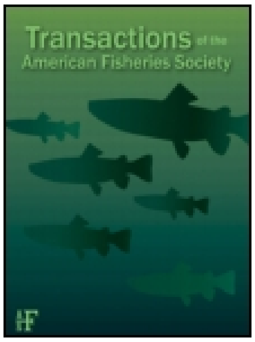

Transactions of the American Fisheries Society

ISSN: 0002-8487 (Print) 1548-8659 (Online) Journal homepage: http://afs.tandfonline.com/loi/utaf20

A Classification of Habitat Types in a Large River and Their Use by Juvenile Salmonids

T. J. Beechie , M. Liermann , E. M. Beamer & R. Henderson

To cite this article: T. J. Beechie , M. Liermann , E. M. Beamer & R. Henderson (2005) A Classification of Habitat Types in a Large River and Their Use by Juvenile Salmonids, Transactions of the American Fisheries Society, 134:3, 717-729, DOI: 10.1577/T04-062.1

To link to this article: http://dx.doi.org/10.1577/T04-062.1

Transactions of the American Fisheries Society 134:717–729, 2005

DOI: 10.1577/T04-062.1

[Article]

A Classification of Habitat Types in a Large River and Their Use by Juvenile Salmonids

T. J. BEECHIE* AND M. LIERMANN
National Marine Fisheries Service, Northwest Fisheries Science Center,
2725 Montlake Boulevard E., Seattle, Washington 98112, USA

E. M. BEAMER AND R. HENDERSON
Skagit River System Cooperative,
Post Office Box 368, La Conner, Washington 98257, USA

Abstract.—We describe six habitat types for large rivers (>100 m bank-full width), including pools, riffles, and glides in midchannel and bank edges, bar edges, and backwaters along channel margins. Midchannel units were deeper and faster than edge units on average. Among edge habitat types, backwater units had the lowest velocities and contained complex cover consisting mainly of wood accumulations and aquatic plants. Banks and bars had similar velocity distributions, but banks had more complex cover such as rootwads and debris jams. Because sampling of juvenile salmonids was ineffective in the midchannel units (electrofishing capture efficiency was low, and the units were too deep and fast to snorkel), we focused our sampling efforts on juvenile salmonid use of edge habitats during winter, spring, and late summer. Densities of juvenile Chinook salmon *Oncorhynchus tshawytscha* and coho salmon *O. kisutch* were highest in bank and backwater units in winter, whereas age-0 and age-1 or older steelhead densities were highest in bank units in winter. In summer, only coho salmon densities were significantly different among edge unit types, densities being highest in banks and backwaters. Microhabitat selection (velocity, depth, and cover type) by juvenile salmonids mirrored that in small streams, most fish occupying areas with a velocity less than 15 cm/s and wood cover. Among ocean-type salmon, Chinook and chum salmon fry were captured in large numbers in all edge units and exhibited only slightly higher densities in low-velocity areas (<15 cm/s).

An important challenge to understanding how habitat abundance and quality influence salmonid populations is quantifying juvenile salmonid use of habitats in large rivers. Studies of juvenile salmonid habitat use in large rivers are rare, mainly because of the difficulties inherent to sampling fast, deep water (e.g., Murphy et al. 1989). Consequently, most studies of juvenile salmonid habitat preferences are in small streams, where decades of research have shown that habitat preferences vary among species and by body size and season (Bustard and Narver 1975; Sullivan 1986; Hillman et al. 1987; Bisson et al. 1988; Taylor 1988; Nickelson et al. 1992; Fausch 1993). Studies of small streams have also shown that habitat changes such as riprapping of banks or creation of specific habitat types affect individuals and populations (e.g., Knudsen and Dilley 1987; Nickelson et al. 1992). Most work on salmonid use of large river channels (>50 m bank-full width) has focused on impacts of specific management practices such as gravel removal (Weigand 1991), effects of riprap (Peters et al. 1998; Garland et al. 2002), or shoreline development (Ward et al. 1994). Only Murphy et al. (1989) attempted a general description of habitat types and fish distributions in a large river (the Taku River in Alaska), but they were unable to effectively sample the turbid main channel.

Most juvenile salmonids occupy relatively shallow and low-velocity areas in small streams (<1 m deep and <40 cm/s velocity; Bjornn and Reiser 1991) and exhibit specific cover-type preferences (Fausch 1993; Rosenfeld et al. 2000). However, most of the habitat area in large rivers is more than 1 m deep and velocity exceeds 40 cm/s throughout the year. Therefore, we anticipated that most juvenile salmonids would be found near channel margins, where velocities are lower and cover is more abundant (Hillman et al. 1987; Murphy et al. 1989). Microhabitat preferences (depth, velocity, and cover type) vary among species (e.g., Bustard and Narver 1975; Taylor 1988; McMahon and Hartman 1989; Shirvell 1990), reflecting body size (Bjornn and Reiser 1991) and morphological ad-

---

* Corresponding author: tim.beechie@noaa.gov

Received April 6, 2004; accepted November 16, 2004

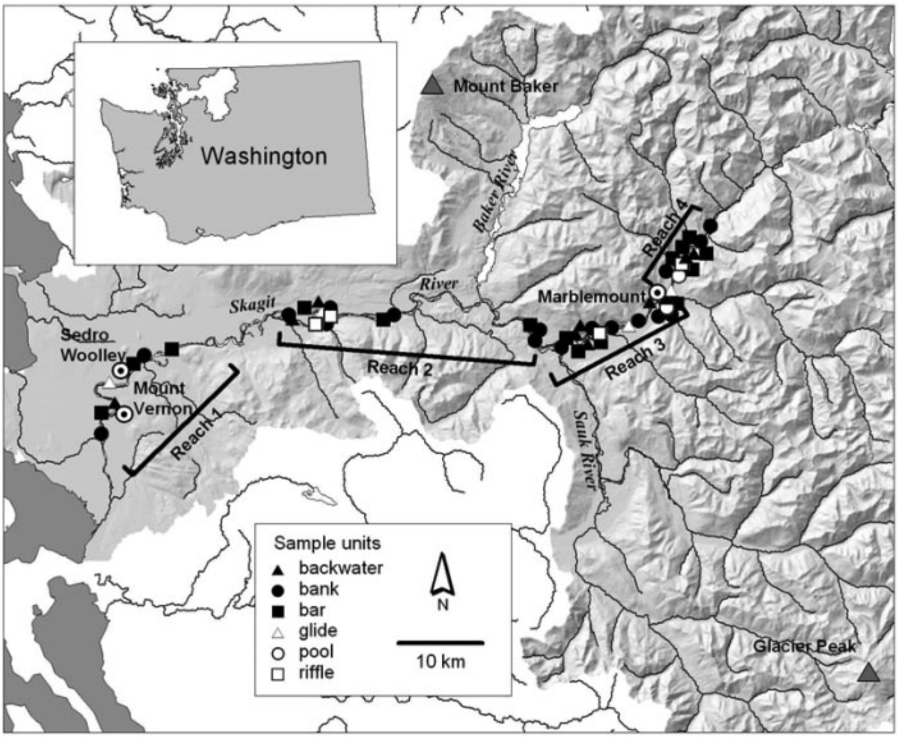

FIGURE 1.—Location of sample reaches and sampled habitat units in the Skagit River basin. Inset shows location of Skagit River basin within Washington State. Circled dots indicate towns near which stream gauges are located.

aptations to different environments (Bisson et al. 1988). Hence, we expected that microhabitat selection along the margins of large rivers would mirror those observed in small streams, and that habitat characteristics and fish abundance would differ among unit types.

