CHAPTER 2

Characterizing Habitat for and Selection by Juvenile Anadromous Salmonids at Multiple Spatial Scales Over Multiple Years (1988-1994) in the Elk River, Oregon

K.M. Burnett
U.S.D.A. Forest Service
Pacific Northwest Research Station
and Department of Fisheries and Wildlife
Oregon State University
Corvallis, Oregon

G.H. Reeves
U.S.D.A. Forest Service
Pacific Northwest Research Station
Corvallis, Oregon

and R.E. Gresswell
U.S.G.S. Biological Resources Division
Forest and Rangeland Ecosystem Science Center
Corvallis, Oregon

ABSTRACT

Although management and study of freshwater ecosystems can benefit from multi-scale analysis, research has generally focused on only the shortest temporal and the finest spatial scales. Habitat availability and selection were examined for the juvenile anadromous salmonid assemblage in the Elk River, Oregon at multiple spatial scales over 7 years. Means of few instream habitat characteristics differed among years at either the stream system or valley segment scales. Within individual years, most habitat characteristics differed between the two stream system types (i.e., the mainstem and tributaries of Elk River) but not among the three valley segment types (i.e., unconstrained valleys, alluviated canyons, and constrained canyons). Habitat selection was quantified at the stream system, valley segment, and channel unit scales by selection ratios and confidence intervals calculated with bootstrapping methods. Unconstrained valleys in the tributaries and pools in the mainstem were often selected by ocean-type chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), and cutthroat trout (*O. clarki*) but were often avoided by steelhead (*O. mykiss*). All species selected pools in the tributaries. Steelhead was the only species for which stream discharge or water temperature variables explained a significant proportion of the interannual variation in selection ratios. Intraspecific competition may have influenced selection by chinook salmon for constrained canyons in the mainstem, and competition with this species may have influenced selection for tributaries by coho salmon. Had this study been of shorter duration, one or two years as is common when relating fish and their habitat, interannual variation in selection ratios was often sufficient to have altered conclusions depending upon the years examined. Because habitat types were selected at each spatial scale, salmon conservation strategies that protect and restore habitat at multiple spatial scales may have the highest likelihood of success.

INTRODUCTION

Application of hierarchy theory has become an important theme in ecology over the past two decades. The theory stems naturally from a recognition that ecosystems are scaled in time and space with subsystems arranged as nested hierarchies (O'Neill 1989; Allen and Hoekstra 1992). Each level of the hierarchy is differentiated by specific process rates and structures. Higher levels are driven by slower processes that generate patterns at coarser spatial and longer temporal scales, while lower levels are driven by faster processes that generate patterns at finer spatial and shorter temporal scales. The concept of constraint is an important consequence of hierarchical arrangement; that is, each level is limited from above by its biotic and abiotic context and from below by its components (O'Neill 1989). To effectively characterize ecosystems, it is necessary to consider multiple levels of the hierarchy (Allen and Hoekstra 1992): 1) the focal level or the level of interest, 2) levels above to identify context and relevance, and 3) levels below to identify mechanisms. Methods to translate explanation and prediction across scales may be 'top-down' in which understanding at finer scales derives from system context or 'bottom-up' in which fine-scale measurements are summed over broad scales, with the caution that heterogeneity may exert non-linear influences (Turner et al. 1989).

Management and study of freshwater ecosystems have been influenced by hierarchy theory. Numerous issues in stream ecology were examined across two or more spatial scales, from regional to local. These include controls on fish diversity (e.g., Poff 1997; Angermeier and Winston 1998); individual and population distribution and regulation (e.g., Fausch 1998; Torgersen et al. 1999; Labbe and Fausch 2000); fish habitat classification, conservation, and restoration (e.g., Frissell et al. 1986; Lewis et al. 1996; Rabeni and Sowa 1996); land-use effects on water quality, biotic integrity, and habitat condition (e.g., Hunsaker and Levine 1995; Roth et al. 1996); and modeling, planning, and managing of salmonids (e.g., FEMAT 1993; Lee and Grant 1995; Armstrong et al. 1998). Baxter and Hauer (2000) demonstrated multi-scale hierarchical analyses and the unique insights that can be obtained. Numbers of redds for bull trout (*Salvelinus confluentus*) in tributaries of the Swan River basin, Montana were positively correlated with areas of groundwater upwelling at the three coarsest spatial scales examined but with areas of downwelling at the finest spatial scale. Their findings indicated that, although hyporheic exchange was important at all four spatial scales, geomorphic features and mechanisms affecting bull trout spawning selection and use differed among scales. Focus on scale may particularly benefit aquatic system applications because physical and biological components may scale more similarly in aquatic systems than in terrestrial systems where biological features frequently dominate structure and mediate physical influences (Wiens 1989).

Despite advantages of hierarchical analysis, most research on salmonid distribution and abundance in streams has been at fine spatial and short temporal scales (for discussion see Platts and Nelson 1988; Folt et al. 1998). Wiens (1989) stressed the importance of matching the scale of inquiry to the question. Investigations targeting finer scales (i.e., channel unit (100-101 m) or below and <1 year) may be appropriate for many questions, such as how habitat mediates interactions between a fish and conspecifics. For other questions, particularly those related to freshwater habitat influences on population persistence, relevant information is most likely to derive from coarser spatial scales (i.e., watershed (103-104 m) or above and >10 years) (Reeves et al. 1995). Most fish-habitat research has had a temporal extent of #2 years and a spatial extent of reach(es) (101-102 m) or channel unit(s).

Studies over multiple years can be valuable when relating fish and their habitat. Population abundances of stream fish and factors influencing these abundances may fluctuate from year to year (Platts and Nelson 1988; Grossman et al. 1990). An extended investigation can reveal interannual patterns and provide a context for interpreting the results from any one year. Transferability of fish habitat models and results to other years may be limited by the failure to account for interannual variation. Documenting and understanding temporal variability can also aid in designing programs to monitor trends. The effectiveness of conservation strategies may be improved if the suite of habitat elements affecting fish over longer periods is known.

As abundances of many Pacific salmon and trout populations (*Oncorhynchus spp.*) declined near or to extinction (Nehlsen et al. 1991), knowledge gaps resulting from fine-scale studies became obvious and a watershed perspective was often recommended in strategies to understand and reverse these trends (Doppelt et al. 1993; FEMAT 1993; NRC 1996). However, relatively few investigations examined relationships between fish and their habitats throughout a watershed (e.g., Dolloff et al. 1994; Roper et al. 1994; Scarnecchia and Roper 2000). Longer-term studies (i.e., one or more generations) over the spatial extent of a watershed are even less common (e.g., but see Reeves et al. 1997).

Use by an organism of habitat at any spatial scale may reflect availability of, rather than selection for, a particular habitat type; therefore, metrics to quantify selection were developed (Manly et al. 1993). Selection by salmonids in freshwater has been assessed at different spatial scales (e.g., Dambacher 1991; Nislow et al. 1999; Torgersen et al. 1999), but most often at the reach scale or below. A variety of habitat selection indices have been used in such studies [e.g., Chesson's alpha (Chesson 1978), Jacobs D (Jacobs 1974), and Ivlev's electivity index (Ivlev 1961)]. Manly et al. (1993) articulated an integrated statistical theory of habitat selection based on a resource selection function that estimated the probability of a given habitat being used. Univariate and multivariate methods were developed to calculate values of resource selection functions and their normally approximated standard errors. Erickson et al. (1998) demonstrated bootstrapping methods to estimate a resource selection function and standard errors for moose winter habitat selection. Such an approach can overcome limitations of the normal approximation but has not been applied to estimate salmonid habitat selection at any spatial scale.

The goal of this research was to understand summer habitat availability and selection for a juvenile salmonid assemblage over multiple years and at multiple spatial scales in a watershed. Specific objectives were to: 1) describe inter-annual variability over 7 years (1988-94) for fish-habitat characteristics in the Elk River, Oregon, USA (Fig. 2.1) summarized at the stream system and valley segment scales; 2) compare fish-habitat characteristics in each year between stream system types and between valley segment types; 3) evaluate habitat selection in each year by juvenile ocean-type chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), coastal cutthroat trout (*O. clarki*) and steelhead (*O. mykiss*) at the stream system, valley segment, and channel unit scales (Fig. 2.2) using bootstrapping techniques to estimate selection ratios and con-
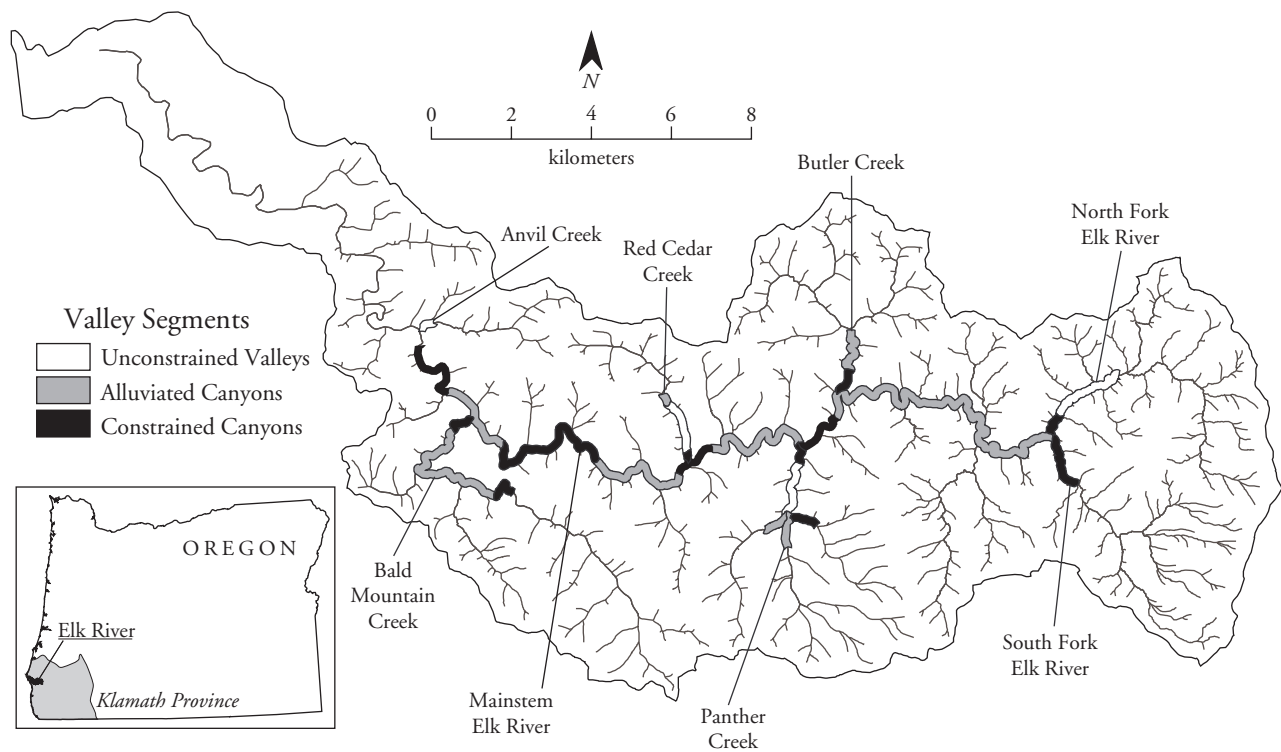
Figure 2.1. Location and map of the Elk River, Oregon with valley segments identified for anadromous fish-bearing sections of the mainstem and its tributaries.

fidence intervals; and 4) explain interannual variation in species-specific selection with environmental conditions and salmonid densities as potential indicators of competition.

