrast, Hells Canyon Reach populations have declined because habitat quantity or quality was low (limited spawning area), former core populations were effectively

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'closed-off' from important upriver production areas, and conditions imposed on downstream migrating juveniles were more severe than those experienced by Hanford Reach populations (more mainstem reservoirs). We attribute much of the reduction in production for Snake River populations to lack of access to former core production areas and to changes in biotic conditions (i.e. temperature and flow regimes) that may limit completion of critical life history needs.

A major factor limiting recovery of Snake River spawning populations may be whether sufficient habitat patches remain for colonization (Reeves *et al*., 1995). For example, a primary biotic variable in maintaining viable populations of salmonids is the ability of the existing satellite or core population (metapopulation) to successfully colonize suitable habitat (Rieman *et al*., 1993; Rieman and McIntyre, 1995). One concern is that elimination of upstream and downstream populations (through migration blockage and habitat inundation, respectively) has dramatically increased the distance between the Hells Canyon Reach population and adjacent populations (after MacArthur and Wilson, 1967; Wilcox, 1980). Snake River fall chinook salmon probably respond to these metapopulation processes. The overall effect of increasing travel distance between potential colonists is a reduction in production potential of the Hells Canyon Reach.

Our hierarchical-based approach to habitat assessment provides one 'view' of factors affecting fall chinook salmon populations in the Columbia River basin. While our focus was on spawning habitat, we recognize that other biotic and abiotic forces shape their survival. In particular, availability of freshwater rearing and migration habitats with suitable temperatures, water quality and food web characteristics, must be overlayed against available spawning habitat (Independent Scientific Group, 1996; Stanford *et al*., 1996). River level fluctuations, a result of power-peaking of hydroelectric dams, is a concern for juvenile salmon because they rear in shallow, nearshore areas (Becker *et al*., 1981). Mortality during their downstream migration interval is also a consideration for the freshwater phase of fall chinook salmon life history (Raymond, 1979). Restoration and protection of suitable spawning habitats provides just one essential link required for sustaining these salmonid resources.

CONCLUSION

The distribution and abundance of fall chinook salmon populations that spawned throughout the mainstem Columbia River system has changed dramatically during the latter half of the 20th century. Populations from the Columbia and Snake Rivers have responded differently, as access to former spawning habitats was eliminated because of hydroelectric dam construction and operation. Populations of fall chinook salmon that return to the Hanford Reach have remained viable, largely because the geological template there appears highly compatible with their life history requirements. The realized production (after Warren *et al*., 1979) of fall chinook salmon in the Hanford Reach is now higher than it was 30 years ago. Production in the Hells Canyon Reach appears to limited to near historic levels because the channel is more confined, it has a steeper hydraulic gradient, and alluvium is less abundant. Snake River populations must also overcome a greater discontinuum in environmental conditions in order to successfully carry out their life history requirements. This discontinuum, created primarily by hydroelectric dams, has reduced both the potential and realized production of Snake River fall chinook salmon. Both the extent of 'recovery' and time required for 'recovery' of depressed Snake River populations will depend on whether present populations can be 'connected' to additional habitats and if neighboring populations are sustained.

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