In this paper we describe a suite of six habitat types for large rivers (greater than ~100 m bank-full width): pools, riffles, and glides in mid-channel and bank edges, bar edges, and backwaters along the channel margins. We describe physical differences between midchannel and edge units, but we were unable to effectively sample juvenile salmonids in the deep and fast midchannel units. Therefore, we focused our fish-sampling efforts on edge habitat types. We compare juvenile salmonid use among the three edge habitat types and evaluate how velocity, depth, and cover type influence salmonid abundance within units to help explain patterns observed at the unit scale.

Study Area

The Skagit River basin drains an area of 8,544 km^2 in the North Cascades of Washington (Figure 1). Precipitation ranges from 90 cm/year at sea level to 460 cm/year in the area of 3,275-m-high Glacier Peak. Historically, dense coniferous forests covered hillslopes and terraces, and mixed deciduous and conifer forests covered the valley bottoms (Ayers 1899; Gannett 1899). By 1898, logging had cleared virtually all lands near the coast and on the floodplain of the Skagit River up to the Sauk River (Gannett 1899). Present floodplain and riparian forests reflect extensive modification for agriculture and residential uses even upstream of the Sauk River (Lunetta et al. 1997), and the lower river reaches (from Sedro Woolley to the mouth) have been diked to protect agricultural lands from flooding (Beechie et al. 2001).

The study reaches extended from river kilometer, as measured from the river's mouth, 13.7 (near Mount Vernon) to river kilometer 137 (near Marblemount; Figure 1). The Skagit River has a drainage area of 3,580 km^2 at river kilometer 137, and 8,017 km^2 at river kilometer 13.7. Bank-full channel widths ranged from 95 to 226 m, and average reach slopes ranged from 0.0002 to 0.0015 m/m. Mean annual discharges are 157 and 451 m^3/s at the Marblemount and Sedro Woolley gauges, respectively, and peak flows of 2-year recurrence

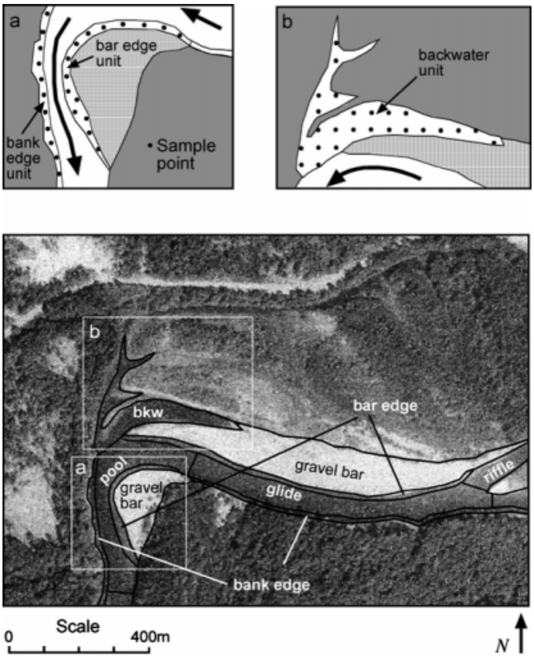

FIGURE 2.—Typical position of different unit types in the main-stem Skagit River, and examples of sample point distribution within edge units (panels a and b). Note that bank units tend to be at the outside edge of meander bends, whereas bar units tend to be at the inside edge (along gravel bars). Backwater units are most commonly located where side channels or tributaries join the main stem. Because bank and bar edges are generally narrow, sample points were typically arranged in a single line or two parallel lines. Backwater units more often had a large enough area to arrange a grid of sample points.

interval are 593 and 2,673 m^3/s (Williams et al. 1985; Sumioka et al. 1998).

Eight anadromous salmonids inhabit the Skagit River basin: Chinook salmon *Onchorhynchus tshawytscha*, pink salmon *O. gorbuscha*, chum salmon *O. keta*, sockeye salmon *O. nerka*, coho salmon *O. kisutch*, steelhead *O. mykiss*, cutthroat trout *O. clarkii*, and bull trout *Salvelinus confluentus*. Dolly Varden *S. malmo* are also found in the basin, but only above anadromous barriers (Ed Connor, Seattle City Light, Seattle, Washington, unpublished data). Chinook, pink, and chum salmon exhibit predominantly ocean-type life histories (i.e., juveniles migrate to saltwater soon after emerging from the gravel), sockeye salmon juveniles rear in Baker Lake for 1–3 years, and the remaining species exhibit primarily stream-type life histories (i.e., juveniles rearing in freshwater for 1 or more years before migrating to saltwater) (Williams et al. 1975; WDF et al. 1993; WDFW 1998; Blakley et al. 2000).

Methods

Habitat unit definition.—We identified six unit types in large main-stem rivers (Figure 2): three midchannel unit types (pools, riffles, and glides) and three edge unit types (banks, bars, and backwaters). The main channel units were defined by bed morphology and flow characteristics as in Sullivan (1986) and Bisson et al. (1988). Pools were defined by an obvious scoured depression in the bed; in the terminology of Bisson et al. (1988), these would be classified as lateral scour pools. Glides were slightly steeper and faster than pools, with no obvious depression in the bed and little surface turbulence. Riffles were the steepest units, with high water velocities and pronounced surface turbulence. Rapids and cascades as defined by Bisson et al. (1988) were not found in the study reaches.

The boundary between edge and midchannel units was a visible current shear line, the edge units having lower velocity. Banks had a vertical, or nearly vertical shore; bars had a shallow, low-gradient interface with the shore; and backwaters were partially enclosed, low-velocity areas separated from the main river channel. Bank habitat was further defined as either ''natural'' or ''riprapped'' based on the presence of riprap or other anthropogenic bank modifications. In this paper we examine only natural bank units to understand differences among the six unmodified unit types and their use by salmonids. Natural and riprapped banks are compared in Beamer and Henderson (1998).

Sample unit selection.—We first identified four sampling reaches of the main-stem Skagit River based on discharge patterns and spawner abundance (Figure 1). Reaches 1 and 2 have a discharge pattern that reflects the combined flow of the Skagit River and its main tributaries: the regulated Baker River, the regulated upper Skagit River, and the unregulated Sauk River (Figure 3). However, Reach 1 does not contain a spawning population of salmon, whereas Reach 2 is within the main-stem spawning area of fall Chinook salmon, chum salmon, and steelhead in the lower Skagit, as well as tributary populations of coho salmon. Reaches 3 and 4, both contained within the regulated portion of the upper Skagit River (upstream of the Sauk River confluence), were distinguished primarily by differences in spawner densities among species.