METHODS

Study Area and Salmonid Community

Elk River is located in southwestern Oregon, USA (Fig. 2.1). The mainstem flows primarily east to west, entering the Pacific Ocean just south of Cape Blanco (42°5' N latitude and 124°3' W longitude). The Elk River basin (236 km²) is in the Klamath Mountains physiographic province (Franklin and Dyrness 1988) and is similar to other Klamath Mountain coastal basins in climate, land form, vegetation, land use, and salmonid community (Chapter 4). The upper mainstem of Elk River (i.e., upstream of Anvil Creek) and its tributaries (Fig. 2.1) provide spawning and rearing habitat for native ocean-type chinook salmon, coho salmon, coastal cutthroat trout, and winter-run steelhead. A small population of chum salmon (*O. keta*) occurs with these species in the lower mainstem. The Elk River is highlighted in both state and federal strategies to protect and restore salmonids (USDA and USDI 1994; State of Oregon 1997).

Valley Segments

Valley segments encompass sections of stream accessible to anadromous salmonids. Accessibility was determined in the field based on the absence of physical features considered to be barriers for adult fish migrating upstream. The type and boundaries of each valley segment were determined through field reconnaissance. Valley segments were classified as one of three types (Table 2.1) (adapted from Frissell 1992). Unconstrained valleys (UV) in the upper Elk River basin occur only in the tributaries. These contain stream channels that are generally lower gradient and less confined (i.e., valley floor width >2 x active channel width) than other valley segments in the tributaries. Any confinement is imposed by channel-adjacent terraces. Constrained canyons (CC) contain stream channels that are relatively high gradient for the stream system type where they occur and are confined by valley walls (i.e., valley floor width - active channel width). Alluviated canyons (AC) contain stream channels that are intermediate in gradient and confinement to those in the former two valley segment types for the stream system type where they occur. Twenty-five valley segments were identified and mapped (Table 2.1 and Fig. 2.1); eight are in the upper mainstem between Anvil Creek and the confluence of the North and South Forks of Elk River, and 17 are in the tributaries. The mainstem is a 5th order channel, and surveyed tributaries are either 3rd or 4th order channels (Strahler 1957). Drainage area of valley segments did not differ significantly (P>0.05) by valley segment type in either the mainstem or tributaries.

Channel Unit Features and Juvenile Salmonid Densities

Data for channel units and juvenile salmonid abundance were collected in the Elk River basin each year from 1988 to 1994. Annual data collection began in late July to mid-August and continued approximately three weeks. Data were collected for twenty-three valley segments in 29 km of the upper mainstem and 20 km of the tributaries for every year. Surveys included an additional 0.5 km in Anvil Creek for 1991-1994 and 0.9 km in the East Fork of Panther Creek for 1990 and 1992-1994.
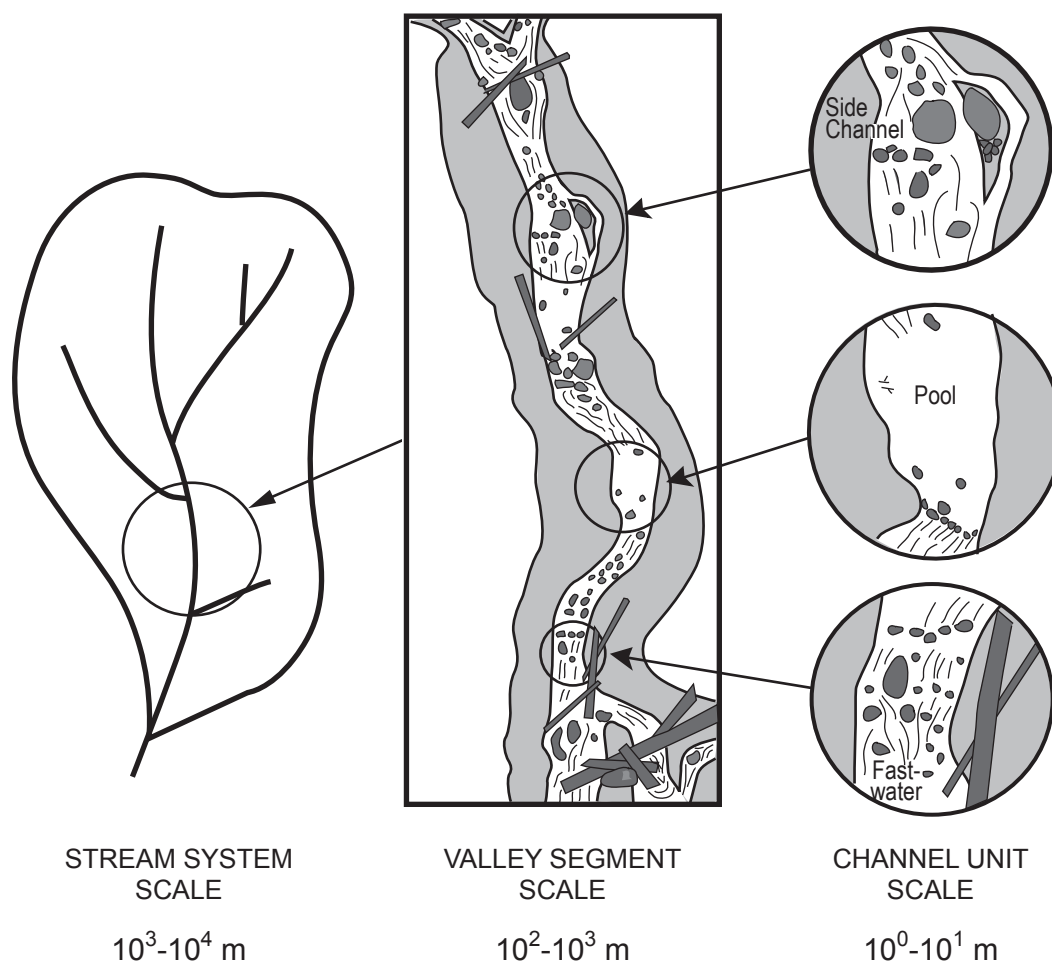
Figure 2.2. Spatial scales examined in the Elk River, Oregon. Linear spatial scale approximates units in 3rd-5th order channels (figure adapted from Frissell et al. 1986).

Each channel unit was classified by type [as pool, fastwater (Hawkins et al. 1993), or side channel (<10% flow)]. The length, mean wetted width, and mean depth of each channel unit was estimated using the method of Hankin and Reeves (1988). Channel units were at least as long as the estimated mean active channel width (10^0-10^1 m). Dimensions were measured for approximately 15% of all channel units. A calibration ratio was derived from the subset of channel units with paired measured and estimated values. Separate calibration ratios were developed annually for each person estimating channel unit dimensions. All estimated dimensions were multiplied by the appropriate calibration ratio, and only calibrated estimates were analyzed. For each channel unit, the dominant substrate by percent area (defined as small gravel 3-10 mm, large gravel 11-100 mm, cobble 101-299 mm, boulder >300 mm, and bedrock) was estimated visually and the number of wood pieces (≥3 m long and ≥0.3 m diameter) was counted. Maximum depth of each pool was measured if ≤1 m and was estimated otherwise.

A systematic sample of channel units was selected annually for estimating fish abundance. Species were chinook and coho salmon that emerged the previous spring (i.e., age 0) and of steelhead and cutthroat trout that were thought to have reared in the basin for at least a year (i.e., ≥ age 1). Every 4th pool, 10th fastwater habitat, and 2nd side channel were chosen annually using an independent random start for each channel unit type in the mainstem and in

each tributary. Abundance estimates were derived from fish counted while snorkeling in these selected units (Hankin and Reeves 1988) between 10:00 AM and 4:00 PM. Snorkeling counts were not calibrated with electroshocking estimates of fish abundance in a departure from Hankin and Reeves (1988). Consequently, estimates from snorkeling counts were assumed to be negatively biased (Rodgers et al. 1992; Thompson and Lee 2000) but to provide measures of relative abundance. Valley segments Anvil Creek 1 from 1988-1990, Red Cedar Creek 3 from 1988, E. Fork Panther Creek 1 from 1988,1989, and 1991, and Mainstem 8 from 1990 were excluded from analyses because fish data were not collected in these years. Valley segments Bald Mountain Creek 2 and 3 were excluded from all analyses for chinook and coho salmon because a barrier prevented access by adults of these species.

Habitat and fish abundance data for each channel unit were geo-referenced to the digital stream network with Dynamic Segmentation in ARC/INFO[1] (Byrne 1996). A separate channel unit coverage was created for each year that data were collected. Geo-referenced channel unit data were summarized for each year to derive channel unit features and estimates of fish density for subsequent analyses. Channel unit data by type were summarized for valley segments to

[1]The use of trade or firm names is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.

Valley Segment	Valley segment type	Length (m)	Mean (SD) % gradient	Drainage area (ha)
Mainstem 2	CC	1,977	1.3 (1.7)	18,286
Mainstem 4	CC	4,887	0.8 (1.0)	14,925
Mainstem 6	CC	1,342	0.6 (0.9)	13,328
Mainstem 8	CC	1,531	0.9 (0.1)	9,254
Mean (SD)			0.9 (0.3)	
Mainstem 3	AC	2,248	0.2 (0.3)	17,920
Mainstem 5	AC	2,923	0.8 (0.7)	14,203
Mainstem 7	AC	3,471	0.7 (0.8)	12,397
Mainstem 9	AC	10,629	0.9 (0.8)	7,226
Mean (SD)			0.7 (0.3)	
Anvil Creek 1	UV	532	0.1 (0.1)	687
North Fork Elk River 2	UV	2,511	1.6 (2.9)	2,302
Panther Creek 2	UV	1,697	2.3 (2.0)	2,275
Red Cedar Creek 2	UV	1,418	2.1 (1.9)	736
Mean (SD)			1.5 (0.9)	
Bald Mountain Creek 2	AC	4,251	2.4 (2.7)	2,678
Butler Creek 2	AC	1,588	1.2 (1.8)	1,724
Panther Creek 3	AC	1,165	1.9 (1.9)	928
W. Fork Panther Creek	AC	806	2.8 (2.7)	574
Red Cedar Creek 3	AC	419	3.3 (3.4)	564
Mean (SD)			2.3 (0.7)	
Bald Mountain Creek 1	CC	826	3.1 (3.8)	2,715
Bald Mountain Creek 3	CC	965	2.3 (2.6)	1,510
Butler Creek 1	CC	763	3.3 (4.3)	1,752
North Fork Elk River 1	CC	648	3.3 (4.9)	2,456
Panther Creek 1	CC	727	0.6 (0.8)	2,346
E Fork Panther Creek 1	CC	888	1.8 (3.2)	569
Red Cedar Creek 1	CC	344	4.7 (3.3)	743
South Fork Elk River 1	CC	1,544	5.6 (6.2)	1,988
Mean (SD)			3.2 (1.6)	

Table 2.1. Characteristics of mainstem and tributary valley segments in the Elk River, Oregon. Valley segments are numbered starting downstream. Valley segment types are unconstrained valleys (UV), alluviated canyons (AC), and constrained canyons (CC) (adapted from Frissell et al. 1992). Mean percent gradient and drainage area were derived from US Geological Survey (USGS) 30 m digital elevation models (DEM) (Chapters 3 and 4).

obtain channel unit features of mean length (m), mean wetted width (m), mean maximum depth of pools (m); mean volume (m^3); mean density of wood (number of pieces/100 m); percent area; frequency (number/km); and percent area with bedrock as dominant substrate, boulders as dominant substrate, cobble as dominant substrate, large gravel as dominant substrate, and small gravel as dominant substrate. Total relative fish density (number/100 m^2) by species and associated standard errors, stratified by habitat type (Cochran 1977), were estimated for each year over the entire basin (Table 2.2). Estimates were also calculated for the mainstem and tributaries separately (Table 2.3).