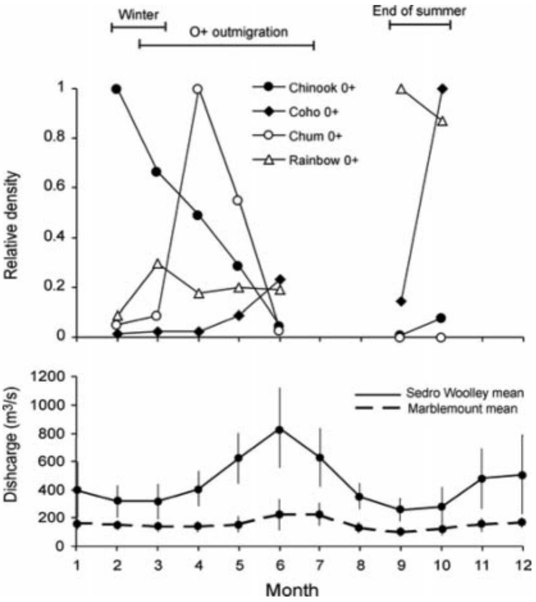

FIGURE 3.—Discharge patterns in lower and upper Skagit (Sedro Woolley and Marblemount gauges, respectively) and relative densities of juvenile salmonids for the four most abundant species age-classes captured during this study. Also shown are sample seasons encompassing end of summer rearing and winter rearing for stream-type fish (coho salmon, steelhead, bull trout, and cutthroat trout), as well as the out-migration period for ocean-type fish (Chinook, chum, and pink salmon).

TABLE 1.—Mean number of juvenile salmonids stunned per grid point, percent of stunned fish that were captured in dip nets, mean depth, and percent high-velocity (>45 cm/s) points by unit type for the pilot study. The estimated effective sampling area at each grid point was 3 m^2 (a circle 2 m in diameter). Mean depths differed significantly among unit types (Kruskal–Wallis test: $P < 0.001$). Mean depths with the same lowercase letter were not significantly different among those unit types.

Unit type	Fish/ grid point	Fish captured in dip nets (%)	Mean depth (m)	High-velocity points (%)
Pool	0.02	0	2.53 z	73
Glide	0.05	46	1.35 y	98
Riffle	0.10	47	0.86 x	99
Bar	0.91	81	0.51 w	2
Bank	2.62	77	0.75 wx	9
Backwater	2.88	81	0.69 wx	0

During 1993, the pilot study year, we selected 10 midchannel units and 24 edge units to evaluate the efficacy of electrofishing in a large river and to refine methods. Each unit was sampled in winter and summer (except for 1 midchannel and 1 edge unit, which were sampled in only one season because of logistical problems). We found that midchannel units were very difficult to electrofish effectively, and that we captured one to two orders of magnitude more juvenile salmon and trout in edge units than in midchannel units (Table 1). The proportion of fish stunned but not captured in midchannel units was very high compared to edge units (Table 1), which suggests that sampling midchannel units would not yield reliable results. Because water in mid-channel units was much faster and deeper than in edge units (Table 1), neither electrofishing nor snorkel surveys could be conducted effectively.

Given the difficulty of sampling the midchannel units, we focused the remainder of the study on edge units. Between 1995 and 1998 we sampled

TABLE 2.—Number of unique units sampled by year, season (W = winter, Spr = spring, and Smr = summer), reach (1, 2, 3, or 4), and unit type (BW = backwater, BR = bar edge, and NB = natural bank edge).

		1			2			3			4		
Year	Season	BW	BR	NB	BW	BR	NB	BW	BR	NB	BW	BR	NB
1993	W	1	2	1	2	1	3	2	2	2	2	2	3
	Spr												
	Smr	1	2	1	2	1	3	2	2	2	3	2	3
1995	W		1	1		1	1	3	1	3	1		3
	Spr		1	1		1	1	3	3	3	1		3
	Smr					1	1	3	2	1	1		
1996	W		1	1		1	1	3	3	3	2	3	3
	Spr		1	1		1	1	3	3	3	1	3	
	Smr												
1997	W							3	2	3	1	2	
	Spr						3	1	1	1	2	3	
	Smr												
1998	W							1	1	1			
	Spr							2		1			
	Smr									1			

TABLE 3.—Definitions of cover types within habitat units. The ''other'' category included less than 5% of all sample points and was not included in analyses.

Cover type	Definition
Wood	Anchored brush, bank roots, debris piles or jams, root wads, logs, and branches
Aquatic plants	Live, nonwoody aquatic vegetation
Cobble–boulder	Bed material predominantly boulders (≥256 mm in diameter) and cobble (64–256 mm in diameter)
Other	Undercut banks (submerged area underneath an overhanging bank without bank roots), bedrock (exposed solid rock), and detritus (leaves and other particulate organic matter); rare occurrences of riprap
No cover	No previously defined cover type present

108 units (41 unique units sampled in multiple seasons and years; Table 2), the bulk of the sampling effort occurring in 1995 and 1996. Sampled units were selected to represent typical slope, unit width, and cover types within each reach. During the winter months we sampled 16 bar units, 15 bank units, and 9 backwater units; in spring we sampled 11 bar units, 8 bank units, and 5 backwater units; and in summer we sampled 8 bar units, 12 bank units, and 9 backwater units. We focused our efforts on Reach 3, the region where mean fish densities were consistently highest.

Habitat and fish sampling procedures.—Units were sampled from February through June and in September and October to capture out-migration peaks of ocean-type salmonids (primarily Chinook, chum, and pink salmon), as well as the midwinter and late-summer rearing periods for stream-type salmonids (primarily coho salmon and steelhead; Figure 3). Stream discharges during the sampling period ranged from 56 to 586 m^3/s, the range of discharges sampled being approximately the same in all seasons (87–586 m^3/s in February and March, 77–532 m^3/s in June, 56–409 m^3/s in September and October) in order to minimize the effects of flow and turbidity levels on habitat use by juvenile salmonids. Thus, differences in salmonid use among unit types primarily reflect seasonal changes in stream temperature and fish behavior. Stream temperatures ranged from 3.5°C to 8.3°C in winter and from 11.1°C to 18.3°C in summer.

Each channel unit was electrofished from a stationary boat, using a grid-point sampling system adapted from Weigand (1991). We used a pulsed DC, Smith-Root GPP 7.5 electrofisher with a single 28-cm-diameter ring anode mounted on a telescoping fiberglass pole (500 V, 60 pulses/s, 60 A). Grid-point spacing ranged from 15 m in small units to 30 m in large units, for a total of 12–38 grid points sampled in each channel unit (Figure 2). Grid-point spacing within each unit was chosen to balance the competing goals of (1) achieving a large sample size and (2) limiting the influence of sampling activities on fish use at adjacent points. A spacing of 15-m was the smallest we could use while avoiding effects between points (based on snorkeler observations of fish movements as the boat approached). Therefore, in small units we used a grid-point spacing of 15 m and the sample size was sometimes less than our target of 30 grid points. Where we could use wider grid-point spacing and still maintain our target sample size, we set grid-point spacing as high as 30 m.

After electrofishing each grid point, we recorded water depth, surface water velocity, substrate type, and cover type, according to the dominant condition within a 2-m-diameter circle. Water depth was measured with a stadia rod to the nearest 0.1 m. Surface water velocity was calculated by dropping a chip of wood into the river and recording how long it took the chip to float the length of the boat when the boat was held stationary. We classified velocity as high (>45 cm/s), medium (15–45 cm/s), or low (<15 cm/s) according to Weigand (1991). Substrate types were boulder (>256 mm), cobble (64–256 mm), gravel (2–64 mm), sand (0.06–2 mm), silt/clay (<0.06 mm), detritus (generally leaf litter), and bedrock. Cover type definitions are listed in Table 3. Fish were collected at each grid point by turning the electrofisher on for 10 s, off for 5 s, and back on for 10 s. Stunned fish were retrieved with dip nets, and species and age-classes were recorded. Missed fish (stunned and seen, but not netted) were also recorded and classified as age-0 salmonid, age-1 salmonid, or other.

Data analysis.—To examine differences in microhabitat characteristics among unit types, we summarized velocity, substrate, and cover data for three different time periods (winter, end of spring, and end of summer). We calculated mean values of continuous data (depth) for each unit and tested for differences among unit types, using one-way nonparametric analysis of variance (Kruskal–Wallis; Zar 1996). In cases where a significant difference was found, we applied a multiple comparison procedure (Munzel and Hothorn 2001). For categorical data (velocity class, substrate type, and cover type), we summarized the proportion of total grid points in each class graphically. Because sampling was restricted to relatively low discharges in all seasons, the summarized habitat characteristics do not represent habitat differences among seasons, but rather describe habitat characteristics experienced by fish on each sample date.

We assessed differences in the number of fish per grid point among unit types by averaging across year and grid point to produce a single average value for each unit. We normalized for variation in yearly abundance by dividing by an index of yearly abundance before averaging across year. We constructed the index by calculating the average fish per grid point for units that were sampled in every year of the study (during the season of interest) and then dividing this by the yearly average. An example of a single datum used in the analysis would be the average number of coho per point (after correcting for year effect) in backwater unit 68 in winter. The unit averages for the different unit types were compared by using a one-way nonparametric analysis of variance (Kruskal–Wallis; Zar 1996), followed by a multiple comparison procedure when the test was significant (Munzel and Hothorn 2001). The analyses were repeated for the eight species–age-class–season combinations: Chinook salmon winter, age-0 coho salmon winter and summer, age-0 rainbow trout winter and summer, age-1 rainbow trout winter and summer, and chum salmon spring. We applied a cube-root transformation when plotting the data (not for the analysis) to make visual interpretation of the results more straightforward.

Changing priorities over time led to an unbalanced and incomplete design (Table 2). Consequently, year, season and reach are all potentially confounded with the variables of interest. For example, most of the backwater units sampled in spring were in Reach 3. Therefore, high fish per point values in backwater units could also be attributed to higher values in Reach 3. To address this problem, we first attempted to apply more complex analyses (mixed effects models; e.g., Pinheiro and Bates 2000). However, the combination of unbalanced design, high variability, and small sample sizes made effective parameterization of these models not feasible. Therefore, we addressed this problem by repeating the analyses on a subset of data that is approximately balanced (Reaches 3 and 4, for years 1993, 1995, and 1996). Only results that held up for this additional test are reported here.

To compare fish per grid point values across grid-point characteristics (velocity class and cover type), we calculated averages for each year–unit combination, since the location of the grid points within a unit varied between years (because of different river levels and physical changes to the unit). An example of a single datum would be the average number of coho salmon per point (after correcting for year effect) in complex wood cover, in unit 61, in the winter of 1996. We displayed these data graphically, but avoided direct analysis of grid-point data because of the high proportion of zeros (e.g., Chinook salmon, the most abundant species, was present in less than 30% of the grid points sampled during the peak months of outmigration) and the potential for correlation in space (adjacent grid points within a unit) and time (units sampled multiple times). As with the unit-type analysis, we applied a cube-root transformation when plotting the data.

Results

Among edge units, bars and banks tended to have similar velocity distributions, while backwaters were made up exclusively of low-velocity points (Figure 4). Velocities at sample points in bank and bar units were 40–75% low velocity ($<$15 cm/s) compared with 100% low-velocity points in backwater units. Mean depths differed significantly among unit types (Kruskal–Wallis, $P < 0.001$), bars being shallower on average than banks or backwaters (Table 4). Banks had the most abundant wood cover, whereas backwaters contained aquatic plants and wood cover. Bars contained mainly cobble–boulder cover.

The number of fish per point differed among edge unit types for most combinations of species and season (Figure 5). Bank units had higher densities than bar units for all species in winter and also for coho salmon in summer. This pattern was most pronounced for coho salmon. Chinook, coho, and chum salmon also tended to have higher densities in backwaters, whereas rainbow trout densities were comparable in bar and backwater units. We captured too few age-1 Chinook salmon, pink salmon, cutthroat trout (all ages), and juvenile char (all ages) to analyze differences in density.

Densities of Chinook, chum, and coho salmon (winter) were highest in low-velocity points, whereas densities of rainbow trout (winter) and coho salmon (summer) were comparable in low- and medium-velocity points (Figure 6). Densities

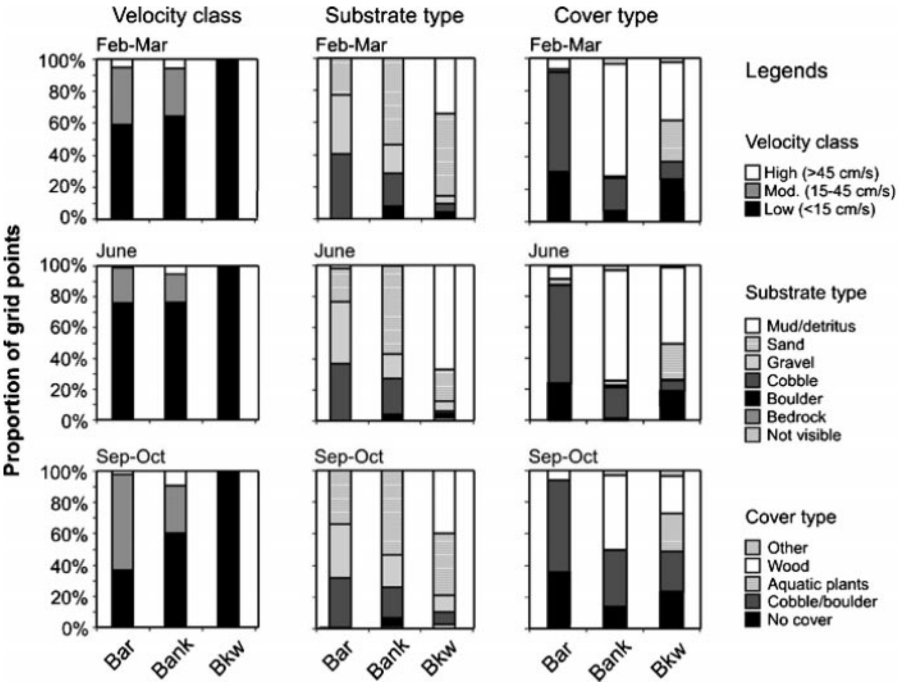

FIGURE 4.—Summary of velocity, substrate, and cover characteristics of edge habitat units in winter (February–March), spring (June), and end of summer (September–October).

of age-0 and age-1 rainbow trout did not vary by velocity class in summer. In winter, age-0 coho salmon and age-0 rainbow trout exhibited higher densities in wood cover (Figure 7). Densities of age-0 rainbow trout were comparable in wood and cobble–boulder cover (both summer and winter). Chinook and chum salmon (the two ocean-type fish with large enough sample sizes for analysis) occupied the broadest range of cover types, and both showed comparable patterns of relative density across velocity class and cover type. Proportion of fish stunned but not captured varied little by cover type (ranging from 16% in aquatic plants to 25% in wood cover).