Stream Discharge and Water Temperature

Stream discharge data were obtained from the USGS gauge (no. 14327250) on the mainstem of Elk River at the State of Oregon Salmon Hatchery. Water temperature data were recorded continuously by a thermograph at the same location. Because of their potential to influence habitat and selection, the following four variables were estimated for each sampled year (Table 2.4): 1) maximum daily average stream discharge during spring (March 21-June 20); 2) annual minimum daily average stream discharge for the water year (October 1-September 30); 3) maximum daily water temperature during summer (June 21-September 20); and 4) annual maximum daily average stream discharge for the water year (October 1-September 30).

Selection by Juvenile Salmonids

Selection was evaluated for juveniles of each salmonid species at three spatial scales in the Elk River basin using a selection function (Manly et al. 1993) calculated with nonparametric bootstrapping methods (Manly 1998; Erickson et al. 1998). In each of seven years for each species, selection functions were developed for each of the two types at the stream system scale (mainstem and tributaries); for each of the three types at the valley segment scale (unconstrained valleys, alluviated canyons, and constrained canyons) in the mainstem and in the tributaries; and for each of the three types at the channel unit scale (pools, fastwater, and side channels) in the mainstem and in the tributaries. Selection functions reduce to selection ratios when habitat is characterized by a single categorical variable (Manly et al. 1993), which in this study was the type at each spatial scale. For each species, type, and stratum (i.e., the stratum is the year at the stream system scale and is the year and mainstem or tributaries at the valley segment and channel unit scales), 5,000 samples were drawn with replacement from the original data. Sample size was equal to the number of snorkeled units for that species, type, and stratum. A snorkeled unit, instead of a single fish, was considered an observation because the presence of an individual fish may not have been independent of conspecifics. The total number of fish observed and the total area snorkeled were determined for each of the 5,000 samples for each species, type and stratum. For each species and stratum, selection ratios for type were calculated (Manly et al. 1993):

$$(1) \qquad w_i = o_i / p_i$$

where i was the type, o_i was the number of fish observed in type i divided by the total number of fish observed in all types at that scale, and p_i was the area snorkeled of type i divided by the total area snorkeled of all types at that scale (Table 2.5). The pairwise difference between selection ratios ($w_i - w_j$) was calculated also.

Means and confidence intervals were generated for selection ratios and for their pairwise differences from the bootstrapped sample distributions for each species, type, and stratum. Hereafter, selection ratio refers to a mean calculated from annual bootstrapped estimates. Confidence intervals were developed with the percentile method, the simplest and most commonly used approach (Dixon 1993), by determining the $100*(\alpha/2)$ and the $100*(1-\alpha/2)$ percentiles of each bootstrapped sample distribution. We used $\alpha=0.1$ and a Bon-

Year	Chinook salmon density	Coho salmon density	Cutthroat trout density	Steelhead density
1988	8.24 (1.00)	0.04 (0.01)	0.35 (0.05)	4.76 (0.33)
1989	15.18 ((1.34)	0.02 (0.00)	0.34 (0.04)	6.86 (0.45)
1990	1.49 (0.28)	0.00 (0.00)	1.39 (0.21)	8.26 (0.76)
1991	3.85 (0.50)	0.33 (0.16)	0.51 (0.12)	8.20 (0.66)
1992	0.66 (0.15)	0.03 (0.01)	0.47 (0.05)	8.21 (0.62)
1993	1.92 (0.48)	0.15 (0.05)	0.23 (0.03)	7.38 (0.44)
1994	2.47 (0.31)	1.13 (0.15)	0.26 (0.03)	8.74 (0.62)

Table 2.2. Estimated total relative density (standard error) of juvenile salmonids in the Elk River, Oregon (1988-1994). Density is expressed as the number of fish per 100 m^2.

ferroni adjustment when appropriate. The lower and upper confidence limits were: 1) the 2.5 and 97.5 percentiles for the two selection ratios at the stream system scale, and the 5 and 95 percentiles for the single pairwise difference between these selection ratios; and 2) the 1.67 and 98.3 percentiles for the three selection ratios and for the three pairwise differences between these selection ratios at the valley segment scale and at the channel unitscale. Although the nominal confidence interval calculated with the percentile method may be inaccurate when the estimated parameter is not the median of the bootstrapped distribution, this was rarely the case for selection ratios or their pair-wise differences.

Selection ratios may range from zero to infinity with a value of one implying no selection. When the confidence interval did not contain the value of one, the null hypothesis was rejected that juveniles of that salmonid species used the habitat type in proportion to its availability (Manly et al. 1993). Consequently, a selection ratio that was significantly >1 indicated selection for the type, and a selection ratio that was significantly <1 indicated avoidance. Similarly, when the confi-dence interval for the pairwise difference between selection ratios did not contain zero, the null hypothesis of no difference between the selection ratios was rejected.

Statistical Analysis

Statistical analyses were performed with SAS/STAT statistical software (Version 6.12, 1997, SAS Institute Inc., Cary, NC) with

significance determined at α=0.05. One-way ANOVA was used to compare means of channel unit features among years for each stream system type (mainstem and tributaries) and each valley segment type (unconstrained valleys, alluviated canyons, and un-constrained canyons). A Bonferroni adjustment was applied for the twenty-one post-hoc comparisons of means between years. Means of channel unit features were compared between the mainstem and tributaries for each year using one-way ANOVA. Means of channel unit features were compared among valley segment types for each year using analysis of covariance (ANCOVA) with drainage area as the covariate. Homogeneity of regression slopes was evaluated, and all cases met this assumption. Reported means were adjusted for the covariate when appropriate. A Bonferroni correction was applied for the three post-hoc comparisons of means between valley segment types in the tributaries.

The presence of outliers and the assumption of normality for each group were assessed by examining normal probability and box plots and with the Shapiro-Wilk test statistic. Homogeneity of variance among groups was evaluated with Levene's test (Snedecor and Cochran 1980). Parametric assumptions were met in ANCOVA for means comparisons of each channel unit feature among valley segment types. Parametric assumptions were not met in ANOVA for within- and among-year means comparisons of a few channel unit features. Identified problems could not be corrected by transforming variables, thus medians for these channel unit features were compared with one-way ANOVA on ranked data.

Relationships between selection ratios and independent variables were evaluated with linear regression. Assumptions of constant variance and normally distributed regression residuals were evaluated with predicted versus residual plots and normal probability and box plots. A value of the Cook's D statistic >2 was used to screen for potential outliers and influential observations. Selection ratios were regressed with stream discharge and water temperature variables to explain interannual variation. Because maximum daily average stream discharge during spring could influence whether juvenile salmonids were found in the mainstem or tributaries later in the year, this variable was regressed with selection ratios only at the stream system scale. To examine potential influence of intra- and interspecific competition, selection ratios for types selected at each spatial scale were regressed with the densities of each species. Selection ratios at the stream system scale were regressed with the estimated total relative fish density of each species in the basin. Selection ratios at the valley segment and channel unit scales were regressed with

Table 2.3. Estimated total relative density (standard error) of juvenile salmonids in the mainstem and tributaries of the Elk River, Oregon (1988-1994). Density is expressed as the number of fish per 100 m^2.

Year	Chinook salmon mainstem	tributaries	Coho salmon mainstem	tributaries	Cutthroat trout mainstem	tributaries	Steelhead mainstem	tributaries
1988	10.1 (1.3)	0.6 (0.20)	0.05 (0.01)	0.00 (0.00)	0.35 (0.06)	0.34 (0.05)	4.6 (0.4)	5.3 (0.4)
1989	18.5 (1.7)	1.90 (0.30)	0.02 (0.01)	0.00 (0.00)	0.33 (0.05)	0.37 (0.05)	7.3 (0.6)	5.6 (0.5)
1990	1.9 (0.3)	0.10 (0.04)	0.00 (0.00)	0.00 (0.00)	1.44 (0.28)	1.26 (0.18)	8.1 (0.9)	8.7 (1.5)
1991	4.7 (0.6)	0.30 (0.08)	0.40 (0.20)	0.03 (0.01)	0.63 (0.17)	0.21 (0.03)	8.8 (0.9)	6.6 (0.4)
1992	0.8 (0.2)	0.04 (0.02)	0.00 (0.00)	0.15 (0.07)	0.36 (0.06)	0.73 (0.11)	9.0 (0.9)	6.3 (0.4)
1993	2.4 (0.6)	0.11 (0.02)	0.13 (0.07)	0.20 (0.04)	0.25 (0.04)	0.19 (0.03)	8.0 (0.6)	5.8 (0.4)
1994	3.0 (0.4)	0.40 (0.05)	0.77 (0.16)	2.57 (0.42)	0.25 (0.05)	0.29 (0.04)	9.3 (0.8)	7.2 (0.4)

Year	Maximum daily average stream discharge during spring (m^3/s)	Annual minimum daily average stream discharge (m^3/s)	Maximum daily water temperature during summer (C^o)	Annual maximum daily average stream discharge (m^3/s)
1988	30.80	0.81	20.89	285.60
1989	65.52	1.01	20.33	181.16
1990	34.72	0.98	20.33	192.36
1991	32.48	0.98	20.89	161.84
1992	83.16	0.84	20.89	112.28
1993	171.92	0.76	20.33	171.92
1994	31.36	0.76	19.78	118.16

Table 2.4. Estimated stream discharge and water temperature in the Elk River, Oregon (1988-1994). Data were obtained from the USGS gage (no. 14327250) on the mainstem of Elk River at the State of Oregon Salmon Hatchery and from a thermograph at the same location. Annual daily average stream discharges are for the water year (October 1-September 30).

the estimated total relative fish density of each species in either the mainstem or tributaries. Residuals from linear regressions with fish density data were typically not normally distributed. Thus, rank regression (Inman and Conover 1979) was used to develop all relationships between juvenile salmonid densities and selection ratios. Regressions were not conducted with coho salmon in the tributaries at the valley segment or channel unit scales because degrees of freedom (df = 3) were considered too few to yield meaningful results.

RESULTS

Habitat Characterization

Stream system scale

In general, means of channel unit features did not differ significantly among years in either the mainstem or tributaries (Table 2.6). Mean density of wood in pools, frequency of pools, and percent area of fastwater with large gravel as dominant substrate differed significantly among years in the mainstem. In the tributaries, significant among-year differences were observed for the frequency of pools,

percent area of pools with boulders as dominant substrate, and percent area of fastwater with large gravel as dominant substrate.

Annual means of several channel unit features differed consistently between the two stream system types (Table 2.6). Means of channel unit features describing the dimensions of pools (mean length, mean wetted width, mean maximum depth, and mean volume) and the percent area of pools were significantly greater for the mainstem than for the tributaries in each year. In contrast, the mean density of large wood in pools and the frequency of pools were significantly greater for the tributaries than for the mainstem in each year. Results of annual means comparisons between the mainstem and tributaries for substrate characteristics were less consistent, and any differences were often less statistically significant than for other channel unit characteristics.

Valley segment scale

Few channel unit features differed significantly among years for valley segment types in either the mainstem or tributaries. Means for the frequency of pools, the percent area of pools, and the percent area of fastwater with large gravel as dominant substrate differed significantly among years for alluviated canyons in the mainstem

Year	% Sampled area of basin in		% Sampled area of mainstem in			% Sampled area of tributaries in			% Sampled area of mainstem in			% Sampled area of tributaries in		
	mainstem	tributaries	UV	AC	CC	UV	AC	CC	pools	FW	SC	pools	FW	SC
1988	73	27	_	62	38	27	41	32	75	25	_	44	54	2.1
1989	68	32	_	63	37	22	44	34	72	26	1.7	51	47	1.0
1990	68	32	_	64	36	28	39	33	72	27	0.2	49	48	3.4
1991	66	34	_	65	35	31	38	31	72	26	1.4	56	42	2.0
1992	65	36	_	68	32	30	34	36	74	23	2.9	57	40	2.6
1993	61	39	_	66	34	32	37	31	76	21	2.6	63	35	1.4
1994	67	33	_	67	33	33	37	30	80	19	0.9	65	31	1.1
Mean(SD)	67(4)	33(4)		65(2)	35(2)	29(4)	39(3)	32(2)	74(3)	24(3)	2(1)	55(8)	43(7)	2(1)

Table 2.5. Percent of habitat area sampled for fish (pi) at the stream system, valley segment and channel unit scales in the Elk River, Oregon (1988-1994). Stream system types are the mainstem and tributaries. Valley segment types are unconstrained valleys (UV), alluviated canyons (AC), and constrained canyons (CC). Channel unit types are pools, fastwater (FW), and side channels (SC). No unconstrained valleys were identified in the mainstem. Percent area sampled for fish approximates the percent estimated total area of each type (Appendix 2.1).
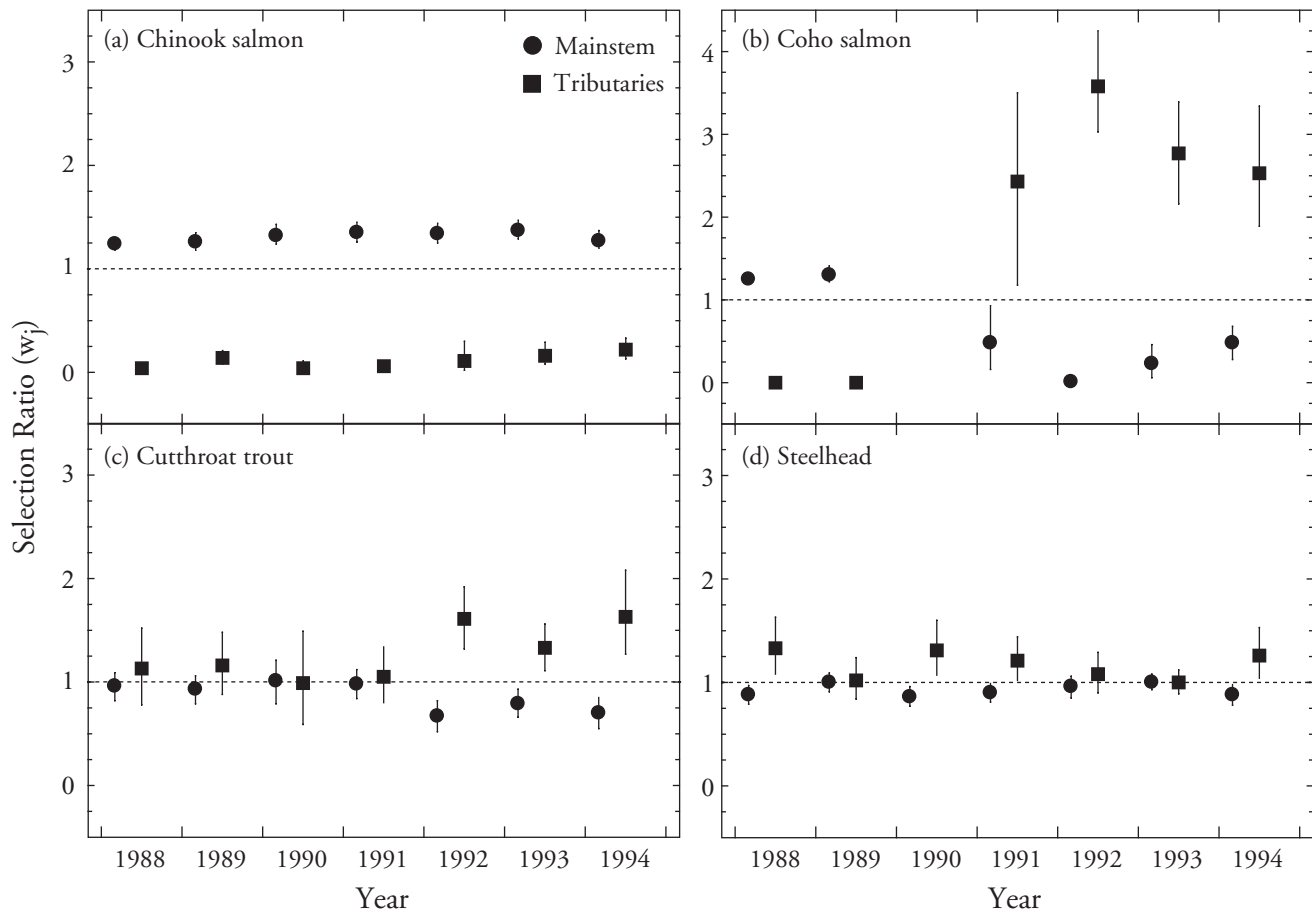
Figure 2.3. Selection ratios of juvenile salmonids for the mainstem and tributaries in Elk River, Oregon (1988-1994) for: (a) chinook salmon; (b) coho salmon; (c) cutthroat trout; and (d) steelhead. Coho salmon were not observed in the basin in 1990. A selection ratio was significant when the Bonferroni-adjusted confidence interval (α=0.1/2) did not include one. For a given year, selection ratios were significantly different (α=0.1) if their confidence intervals did not overlap.

(Table 2.7). Means of channel unit features did not differ significantly among years in constrained canyons in the mainstem. In the tributaries, significant among-year differences were observed for only the frequency of pools in constrained canyons (Table 2.8).

Valley segment types rarely differed significantly for channel unit features in either the mainstem or tributaries (Tables 2.7 and 2.8). Drainage area was a significant covariate more often in the tributaries than in the mainstem when comparing means for channel unit features between valley segment types. Percent area of pools with boulders as dominant substrate and percent area of fastwater with large gravel as dominant substrate were each significantly greater for mainstem alluviated canyons than for mainstem constrained canyons in at least one year. Conversely, the mean length of pools, mean maximum depth of pools, mean volume of pools, and percent area of pools were each greater for mainstem constrained canyons than for mainstem alluviated canyons in at least one year. Valley segment types in the tributaries differed significantly for only three channel unit features: 1) the frequency of pools was significantly greater for constrained canyons than for unconstrained valleys in 1994; 2) the mean depth of fastwater was significantly greater in constrained canyons than in unconstrained valleys in 1989 and 1991; and 3) the percent area of fastwater with small gravel as dominant substrate was

significantly greater for unconstrained valleys than for both alluviated canyons and constrained canyons in 1988.

Habitat Selection

Stream system scale

Selection at the stream system scale differed among the four salmonid species (Fig. 2.3). Based on confidence intervals derived from bootstrapping distributions of selection ratios and pairwise differences between these, chinook salmon selected for the mainstem (P≤0.05) and selected for this stream system type with a higher probability than for the tributaries (P≤0.1) (Fig. 2.3a) in each year. Coho salmon was the only species not found in both stream system types in every year (Table 2.3). For each year that coho salmon were observed in both stream system types (1991, 1993, and 1994), they selected tributaries with a higher probability than the mainstem (P≤0.1) (Fig. 2.3b). Cutthroat trout selected the mainstem and tributaries with similar probabilities (P>0.1) prior to 1992, but in each subsequent year, tributaries were selected over the mainstem (Fig. 2.3c). Steelhead selected tributaries with a higher probability than the mainstem (P≤0.1) in four of seven years (Fig. 2.3d).

Table 2.6. Results of comparing means for channel unit features within and among years at the stream system scale in the Elk River, Oregon (1988-1994). Means (standard error) were compared with ANOVA: 1) between the mainstem (MS) and its tributaries (Trib) in each year (1988 df = 1,20; 1989 df = 1,21; 1990-91 df = 1,22; 1992-94 df = 1,23); and 2) among years in the mainstem (df = 6,49) and tributaries (df = 6,105).