TABLE 4.—Mean depth of edge units by unit type, with SDs in parentheses. Multiple comparisons (indicated by lowercase letters) show that bars were significantly ($P <$ 0.001) shallower than backwaters and banks and that the depths of backwaters and banks were not significantly different.

Unit type	Mean depth (m)
Bar	0.41 y (0.15)
Bank	0.71 z (0.18)
Backwater	0.70 z (0.17)

Discussion

Physical Characteristics of Edge Units

At the outset of this study we hypothesized that juvenile salmon and trout microhabitat preferences (depth, velocity, cover) are similar in both large rivers and small streams, but that preferred habitat characteristics in large rivers are predominantly found in the edge units. Although we were unable to fish the midchannel units effectively, our physical characterization of units was sufficient to illustrate the stark contrast in microhabitat characteristics between the midchannel units and the edge units. As expected, surface water velocities in edge units were typically less than 15 cm/s, within the range of average velocities occupied by juvenile salmonids in earlier studies (<20 cm/s; Bisson et al. 1988). Average water column velocities are approximately 90% of surface velocity in flows 0.18 m deep and approximately 96% of surface water velocity in flows 3.5 m deep (ASCE 1975). Hence, both surface water and average water column velocities in the edge units (average depth 0.51 to 0.75 m) would be largely within the range preferred by most juvenile salmonids. By contrast, surface water velocities in midchannel units (typically greater than 45 cm/s in pools, rif-

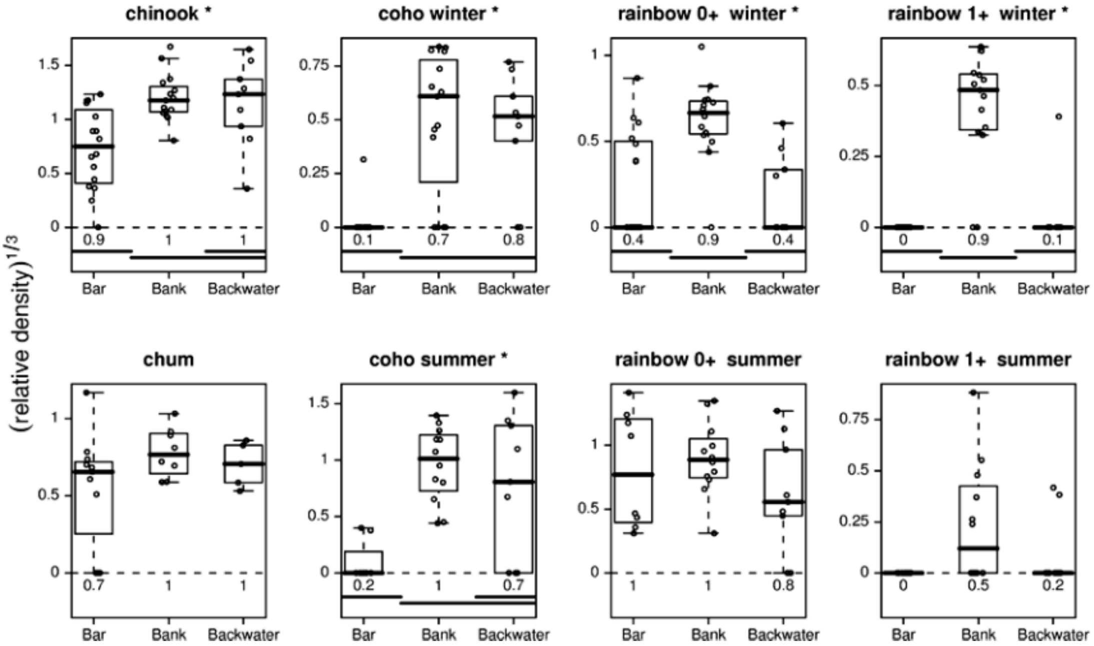

FIGURE 5.—Relative fish density (fish per point standardized by year) by species, age-class, and edge unit type. Asterisk indicates that a Kruskal–Wallace nonparameteric ANOVA resulted in a statistically significant difference among unit types (α = 0. 05). Numbers below *x*-axis indicate the proportion of points at which fish of that species were captured. Bars below *x*-axis indicate results of multiple comparisons (bars at similar heights indicate that differences are not significant).

fles, and glides) exceeded the average velocities occupied by most juvenile salmonids. Therefore, water column velocities in midchannel units (average depth 0.86–2.56 m) would probably exceed preferred velocities throughout most of the water column, except for velocities near the bed or in the lee of flow obstructions such as wood debris.

Juvenile salmonids selected mean depths and cover types found most commonly in edge units, and dominant cover types reflected the morphological position of units in the channel. Bars contained high proportions of cobble and boulder as cover, reflecting positions in the river channel that have relatively high basal shear stress and therefore tend to have coarse substrate, sparse aquatic plant cover, and little accumulated wood debris. By contrast, backwaters tended to have fine substrate, abundant aquatic plants, and greater accumulations of wood debris. Banks contained abundant wood cover because they were at the outside of meander bends where wood tends to accumulate in large rivers (Fetherston et al. 1995; Abbe 2000; Montgomery et al. 2003).

Edge Habitat Use by Juvenile Salmon and Trout

Past research indicates that, during summer, age-0 coho salmon tend to occupy low-velocity habitats, whereas age-0 and age-1 or older steelhead occupy a wide range of focal velocities (Bisson et al. 1988; Shirvell 1990; Fausch 1993; Kruzic et al. 2001). Bisson et al. (1988) argued that this pattern reflects the suitability of coho salmon and steelhead body forms to differing focal velocities and feeding strategies. The laterally compressed body form and large fin surfaces of coho salmon are better suited to low-velocity habitats, where increased maneuvering ability is advantageous for feeding on surface drift and for defending foraging stations. By contrast, the more cylindrical body form of steelhead is better suited to holding feeding positions in faster water. Experimental studies of coho salmon and steelhead support this contention. For example, coho salmon select low velocity over cover when given a choice (Shirvell 1990; Fausch 1993) and have higher growth and survival rates in low-velocity habitats (Kruzic et al. 2001). By contrast, steelhead parr prefer low-velocity locations that are adjacent to faster water and have overhead cover (Shirvell 1990; Fausch 1993).