	Stream System Type	1988 Mean (SE)		1989 Mean (SE)		1990 Mean (SE)		1991 Mean (SE)		1992 Mean (SE)		1993 Mean (SE)		1994 Mean (SE)	
Pools:															
Mean length (m)	MS	78.6†	(4.9)	98.4†	(6.4)	82.3†	(4.8)	67.2†	(4.9)	70.2†	(4.5)	90.9†	(5.0)	78.4†	(5.4)
	Trib	19.5†	(3.7)	22.9†	(4.7)	21.8†	(3.4)	19.7†	(3.5)	20.4†	(3.1)	18.9†	(3.4)	18.3†	(3.7)
Mean wetted width (m)	MS	13.2†	(0.8)	11.5†	(0.4)	11.3†	(0.6)	11.1†	(0.6)	10.8†	(0.5)	11.7†	(0.6)	12.3†	(0.5)
	Trib	6.2†	(0.6)	5.8†	(0.3)	5.7†	(0.4)	5.8†	(0.4)	5.4†	(0.3)	6.1†	(0.4)	5.8†	(0.4)
Mean maximum depth (m)	MS	1.90†	(0.13)	2.28†	(0.14)	2.28†	(0.14)	1.89†	(0.11)	1.78†	(0.09)	1.91†	(0.10)	1.73†	(0.09)
	Trib	0.91†	(0.10)	1.19†	(0.11)	1.02†	(0.10)	0.95†	(0.08)	0.91†	(0.06)	0.89†	(0.07)	0.85†	(0.06)
Mean volume (m^3)	MS	823.5†	(115.8)	1093.1†	(81.2)	1058.3†	(95.6)	722.3†	(71.5)	592.8†	(48.4)	785.7†	(64.5)	889.3†	(99.0)
	Trib[1]	54.7†	(87.6)	57.3†	(59.3)	50.7†	(67.6)	47.9†	(50.6)	49.1†	(33.2)	43.4†	(44.2)	39.2†	(67.9)
Mean density of wood (no./100)	MS	1.1†$_a$[2]	(1.2)	2.2*	(3.9)	1.0*$_b$	(3.6)	1.5†$_c$	(2.6)	4.0*$_{abcd}$	(3.6)	2.6*	(2.7)	1.0*$_d$	(3.5)
	Trib	7.7†	(0.8)	17.7*	(2.8)	14.0*	(2.6)	12.6†	(1.8)	15.2*	(2.7)	13.9*	(1.8)	12.1*	(2.4)
Frequency (no./km)	MS	8.3†	(1.3)	6.1†$_{abcd}$	(1.7)	8.3†	(1.8)	10.0†$_a$	(2.2)	9.8†$_b$	(1.9)	8.9†$_c$	(2.8)	10.7†$_d$	(3.0)
	Trib	18.5†$_a$	(1.0)	15.6†$_{bc}$	(1.3)	18.0†$_{de}$	(1.3)	21.1†	(1.5)	19.9†$_f$	(1.3)	26.5†$_{bd}$	(1.9)	28.5†$_{acef}$	(2.0)
% Area	MS	65.2†	(4.8)	63.5†	(6.1)	69.2†	(5.1)	64.3†	(4.9)	67.5†	(3.9)	79.1†	(4.8)	79.7†	(4.0)
	Trib	35.5†	(3.6)	34.9†	(4.4)	37.7†	(3.6)	38.6†	(3.4)	36.6†	(2.7)	45.5†	(3.3)	46.9†	(2.8)
% Area with bedrock as dominant substrate	MS[1]	5.2	(5.7)	8.9	(4.9)	23.2†	(3.8)	2.8	(2.8)	9.0	(3.0)	10.0	(3.7)	2.8	(3.3)
	Trib	9.5	(4.3)	11.5	(3.6)	4.9†	(2.7)	6.0	(2.0)	6.2	(2.1)	2.9	(2.6)	4.4	(2.2)
% Area with boulders as dominant substrate	MS	43.3*	(8.0)	18.8	(5.0)	20.0	(6.1)	27.5*	(5.6)	40.5†	(5.4)	51.8	(8.8)	37.6*	(7.4)
	Trib	13.5*	(6.0)	12.7	(3.7)	14.1	(4.3)	9.3*$_a$	(3.9)	9.2†$_a$	(3.7)	31.7$_{ab}$	(6.0)	14.7*	(5.1)
Fastwater:															
Mean depth (m)	MS	0.27†	(0.02)	0.31†	(0.03)	0.35†	(0.03)	0.29†	(0.02)	0.26†	(0.02)	0.28†	(0.02)	0.26†	(0.02)
	Trib	0.18†	(0.02)	0.18†	(0.02)	0.15†	(0.02)	0.16†	(0.02)	0.15†	(0.01)	0.15†	(0.01)	0.14†	(0.01)
% Area with cobble as dominant substrate	MS	26.9*	(8.6)	61.9*	(8.3)	54.4	(10.0)	49.4	(5.5)	41.1	(6.7)	41.7	(8.7)	55.8	(8.3)
	Trib	61.9*	(6.5)	40.3*	(6.0)	58.9	(7.1)	49.3	(3.9)	51.5	(4.6)	52.1	(5.9)	60.2	(5.7)
% Area with large gravel as dominant substrate	MS	6.5	(3.2)	7.3	(5.2)	8.1	(3.9)	24.2$_{ab}$[2]	(5.3)	20.1	(7.5)	2.6*$_a$	(4.7)	2.1*$_b$	(5.7)
	Trib	8.3$_{ab}$	(2.4)	16.2	(3.8)	15.4	(2.8)	27.8$_a$	(3.8)	28.8$_b$	(5.2)	15.0*	(3.2)	17.1*	(3.9)
% Area with small gravel as dominant substrate[1]	MS	0.3	(0.6)	5.7	(4.7)	0.8	(0.7)	2.6	(0.9)	8.0	(4.2)	0.1	(0.6)	0.0	(0.0)
	Trib	0.7	(0.5)	5.8	(3.5)	0.6	(0.5)	0.2	(0.7)	0.7	(2.8)	1.3	(0.4)	0.0	(0.0)

†Means for year were significantly (P≤0.001) different.
*Means for year were significantly (P≤0.05) different.
[1]ANOVA for among-year and each within-year means comparison conducted on ranked data.
[2]Means with the same subscript were significantly (P≤0.05 after Bonferroni adjustment for 21 comparisons) different between years.

Table 2.7. Results of comparing means for channel unit features within and among years at the valley segment scale in the mainstem of the Elk River, Oregon (1988-1994). Means (standard error) were compared: 1) between alluviated canyons (AC) and constrained canyons (CC) in each year using ANCOVA with drainage area as the covariate (df = 2,5); and 2) among years within alluviated canyons (df = 6,21) and constrained canyons (df = 6,21) using ANOVA.

	Valley Segment Type	1988 Mean (SE)		1989 Mean (SE)		1990 Mean (SE)		1991 Mean (SE)		1992 Mean (SE)		1993 Mean (SE)		1994 Mean (SE)	
Pools:															
Mean length (m)	AC	68.1	(10.4)	79.2*	(10.8)	67.4*	(7.6)	57.5	(11.1)	62.1	(10.3)	80.5	(11.2)	67.4	(12.6)
	CC	89.1	(10.4)	117.8*	(10.8)	97.2*	(7.6)	76.9	(11.1)	78.2	(10.3)	101.4	(11.2)	89.5	(12.6)
Mean wetted width (m)	AC	*13.9[1]*	*(0.8)*	11.7	(0.4)	*11.7*	*(0.3)*	11.5	(1.3)	10.9	(0.7)	12.2	(0.7)	*12.8*	*(0.5)*
	CC	*12.5*	*(0.8)*	11.2	(0.4)	*10.8*	*(0.3)*	10.7	(1.3)	10.6	(0.7)	11.2	(0.7)	*11.7*	*(0.5)*
Mean maximum depth (m)	AC	1.68	(0.24)	2.08	(0.26)	1.97*	(0.14)	1.66	(0.16)	1.59	(0.16)	1.73	(0.21)	1.53	(0.18)
	CC	2.13	(0.24)	2.47	(0.26)	2.58*	(0.14)	2.11	(0.16)	1.97	(0.16)	2.10	(0.21)	1.93	(0.18)
Mean volume (m^3)	AC	*703.1*	*(169.3)*	895.3	(180.1)	*731.3*	*(80.7)*	567.8	(170.2)	455.6	(105.5)	634.9	(154.6)	628.1	(228.2)
	CC	*943.9*	*(169.3)*	1291.0	(180.1)	*1385.5*	*(80.7)*	876.9	(170.2)	729.9	(105.5)	936.4	(154.6)	1150.4	(228.2)
Mean density of wood (no./100)	AC	1.4	(0.4)	2.1	(0.6)	1.2	(0.5)	1.5	(0.8)	5.3	(1.5)	3.1	(0.4)	1.1	(0.3)
	CC	0.7	(0.4)	2.2	(0.6)	0.9	(0.5)	1.4	(0.8)	2.6	(1.5)	2.2	(0.4)	0.9	(0.3)
Frequency (no./km)	AC	$8.6_a{}^2$	(1.0)	6.2	(0.5)	8.6	(0.5)	9.8	(1.2)	10.1	(0.7)	9.7	(0.6)	11.3_a	(1.2)
	CC	8.1	(1.0)	6.0	(0.5)	7.9	(0.5)	10.2	(1.5)	9.5	(0.7)	8.1	(0.6)	10.0	(1.2)
% Area	AC	58.3	(5.8)	52.6_{bc}	(8.2)	60.3	(6.6)	$55.6*_{de}{}^1$	(3.8)	64.2	(6.5)	76.3_{abd}	(5.9)	75.3_{ce}	(5.0)
	CC	72.0	(5.8)	74.3	(8.2)	78.1	(6.6)	72.9*	(3.8)	70.8	(6.5)	81.9	(5.9)	84.1	(5.0)
% Area with bedrock as dominant substrate	AC^3	3.8	(2.9)	5.2	(5.2)	18.5	(8.2)	1.5	(1.6)	6.4	(4.5)	4.4	(9.0)	2.9	(2.0)
	CC	6.5	(2.9)	12.6	(5.2)	27.8	(8.2)	4.1	(1.6)	11.6	(4.5)	15.7	(9.0)	2.8	(2.0)
% Area with boulders as dominant substrate	AC	50.7	(14.0)	26.5*	(4.5)	27.2*	(4.0)	30.3	(11.4)	49.9	(11.0)	58.9	(11.9)	38.8	(15.1)
	CC	35.8	(14.0)	11.0*	(4.5)	12.8*	(4.0)	24.8	(11.4)	31.1	(11.0)	44.6	(11.9)	36.3	(15.1)
Fastwater:															
Mean depth (m)	AC	0.26	(0.04)	0.32	(0.06)	0.34	(0.06)	0.30	(0.05)	0.26	(0.03)	0.27	(0.05)	0.24	(0.03)
	CC	0.29	(0.04)	0.31	(0.06)	0.36	(0.06)	0.29	(0.05)	0.27	(0.03)	0.28	(0.05)	0.28	(0.03)
% Area with cobble as dominant substrate	AC	28.3	(10.6)	48.7	(11.4)	51.5	(11.4)	44.6	(10.4)	48.8	(10.5)	30.2	(13.7)	42.2	(15.1)
	CC	25.5	(10.6)	75.2	(11.4)	57.2	(11.4)	54.2	(10.4)	33.4	(10.5)	53.2	(13.7)	69.4	(15.1)
% Area with large gravel as dominant substrate	AC	8.0	(6.0)	12.4*	(2.3)	8.8	(5.0)	$22.8_a{}^2$	(8.3)	14.0	(14.1)	3.3	(2.2)	3.1_a	(1.5)
	CC	5.0	(6.0)	2.3*	(2.3)	7.4	(5.0)	25.6	(8.3)	26.2	(14.1)	1.8	(2.2)	1.0	(1.5)
% Area with small gravel as dominant substrate[3]	AC	0.6	(0.4)	8.1	(6.1)	0.0	(1.2)	3.4	(2.5)	0.9	(10.7)	0.2	(0.1)	0.0	(0.0)
	CC	0.0	(0.4)	3.3	(6.1)	1.6	(1.2)	1.7	(2.5)	15.1	(10.7)	0.0	(0.1)	0.0	(0.0)

*Means were significantly (P≤0.05) different between valley segment types for that year.
[1]Means in bold and italic were significantly (P≤0.05) correlated with drainage area and were adjusted for that covariate in ANCOVA.
[2]Means with the same subscript were significantly (P≤0.05 after Bonferroni adjustment for 21 comparisons) different between years.
[3]ANOVA for among-year means comparisons conducted on ranked data.

Table 2.8. Results of comparing means for channel unit features within and among years at the valley segment scale in the tributaries of the Elk River, Oregon (1988-1994). Means (standard errors) were compared: 1) between alluviated canyons (AC) and constrained canyons (CC) in each year using ANCOVA with drainage area as the covariate (1988 df = 3,10; 1989 df = 3,11; 1990-91 df = 3,12; 1992-94 df = 3,13); and 2) among years in unconstrained valleys (df = 6,18), alluviated canyons (df = 6,27), and constrained canyons (df = 6,46) using ANOVA.

	Valley Segment Type	1988 Mean	(SE)	1989 Mean	(SE)	1990 Mean	(SE)	1991 Mean	(SE)	1992 Mean	(SE)	1993 Mean	(SE)	1994 Mean	(SE)
Pools:															
Mean length (m)	UV	21.6	(3.3)	25.1	(5.8)	26.4	(4.5)	20.1	(3.0)	*23.4[1]*	*(2.3)*	*21.1*	*(2.3)*	*20.9*	*(2.2)*
	AC	19.1	(2.9)	24.0	(4.5)	21.1	(3.5)	20.3	(2.7)	*23.4*	*(2.0)*	*21.3*	*(2.1)*	*19.9*	*(2.0)*
	CC	18.8	(2.2)	21.3	(3.8)	20.5	(2.8)	19.0	(2.3)	*16.9*	*(1.6)*	*16.3*	*(1.6)*	*16.0*	*(1.6)*
Mean wetted width (m)	UV	*6.6*	*(0.6)*	*6.1*	*(0.5)*	*5.7*	*(0.5)*	*5.7*	*(0.5)*	*5.8*	*(0.3)*	*7.3*	*(0.7)*	*6.2*	*(0.3)*
	AC	*6.0*	*(0.5)*	*5.7*	*(0.4)*	*5.6*	*(0.4)*	*5.9*	*(0.5)*	*5.3*	*(0.3)*	*5.6*	*(0.6)*	*5.6*	*(0.3)*
	CC	*6.1*	*(0.4)*	*5.7*	*(0.3)*	*5.8*	*(0.3)*	*5.9*	*(0.4)*	*5.3*	*(0.2)*	*5.9*	*(0.5)*	*5.7*	*(0.2)*
Mean maximum depth (m)	UV	*0.93*	*(0.09)*	*1.09*	*(0.13)*	1.03	(0.24)	0.90	(0.14)	0.91	(0.09)	*0.85*	*(0.05)*	*0.85*	*(0.06)*
	AC	*0.80*	*(0.09)*	*1.13*	*(0.11)*	0.97	(0.19)	0.86	(0.12)	0.87	(0.08)	*0.86*	*(0.05)*	*0.83*	*(0.05)*
	CC	*0.97*	*(0.06)*	*1.26*	*(0.09)*	1.05	(0.15)	1.03	(0.10)	0.92	(0.06)	*0.93*	*(0.04)*	*0.86*	*(0.04)*
Mean volume (m^3)	UV	*57.5[1]*	*(6.7)*	65.5	(20.4)	64.6	(20.8)	*48.8*	*(10.9)*	56.2	(8.9)	53.1	(6.5)	45.3	(5.4)
	AC	*49.1*	*(6.0)*	42.3	(15.8)	40.9	(16.1)	*49.6*	*(10.0)*	57.9	(8.1)	44.1	(5.9)	40.2	(4.9)
	CC	*56.6*	*(4.5)*	64.4	(13.4)	51.6	(12.7)	*46.2*	*(8.5)*	40.0	(6.4)	38.1	(4.7)	35.5	(3.9)
Mean density of wood (no./100)	UV	9.0	(2.5)	17.0	(8.0)	19.6	(7.2)	12.5	(4.5)	14.1	(6.6)	15.3	(4.7)	19.7	(5.7)
	AC	7.6	(2.1)	22.2	(6.2)	17.2	(5.6)	16.0	(4.0)	18.5	(6.6)	16.0	(4.2)	13.3	(5.1)
	CC	7.1	(1.6)	14.8	(5.3)	9.9	(4.4)	10.2	(3.4)	13.7	(5.4)	11.8	(4.2)	7.5	(4.0)
Frequency (no./km)	UV	16.1	(2.7)	11.7	(3.4)	15.2	(3.6)	*21.1*	*(3.3)*	18.2	(3.0)	23.7	(4.9)	*21.9**	*(3.8)*
	AC	19.5	(2.3)	17.1	(2.7)	16.3	(2.8)	*18.7*	*(3.0)*	17.2	(2.7)	24.7	(4.4)	*24.1*	*(3.4)*
	CC	19.0_a[2]	(1.8)	16.2_{bf}	(2.3)	20.2_c	(2.2)	22.8_d	(2.6)	22.5_e	(2.2)	29.0_f	(3.5)	$34.6*_{abcde}$	(2.7)
% Area	UV	34.5	(8.6)	28.3	(9.9)	36.9	(8.3)	35.2	(7.1)	37.7	(5.5)	43.6	(7.6)	40.4	(5.9)
	AC	35.2	(7.4)	37.0	(7.7)	33.3	(6.4)	41.1	(6.3)	33.7	(4.9)	45.2	(6.8)	45.7	(5.3)
	CC	36.2	(5.6)	36.3	(6.5)	40.8	(5.1)	38.7	(5.3)	38.0	(3.9)	46.7	(5.4)	51.0	(4.2)
% Area with bedrock as dominant substrate	UV	0.0	(11.4)	3.6	(9.2)	0.0	(4.3)	1.2	(4.7)	3.1	(4.4)	1.3	(2.5)	2.2	(5.6)
	AC	5.4	(9.9)	14.3	(7.1)	6.1	(3.3)	9.6	(4.2)	6.3	(3.9)	3.2	(2.3)	1.7	(5.0)
	CC	16.0	(7.5)	13.0	(6.0)	5.9	(2.6)	6.0	(3.5)	7.8	(3.1)	3.5	(1.8)	7.2	(3.9)
% Area with boulders as dominant substrate	UV	21.1	(11.4)	10.4	(9.0)	3.5	(11.2)	3.5	(6.4)	13.3	(5.3)	26.8	(12.6)	13.1	(8.5)
	AC	2.1	(9.9)	6.9	(7.0)	9.4	(8.7)	6.6	(5.5)	5.3	(4.8)	20.2	(11.3)	7.8	(7.8)
	CC	16.8	(7.5)	17.8	(5.9)	21.0	(6.9)	14.5	(4.6)	9.5	(3.8)	41.4	(8.9)	19.7	(6.0)
Fastwater:															
Mean depth (m)	UV	0.15	(0.03)	*0.15**	*(0.01)*	0.14	(0.02)	*0.13**	*(0.01)*	0.12	(0.02)	*0.14*	*(0.01)*	*0.13*	*(0.01)*
	AC	0.15	(0.03)	*0.18*	*(0.01)*	*0.15*	*(0.02)*	*0.15*	*(0.01)*	0.13	(0.02)	*0.15*	*(0.01)*	*0.14*	*(0.01)*
	CC	0.20	(0.02)	*0.19**	*(0.01)*	*0.16*	*(0.01)*	*0.18**	*(0.01)*	0.18	(0.01)	*0.16*	*(0.01)*	*0.15*	*(0.01)*
% Area with cobble as dominant substrate	UV	58.1	(15.5)	33.3	(13.3)	72.0	(16.5)	49.4	(6.4)	48.5	(9.6)	40.3	(11.2)	61.0	(10.0)
	AC	76.8	(13.4)	48.9	(10.3)	69.5	(12.8)	56.7	(5.7)	54.2	(8.6)	63.3	(10.0)	61.5	(9.0)
	CC	55.0	(10.2)	37.2	(8.7)	47.3	(10.1)	43.9	(4.9)	51.3	(6.8)	50.9	(7.9)	59.1	(7.1)
% Area with large gravel as dominant substrate	UV	*12.0[1]*	*(4.9)*	22.8	(9.5)	24.0	(6.7)	38.7	(6.9)	41.5	(8.8)	*30.1*	*(6.8)*	21.3	(9.1)
	AC	*6.8*	*(4.3)*	*7.7*	*(7.7)*	15.1	(5.2)	19.8	(6.2)	28.5	(7.9)	*12.3*	*(6.2)*	27.7	(8.2)
	CC	*7.5*	*(3.2)*	*19.5*	*(6.4)*	12.2	(4.1)	27.3	(5.2)	22.7	(6.2)	*9.2*	*(4.9)*	8.3	(6.5)
% Area with small gravel as dominant substrate[3]	UV	3.4*§	(0.9)	11.4	(8.2)	0.5	(1.1)	0.9	(0.3)	1.3	(0.6)	1.5	(1.1)	0.0	(0.0)
	AC	0.0*	(0.0)	10.6	(6.3)	0.1	(0.8)	0.0	(0.3)	0.4	(0.5)	1.5	(1.0)	0.0	(0.0)
	CC	0.0§	(0.0)	0.0	(5.3)	1.0	(0.7)	0.0	(0.2)	0.5	(0.4)	1.2	(0.8)	0.0	(0.0)

*Means were significantly (P≤0.05 after Bonferroni adjustment for 3 comparisons) different between valley segment types.

[1]Means in bold and italic were significantly (P≤0.05) correlated with drainage area and were adjusted for that covariate in ANCOVA.

[2]Means with the same subscript were significantly (P≤0.05 after Bonferroni adjustment for 21 comparisons) different between years.

Valley segment scale

The four species differed in their selection of valley segment types in the mainstem, but chinook salmon, coho salmon, and cutthroat trout often selected for unconstrained valleys in the tributaries (Fig. 2.4). Chinook salmon in the mainstem selected constrained canyons with a higher probability than alluviated canyons (P≤0.03) in two years (1993 and 1994), but selection ratios for the two valley segment types did not differ (P>0.03) in any other year (Fig. 2.4a). Unconstrained valleys in the tributaries were either selected or used in proportion to their availability by chinook salmon and for most years (1989, 1991, 1993, and 1994) were selected with a higher probability than the other two valley segment types (P≤0.03) (Fig. 2.4b).

Coho salmon in some years selected alluviated canyons in the mainstem and unconstrained valleys in the tributaries. This species selected alluviated canyons with a higher probability than constrained canyons (P≤0.03) in two of the five years that they were observed in the mainstem (Fig. 2.4c). Coho salmon in the tributaries selected for unconstrained valleys (P≤0.03) in 1991 and 1994. This valley segment type was selected with a higher probability than alluviated canyons (P≤0.03) in three years and with a higher probability than constrained canyons (P≤0.03) in two years (Fig. 2.4d). Alluviated canyons and constrained canyons in the tributaries were either avoided or used in proportion to their availability.

Cutthroat trout generally used valley segment types with equal probability in the mainstem but frequently selected for unconstrained valleys in the tributaries. Cutthroat trout in the mainstem used valley segment types in proportion to their availability for all except one year (1990) when alluviated canyons were selected over constrained canyons (P≤0.03) (Fig. 2.4e). In the tributaries, they generally selected unconstrained valleys and avoided constrained canyons, but alluviated canyons were used in proportion to availability (Fig. 2.4f). Cutthroat trout selected unconstrained valleys with a higher probability than constrained canyons (P≤0.03) in 4 years and alluviated canyons in one year.