Our finding that most coho salmon selected low to moderate velocities (<45 cm/s) in summer is consistent with these earlier studies, except that in this study coho salmon strongly avoided bar units

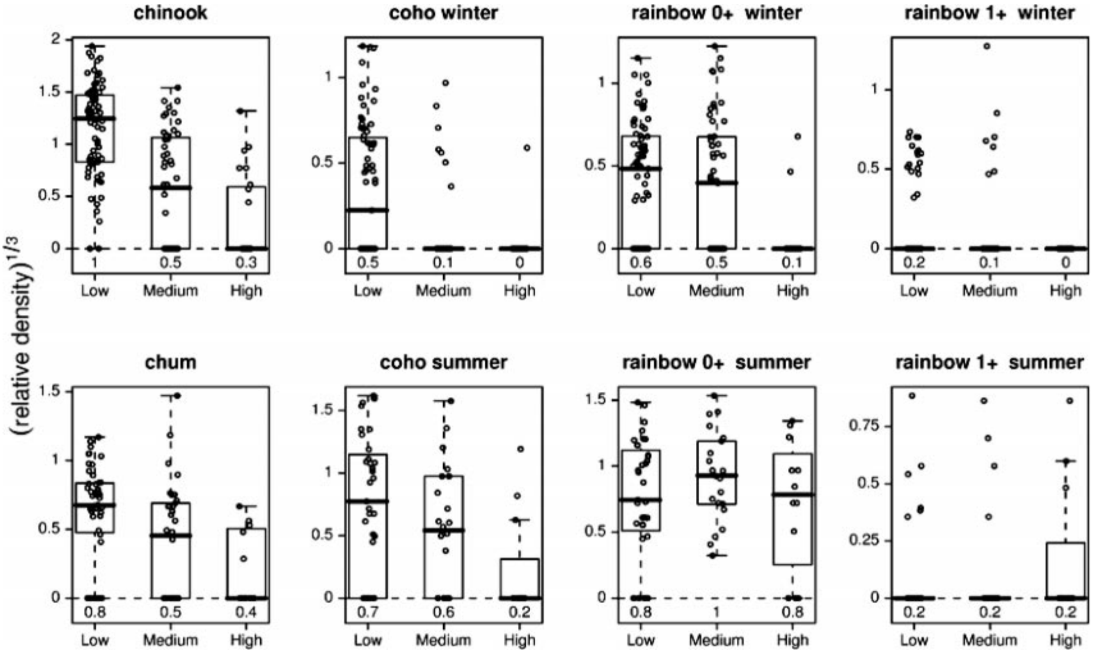

FIGURE 6.—Relative fish density (fish per point standardized by year) by species, age-class, and velocity class. Numbers below *x*-axis indicate the proportion of points at which fish of that species were captured.

even though these units contained nearly 40% low-velocity points. Examination of point characteristics within bar units indicated that low-velocity points were only slightly shallower than in banks or backwaters, but cover was either absent or provided by cobble and boulder. Hence, we found no evidence that depth explains avoidance of bars. However, proximity to complex cover may be an important factor in habitat selection by coho salmon in large rivers.

Age-0 and age-1 or older steelhead were evenly distributed among edge habitat types in summer and were evenly distributed across all velocity classes in the microhabitat analysis. The only suggestion of preference among microhabitats is their association with either cobble–boulder or wood cover. However, earlier studies indicate a preference for overhead cover (Shirvell 1990; Fausch 1993), suggesting that their apparent affinity to cobble–boulder cover may partly be the result of competition with other species, or an artifact of their ability to occupy higher-velocity habitats (Bisson et al. 1988). That is, steelhead may choose habitats based on characteristics other than cover type, and simply the predominance of cobble–boulder cover (more than 50% of sample points with that cover type) suggests the preference.

In winter, coho salmon commonly occupy off-channel ponds and alcoves, but some also remain in low-gradient tributaries or main-stem channels (Peterson and Reid 1984; Scarlett and Cederholm 1984; Nickelson et al. 1992). In channels, coho salmon tend to move closer to complex cover (e.g., rootwads) as discharge increases and water temperature decreases (Bustard and Narver 1975; Taylor 1988; McMahon and Hartman 1989). By contrast, age-0 and age-1 steelhead make little use of ponds and alcoves (Scarlett and Cederholm 1984), but like coho salmon also move closer to complex cover in winter (Bustard and Narver 1975; McMahon and Hartman 1989). Because the backwater units in our study are similar to both alcoves and off-channel ponds, it is no surprise that coho salmon were found there in large numbers in winter. It is also not surprising that age-0 coho salmon, age-0 steelhead, and age-1 or older steelhead all selected bank units, where most of the complex wood cover was located.

Among ocean-type fry, Chinook and chum salmon fry were captured in large numbers in edge units, whereas pink salmon were rarely captured. Chinook and chum salmon tended to occupy low-velocity areas and used all cover types available (aquatic plants, wood, and cobble–boulder), consistent with earlier observations. Chum salmon typically migrate in midchannel at night, but dur-

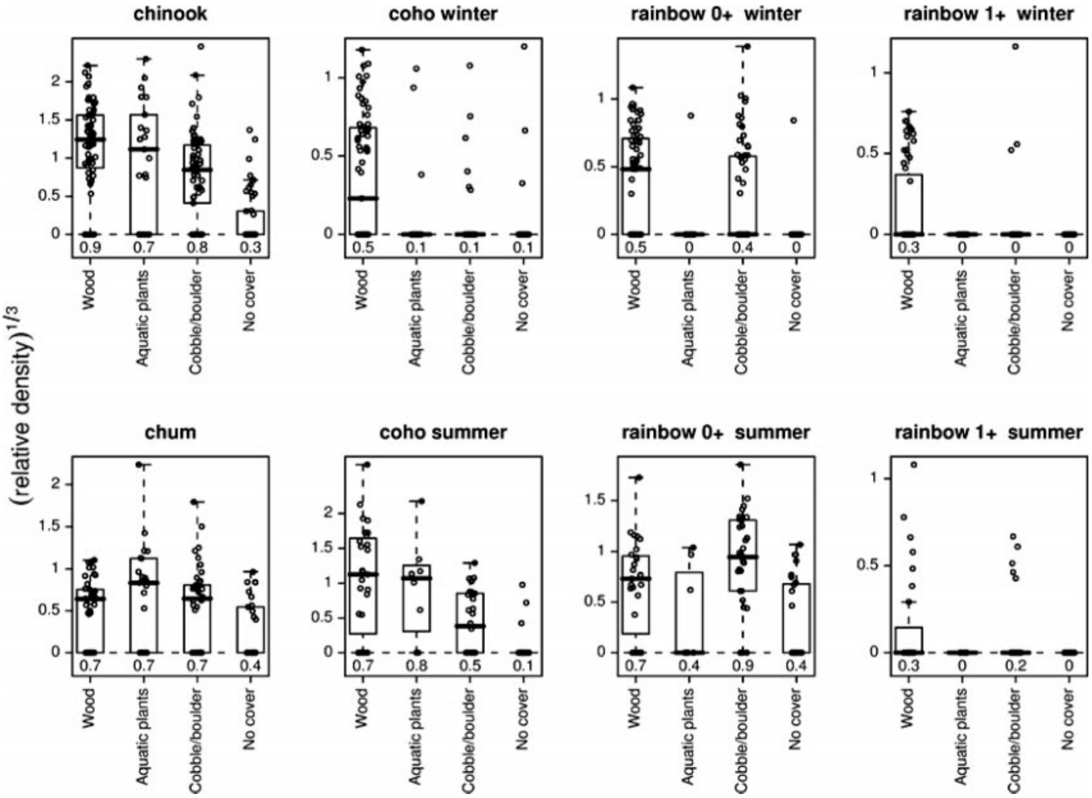

FIGURE 7.—Relative fish density (fish per point standardized by year) by species, age-class, and cover type. Numbers below *x*-axis indicate the proportion of points at which fish of that species were captured.

ing daylight exhibit an affinity for low velocities and shade (Salo 1991). Chinook fry also migrate mainly at night, but they occupy a wide range of edge habitats during daylight (Healey 1991). Peak abundance of Chinook fry was 1–2 months earlier than that of chum fry (see Figure 3). Age-0 pink salmon were not captured in significant numbers, probably because their typical behavior is to migrate downstream in the faster water of midchannel units without moving to edge habitats during daylight hours (Heard 1991).