Steelhead used valley segment types in proportion to their availability in the mainstem (Fig. 2.4g) but often avoided unconstrained valleys in the tributaries. In three years (1988, 1991, and 1993), the probability of selecting unconstrained valleys was less than one (P≤0.03) and less than that of selecting either of the other two valley segment types (P≤0.03) in the tributaries (Fig. 2.4h).

Channel unit scale

All four species selected for pools in the tributaries but selected less strongly for this channel unit type relative to fastwater in the mainstem (Fig. 2.5). Chinook salmon generally selected pools and avoided fastwater and side channels in both the mainstem and tributaries (Figs. 2.5a and b). Pools were selected (P≤0.03) and were selected with a greater probability than fastwater (P≤0.03) for all except one year (1990) in the mainstem and for all years in the tributaries. Chinook salmon either avoided or used side channels in proportion to their availability in the mainstem and in the tributaries (Figs. 2.5a and b).

Selection by coho salmon was relatively inconsistent in the mainstem (Fig. 2.5c), but pools were always selected and the other chan-

nel unit types were avoided in the tributaries (P≤0.03) (Fig. 2.5d). For three of the five years that coho salmon were observed in the mainstem, they selected for pools (P≤0.03) and against fastwater (P≤0.03). Both channel unit types were used in proportion to their availability for the other two years (1989 and 1993). Coho salmon were not seen in tributary side channels in any year, but side channels in the mainstem were selected (1989), avoided (1994), or used in proportion to their availability (1991 and 1993).

Selection by cutthroat trout, except for avoiding side channels, was somewhat ambiguous in the mainstem (Fig. 2.5e), but in the tributaries pools were usually selected over the other two channel unit types (Fig. 2.5f). Cutthroat trout selected pools with a higher probability than fastwater (P≤0.03) for only two years (1992 and 1993) in the mainstem and for all except one year (1990) in the tributaries (Figs. 2.5e and f). Although observed in both mainstem (1992 and 1994) and tributary (1990, 1992, 1994) side channels, cutthroat trout avoided or used this channel unit type in proportion to availability (Figs. 2.5e and f).

Steelhead selected fastwater over pools for some years in the mainstem but always selected pools over fastwater in the tributaries. In the mainstem, steelhead either selected fastwater with a higher probability than pools (P≤0.03) or used both habitat types in proportion to availability (Fig. 2.5g). In the tributaries, they invariably selected pools over fastwater (Fig. 2.5h). Although steelhead were observed in side channels in the mainstem and in the tributaries, their selection ratios for this channel unit type were less than one (P>0.03) in both the mainstem and tributaries for every year (Figs. 2.5g and h).

Interannual Variation in Selection

Interannual variation in selection ratios at most spatial scales was not explained by stream discharge, water temperature, or juvenile salmonid densities (Table 2.9). Steelhead was the only species for which selection ratios of selected habitat types were related to stream discharge or water temperature. Selection ratios of chinook salmon for constrained canyons in the mainstem were negatively related to densities of this species in the mainstem. Selection ratios of coho salmon for tributaries were negatively related to the density of chinook salmon in the basin.

DISCUSSION

Habitat Characterization

Means of most channel unit features differed between stream system types, but means of only a few channel unit features differed among years or among valley segment types. Channel unit features routinely differed between the mainstem and tributaries, which were distinguished primarily based on drainage area and gradient. Streams with larger drainage area generally have higher discharge and greater ability to transport materials (Gordon et al. 1992) so should be deeper, wider, and transport more wood than streams with lower discharge. Accordingly, channel units were larger and the mean density of wood in pools was less in the mainstem of Elk River than in the tributaries for each year. Larger streams may also have lower wood inputs. Pool frequency should be higher and percent pool area lower

Figure 2.4. Selection ratios of juvenile salmonids for unconstrained valleys, alluviated canyons, and constrained canyons in Elk River, Oregon (1988-1994) for: chinook salmon in the (a) mainstem and (b) tributaries; coho salmon in the (c) mainstem and (d) tributaries; cutthroat trout in the (e) mainstem and (f) tributaries; and steelhead in the (g) mainstem and (h) tributaries. Coho salmon were not observed in the mainstem in 1990 and 1992 or in the tributaries in 1988-90. A selection ratio was significant when the Bonferroni-adjusted confidence interval (α=0.1/3) did not include one. For a given year, selection ratios were significantly different (α=0.1/3 Bonferroni adjusted) if their confidence intervals did not overlap.
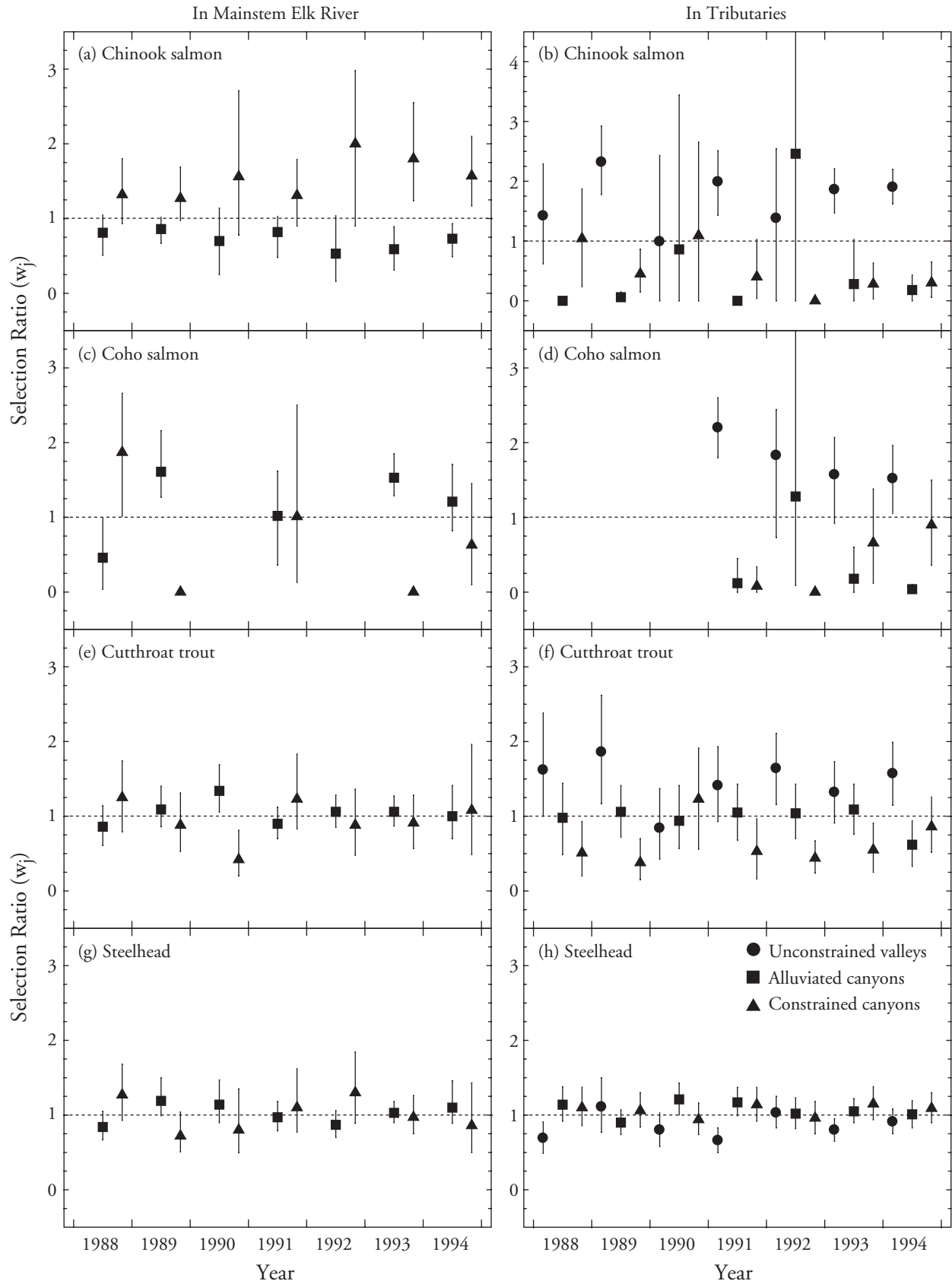
Figure 2.5. Selection ratios of juvenile salmonids for pools, fastwater habitats, and side channels in Elk River, Oregon (1988-1994) for: chinook salmon in the (a) mainstem and (b) tributaries; coho salmon in the (c) mainstem and (d) tributaries; cutthroat trout in the (e) mainstem and (f) tributaries; and steelhead in the (g) mainstem and (h) tributaries. Coho salmon were not observed in the mainstem in 1990 and 1992 or in the tributaries in 1988-90. A selection ratio was significant when the Bonferroni-adjusted confidence interval (α=0.1/3) did not include one. For a given year, selection ratios were significantly different (α=0.1/3 Bonferroni adjusted) if their confidence intervals did not overlap.
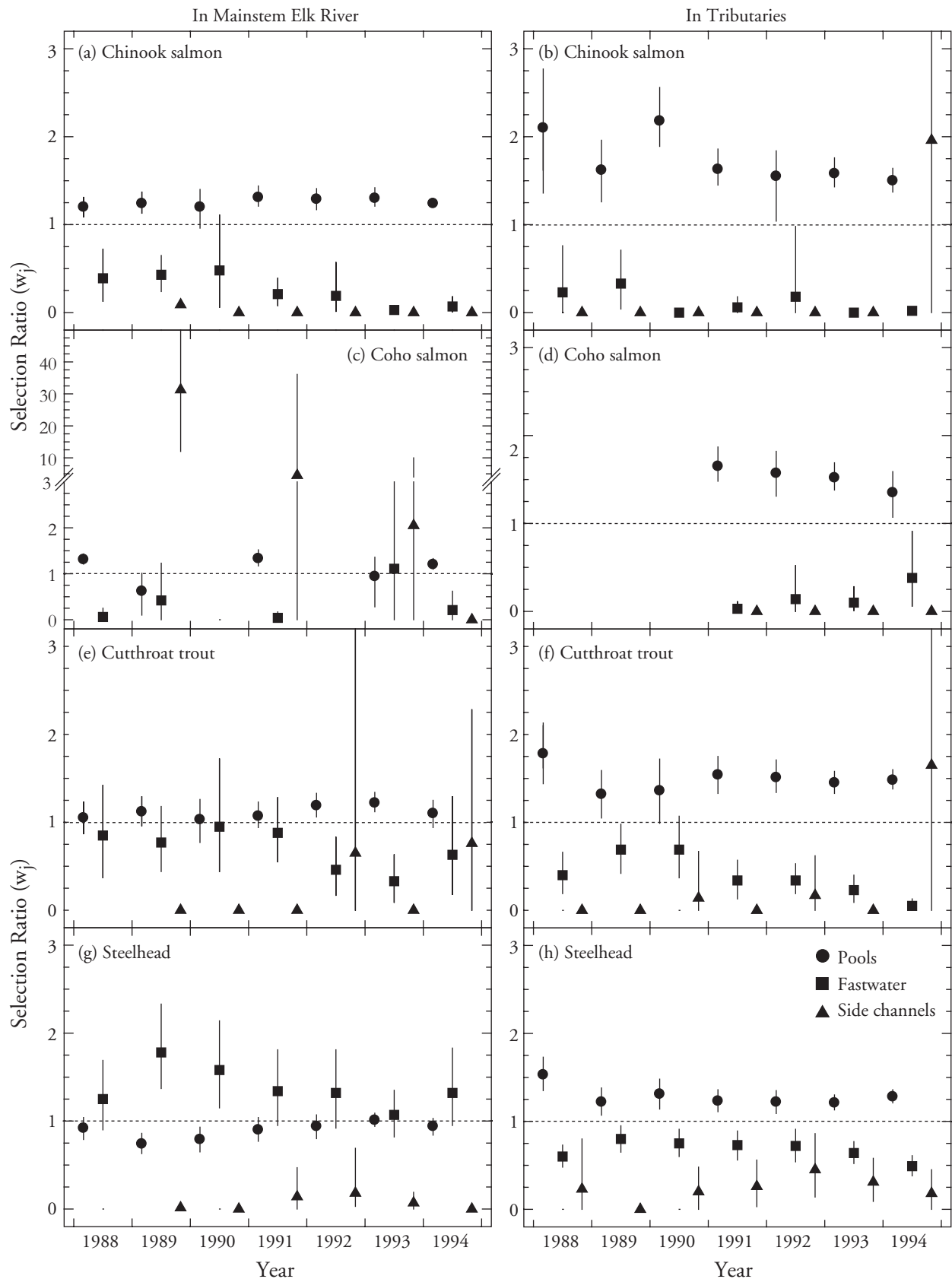
Table 2.9. Results from regressions to explain interannual variation in selection ratios for habitat types selected by juvenile salmonids at three spatial scales in Elk River, Oregon. Selection ratios were regressed with stream discharge and water temperature variables at each spatial scale. Selection ratios were also regressed at the stream system scale with the estimated total density of each salmonid species summarized for the basin and at the valley segment and channel unit scales with the estimated total density of each salmonid species summarized for the mainstem or tributaries. The sign (+/-) preceding selection ratios indicates the direction of relationship with the independent variable.