Limitations of Sampling Method

There are substantial difficulties in attempting to sample fish in large river habitats. Habitats are too deep and fast to effectively snorkel or sample with blocknetting and multipass electrofishing methods, so we elected to electrofish from a stationary boat at fixed points, using a consistent electrofishing time at each point. Thus, although our data underestimate fish density at each point or within units, relative densities among unit types are valid as long as capture efficiency is similar across units. With no independent means of estimating populations within units, we were unable to assess potential differences in capture efficiency directly. However, our records of missed fish (i.e., fish stunned and seen but not netted during electrofishing) suggest that capture efficiencies did not vary significantly among edge units (77% to 83% netted) or cover types (71% to 84% netted). This suggests that our comparisons of juvenile salmonid abundance among edge units were probably not affected by differences in our ability to net stunned fish. On the other hand, we were unable to account for fish within sample areas that were either not stunned or stunned but never seen (i.e., fish that may have been hiding in the various cover types). As all edge-unit types had abundant cover but of different types, it is difficult to speculate how such errors might affect our results. For example, if we missed fish hiding in cobble cover in bars, some differences among unit types may be overestimated by our study. By contrast, if we missed fish in complex cover in banks and backwaters, our results probably underestimate differences among unit types.

How does the presence of the electrofishing boat alter juvenile salmon and trout behavior and position during sampling? Limited snorkel observations of fish movements in bank, bar, and backwater habitat (two units each) as the fully outfitted electrofishing boat was approaching indicated that fish remained within the grid-point area (approximately 2-m-diameter circle centered on the grid point) in bank and bar units, but sometimes moved out of the grid point area in backwater units. In bank and bar units, juvenile salmonids were oriented into the current and held a territory a short distance from cover. As the boat approached, fish sometimes moved closer to cover but remained within the grid-point area and otherwise did not move significantly. In backwater units, fish appeared less territorial and moved throughout the backwater, sometimes in schools. Thus, they were less often near cover before the boat approached and were more likely to move outside the grid-point sampling area as the boat neared their position. These observations indicate that fish captures in backwaters may be biased low relative to captures in banks and bars, and that our data may underestimate preference for backwaters. However, habitat selection by juvenile salmonids in our study was largely consistent with earlier field observations and experimental studies, suggesting that any effect of sampling method on habitat selection was not large enough to fundamentally alter our results.

Management Implications

One of the main limitations in estimating the impact of habitat losses on salmon populations is the lack of knowledge of juvenile salmon habitat use in large rivers (e.g., Beechie et al. 1994). This same lack of knowledge also inhibits our ability to predict how habitat restoration actions in large rivers might contribute to recovery of salmon listed under the Endangered Species Act (Beechie et al. 2002). This study identifies a suite of edge habitat types that effectively stratify microhabitat characteristics and seasonal abundances of juvenile salmonids. These habitat types are both (1) sensitive to anthropogenic change and (2) reasonable predictors of juvenile salmonid abundances. Therefore, they should be useful for evaluating effects of habitat change at the scale of reaches or watersheds, and may also help predict population responses to large-river restoration actions using habitat-specific life cycle models.

Acknowledgments

This study was supported in part by Pacific Coastal Salmon Recovery funds, the Pacific Salmon Treaty, and the U.S. Army Corps of Engineers, Seattle District. We thank Todd Wilbur, Stan Walsh, John Grossglass, Leonard Bill, Sr., Leonard Boome, and Joe McDonald for their assistance with data collection. Steve Riley, Aimee Fullerton, Tracy Hillman, John Buffington, and one anonymous reviewer provided helpful comments on the manuscript.

References

Abbe, T. B. 2000. Patterns, mechanics and geomorphic effects of wood debris accumulations in a forest river system. Doctoral dissertation. University of Washington, Seattle.

ASCE (American Society of Civil Engineers). 1975. Sedimentation engineering. ASCE, Manuals and Reports on Engineering Practice 54, New York.

Ayers, H. B. 1899. Washington Forest Reserve. Pages 283–313 *in* H. Gannett, editor. Nineteenth annual report of the United States Geological Survey, 1897–1898, part V. Forest reserves. U.S. Government Printing Office, Washington, D.C.

Beamer, E., and R. Henderson. 1998. Juvenile salmonid use of natural and hydromodified stream bank habitat in the mainstem Skagit River, northwest Washington. Skagit River System Cooperative, La Conner, Washington.

Beechie, T., E. Beamer, and L. Wasserman. 1994. Estimating coho salmon rearing habitat and smolt production losses in a large river basin, and implications for restoration. North American Journal of Fisheries Management 14:797–811.

Beechie, T. J., B. D. Collins, and G. R. Pess. 2001. Holocene and recent geomorphic processes, land use, and salmonid habitat in two north Puget Sound river basins. Pages 37–56 *in* J. M. Dorava, D. R. Montgomery, Betty B. Palcsak, F. A. Fitzpatrick, editors. Geomorphic processes and riverine habitat. American Geophysical Union, Washington, D.C.

Beechie, T. J., G. Pess, E. Beamer, G. Lucchetti, and R. E. Bilby. 2002. Role of watershed assessments in recovery planning for salmon. Pages 194–225 *in* D. Montgomery, S. Bolton, D. Booth, and L. Wall, editors. Restoration of Puget Sound rivers. University of Washington Press, Seattle.

Bisson, P. A., K. Sullivan, and J. L. Nielsen. 1988. Channel hydraulics, habitat use, and body form of juvenile coho salmon, steelhead, and cutthroat trout in streams. Transactions of the American Fisheries Society 117:262–273.

Bjornn, T. C., and D. W. Reiser. 1991. Habitat requirements of salmonids in streams. Pages 83–138 *in* W. R. Meehan, editor. Influences of forest and rangeland management on salmonid fishes and their habitats. American Fisheries Society, Special Publication 19, Bethesda, Maryland.

Blakley, A., B. Leland, and J. Ames. 2000. Washington state salmonid stock inventory: coastal cutthroat trout. Washington Department of Fish and Wildlife, Olympia.

Bustard, D. R., and D. W. Narver. 1975. Aspects of the winter ecology of juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of the Fisheries Research Board of Canada 32:667–680.

Fausch, K. D. 1993. Experimental analysis of microhabitat selection by juveniles steelhead (*Oncorhynchus mykiss*) and coho salmon (*O. kisutch*) in a British Columbia stream. Canadian Journal of Fisheries and Aquatic Sciences 50:1198–1207.

Fetherston, K. L., R. J. Naiman, and R. E. Bilby. 1995. Large woody debris, physical process, and riparian forest development in montane river networks of the Pacific Northwest. Geomorphology 13:133–144.

Gannett, H. 1899. Nineteenth annual report of the United States Geological Survey, 1897–1898, part V. Forest reserves. U.S. Government Printing Office, Washington, D.C.

Garland, R. D., K. F. Tiffan, D. W. Rondorf, and L. O. Clark. 2002. Comparison of subyearling fall chinook salmon's use of riprap revetments and unaltered habitats in Lake Wallula of the Columbia River. North American Journal of Fisheries Management 22:1283–1289.

Healey, M. C. 1991. Life history of Chinook salmon (*Oncorhynchus tshawytscha*). Pages 311–394 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Heard, W. R. 1991. Life history of pink salmon (*Oncorhynchus gorbuscha*). Pages 119–230 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Hillman, T. W., J. S. Griffith, and W. S. Platts. 1987. Summer and winter habitat selection by juveniles chinook salmon in a highly sedimented Idaho stream. Transactions of the American Fisheries Society 116:185–195.

Knudsen, E. E., and S. J. Dilley. 1987. Effects of riprap bank reinforcement on juveniles salmonids in four western Washington streams. North American Journal of Fisheries Management 7:351–356.

Kruzic, L. M., D. L. Scarnecchia, and B. B. Roper. 2001. Comparison of midsummer survival and growth of age-0 hatchery coho salmon held in pools and riffles. Transactions of the American Fisheries Society 130:147–154.

Lunetta, R. S., B. L. Cosentino, D. R. Montgomery, E. M. Beamer, and T. J. Beechie. 1997. GIS-based evaluation of salmon habitat in the Pacific Northwest. Photogrammetric Engineering and Remote Sensing 63(10):1219–1229.

McMahon, T. E., and G. F. Hartman. 1989. Influence of cover complexity and current velocity in winter habitat use by juvenile coho salmon (*Oncorhynchus kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 46:1551–1557.

Montgomery, D. R., B. D. Collins, J. M. Buffington, and T. B. Abbe. 2003. Geomorphic effects of wood in rivers. Pages 21–47 *in* S. Gregory, K. Boyer, and A. M. Gurnell, editors. The ecology and management of wood in world rivers. American Fisheries Society, Bethesda, Maryland.

Munzel, U., and L. A. Hothorn. 2001. A unified approach to simultaneous rank test procedures in the unbalanced one-way layout. Biometrical Journal 43:553–569.

Murphy, M. L., J. Heifetz, J. F. Thedinga, S. W. Johnson, and K. V. Koski. 1989. Habitat utilization by juvenile Pacific salmon (*Oncorhynchus*) in the glacial Taku River, southeast Alaska. Canadian Journal of Fisheries and Aquatic Sciences 46:1677–1685.

Nickelson, T. E., M. F. Sollazzi, S. L. Johnson, and J. D. Rogers. 1992. Effectiveness of selected stream improvement techniques to create suitable summer and winter rearing habitat for juvenile coho salmon in Oregon coastal streams. Canadian Journal of Fisheries and Aquatic Sciences 49:790–794.

Peters, R. J., B. R. Missildine, and D. L. Low. 1998. Seasonal fish densities near river banks stabilized by various stabilization methods: first year report of the Flood Technical Assistance Project. U.S. Fish and Wildlife Service, Lacey, Washington, D.C.

Peterson, N. P., and L. M. Reid. 1984. Wall-base channels: their evolution, distribution, and use by juvenile coho salmon in the Clearwater River, Washington. Pages 215–225 *in* J. M. Walton and D. B. Houston, editors. Proceedings of the Olympic Wild Fish Conference. Peninsula College, Port Angeles, Washington.

Pinheiro, J. C., and D. M. Bates. 2000. Mixed-effects models in S ans S-Plus. Springer-Verlag, New York.

Rosenfeld, J., M. Porter, and E. Parkinson. 2000. Habitat factors affecting the abundance and distribution of juveniles cutthroat trout (*Oncorhynchus clarki*) and coho salmon (*O. Kisutch*). Canadian Journal of Fisheries and Aquatic Sciences 57:766–774.

Salo, E. O. 1991. Life history of chum salmon (*Oncorhynchus keta*). Pages 231–310 *in* C. Groot and L. Margolis, editors. Pacific salmon life histories. University of British Columbia Press, Vancouver.

Scarlett, W. J., and C. J. Cederholm. 1984. Juvenile coho salmon fall−winter utilization of two small tributaries of the Clearwater River, Jefferson County, Washington. Pages 227–242 *in* J. M. Walton and D. B. Houston, editors. Proceedings of the Olympic Wild Fish Conference. Peninsula College, Port Angeles, Washington.

Shirvell, C. S. 1990. Role of instream rootwads as juvenile coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*O. mykiss*) cover habitat under varying streamflows. Canadian Journal of Fisheries and Aquatic Sciences 47:852–861.

Sullivan, K. 1986. Hydraulics and fish habitat in relation to channel morphology. Doctoral dissertation. Johns Hopkins University, Baltimore, Maryland.

Sumioka, S. S., D. L. Kresch, and K. D. Kasnick. 1998. Magnitude and frequency of floods in Washington.

U.S. Geological Survey, Water-Resources Investigations Report 97-4277, Denver.

Taylor, E. B. 1988. Water temperature and velocity as determinants of microhabitats of juvenile chinook and coho salmon in a laboratory stream channel. Transactions of the American Fisheries Society 117: 22–28.

WDF (Washington Department of Fisheries), WDW (Washington Department of Wildlife), and Western Washington Treaty Indian Tribes. 1993. Washington State salmon and steelhead stock inventory. Olympia, Washington.

WDFW (Washington Department of Fish and Wildlife). 1998. Washington State salmonid stock inventory: bull trout/Dolly Varden. Washington Department of Fish and Wildlife, Olympia.

Ward, D. L., A. A. Nigro, R. A. Farr, and C. J. Knutsen. 1994. Influence of waterway development on migrational characteristics of juvenile salmonids in the lower Willamette River, Oregon. North American Journal of Fisheries Management 14:362–371.

Weigand, D. 1991. Effect of gravel scalping on salmonid rearing habitats in the Puyallup River. Master's thesis. University of Washington, Seattle.

Williams, J. R., H. E. Pearson, and J. D. Wilson. 1985. Streamflow statistics and drainage basin characteristics for the Puget Sound Region, Washington, volume II. Eastern Puget Sound from Seattle to the Canadian border. U.S. Geological Survey, Open File Report 84-144-B, Lakewood, Colorado.

Williams, R. W., R. M. Laramie, and J. J. Ames. 1975. A catalog of Washington streams and salmon utilization, volume 1. Puget Sound. Washington Department of Fisheries, Olympia.

Zar, J. H. 1996. Biostatistical analysis, 3rd edition. Prentice-Hall, Upper Saddle River, New Jersey.