Species	Stream System	Valley Segment		Channel Unit	
		mainstem	tributaries	mainstem	tributaries
Chinook salmon	ns[1] selection ratio for mainstem	r^2=0.73; df=6; P=0.01 -selection ratio for constrained canyons vs. density of chinook salmon in the mainstem	ns selection ratio for unconstrained valleys	ns selection ratio for pools	ns selection ratio for pools
Coho salmon	r^2=0.97; df=4; P=0.003 -selection ratio for tributaries vs. density of juvenile chinook salmon in the basin	No habitat type selected	selection ratio for unconstrained valleys[2]	No habitat type selected	selection ratio for pools[2]
Cutthroat trout	ns selection ratio for tributaries	No habitat type selected	ns selection ratio for unconstrained valleys	ns selection ratio for pools	ns selection ratio for pools
Steelhead	r^2=0.63;df=6; P=0.03 -selection ratio for tributaries vs. maximum daily stream flow during spring[3]	No habitat type selected	ns selection ratio for unconstrained valleys (avoided)	r^2=0.66; df=6; P=0.03 +selection ratio for fastwater vs. annual minimum daily stream flow	ns selection ratio for pools

in smaller, steeper channels with more wood because pool spacing is scaled to channel width and decreases with increased gradient and amount of wood or boulders (Grant et al. 1990; Montgomery and Buffington 1997). Consistent with this, we found that the frequency of pools was greater and the percent area of pools was less in the tributaries than in the mainstem for every year. Differences between stream system types were identified for some dominant substrate classes, but both the level of statistical significance and the consistency of relationships were less than for the previously discussed channel unit features. This may stem from weaker relationships of substrate classes to drainage area and gradient or from greater bias associated with ocular estimation of dominant substrate.

Possible reasons we rarely found significant differences among valley segment types in channel unit features included that valley segment types were truly not different or that real differences were not detected due to small sample size and error associated with observer bias. Differences in channel unit features should have been apparent if influences of channel gradient and confinement, the primary characteristics we used to identify valley segment types, were expressed. Valley segment types have been shown to differ significantly for some of the same channel unit features that we evaluated (Cupp 1989; Frissell 1992). However, the spatial extent of these studies was much larger and encompassed a broader range of valley segment types than those examined here. Lithologies and geologic structures, from which valley segment types originate (McHugh 1986; Cupp 1989; Frissell 1992), may not have varied enough in the Elk River basin to cause statistically discernible differences in channel unit features. This could be particularly true for the mainstem of

Elk River where only two similar valley segments types were identified.

Land use effects in the Elk River basin may have masked differences among valleys segment types, especially in the tributaries. Timber harvest activities have been concentrated in Butler Creek and on the south and east sides of the Elk River basin (USDA 1998). Thus, valley segments of the same type had different land use histories that were thought to be manifested in their stream channels (McHugh 1986; Ryan and Grant 1991). Streams affected by timber harvest may contain less wood (Bilby and Ward 1991; Montgomery et al. 1995) and respond to increased sediment loads by aggrading and widening (McHugh 1986; Ryan and Grant 1991). These effects may have increased the variability of channel unit features within a valley segment type thus decreased the likelihood of distinguishing among valley segment types.

Small sample size and observer bias may have reduced the probability of identifying differences among valley segment types in means of channel unit features. Ability to consistently detect differences could have been limited by small sample size unless differences among valley segment types were large, approaching the order of magnitude for those between stream system types. For a subset of channel unit features, valley segment types did differ significantly. Valley segment types were ordered similarly in other years for these channel unit features, suggesting that identified differences occurred by chance or low statistical power prevented their detection in other years.

Errors associated with observer bias in delineating, classifying, and estimating dimensions of channel units can have serious ramifi-

cations when characterizing streams (Roper and Scarnecchia 1995; Poole et al. 1997). Bias of different observers reduces repeatability and precision of estimates (Poole et al. 1997) and might have allowed differences among valley segments types to remain undetected. However, field crews for Elk River were uniformly trained and were required to distinguish among a limited number of channel unit types. Both factors have been shown to reduce bias in stream surveys (Roper and Scarnecchia 1995). Observer bias does not fully explain results for all channel unit features. Differences among valley segment types in the mean maximum depth of pools were not identified even though this variable was measured instead of estimated. Furthermore, confidence intervals for channel unit dimensions in the Elk River were typically less than 20% of the corrected estimates. Thus, smaller differences between means of channel unit features may not have been discerned.

Habitat Selection

Juvenile anadromous salmonids in the Elk River basin selected for specific types at the stream system, valley segment, and channel unit scales. The types selected at each scale varied among species and among years. Year-to-year consistency, strength of selection, and possible reasons for observed temporal patterns also varied among species and spatial scales. We recognize that habitat types used by juvenile salmonids at the stream system and valley segment scales may have been determined in part by where adults spawned. Spatially explicit data on the number of spawning adults and the movements of juveniles are not available for Elk River, thus selection at the stream system and valley segment scales cannot be apportioned between juvenile and adult choice.

Stream system scale

The temporal pattern of selection for steam system types varied among species in the Elk River basin. Chinook salmon selected the mainstem over the tributaries in each of the seven years of study. In the Elk River basin, chinook salmon are thought to spawn primarily in low gradient areas of the mainstem and larger tributaries (Burck and Reimers 1978). Many of the juveniles that originated in these tributaries appear to have entered the mainstem at the time of our surveys. This is consistent with their ocean-type life history (Taylor 1990; Healey 1991) and with smolt trapping data from the Elk River that indicated a large proportion of each chinook salmon cohort was migrating downstream during the spring and summer (Downey et al. 1987; K.M. Burnett and G.H. Reeves, unpublished data).

The stream system type selected by coho salmon in the Elk River basin varied among years and may have been influenced by competition with chinook salmon. Coho salmon selected for the mainstem in some years and for the tributaries in others. The summer distribution of juvenile coho salmon in the Elk River basin is similar to that in other river systems where these fish are found in mainstem rivers and lower gradient tributaries (Stein et al. 1972; Sandercock 1991; Rosenfeld et al. 2000). Coho salmon selected for the tributaries more strongly in years when densities of chinook salmon in the basin where lower. Both species selected pools over other channel unit types, and tributaries have less of their surface area in pools than the mainstem. Concordant with ideal free distribution theory

(Fretwell and Lucas 1970), coho salmon may have moved into or stayed in the mainstem to reduce competition with chinook salmon when densities of that species were high.

The relationship between chinook and coho salmon was the only evidence suggesting that interspecific competition may have influenced selection. In fine scale studies, juvenile coho salmon often prevail in competitive encounters with steelhead (Hartman 1965), cutthroat trout (Glova 1986), and chinook salmon (Stein et al. 1972). However, densities of these three species in the Elk River basin exceeded those of coho salmon for almost every year. This may have diminished the competitive ability of coho salmon and favored chinook salmon when the two species interacted. Although interspecific competition is well documented for juvenile salmonids at fine spatial scales (see Hearn 1987 for review), its role in determining habitat use at coarser spatial scales is seldom studied (e.g, Fausch et al.1994) so may not be well understood (Fausch 1998).

Cutthroat trout and steelhead selected tributaries over the mainstem of Elk River in some years, but in others, they used both stream system types with equal probability. These species typically occur in a range of stream sizes from mainstem rivers to small, steep tributaries (Meehan and Bjornn 1991; Trotter 1997). Although interannual variation in selection of cutthroat trout for tributaries could not be explained, selection ratios of steelhead for tributaries were negatively related to maximum daily average stream discharge during the previous spring. In years with relatively high spring flows, steelhead may have either avoided tributaries during late summer, or perhaps more likely, moved downstream and out of them before we surveyed. If the latter is true, the mainstem and tributaries may not be equally available to steelhead during summer in years when spring flows were high. Determination of habitat availability is critical in interpreting habitat selection (Johnson 1980; Rosenberg and McKelvey 1999). If a habitat type is less available to a species than its area would indicate due to factors such as patch shape or location (Otis 1997; Rosenberg and McKelvey 1999), presence of predators or competitors, and weather, selection ratios will underestimate the true preference for the habitat type. Steelhead was the only species for which examined environmental variables explained a significant proportion of the inter-annual variation in selection ratios for selected types at any spatial scale. Relationships may have been more apparent if stream discharge and water temperature data had been collected at locations in addition to the USGS gauge on the mainstem of Elk River.

Valley Segment Scale

Juvenile salmonids generally used mainstem valley segment types in proportion to availability. Cutthroat trout and coho salmon selected for mainstem alluviated canyons in one and two years, respectively, and chinook salmon selected for mainstem constrained canyons in two years. Infrequent or no selection for valley segment types supports the hypothesis that alluviated canyons and constrained canyons in the mainstem were similar regarding channel unit features and indicates that any physical differences between these valley segment types had limited influence on distribution of juvenile salmonids during the summer. Valley segment location, but not type, affected abundances of juvenile chinook and coho salmon in the mainstem of Drift Creek, Oregon (Schwartz 1990). However, in Drift Creek and other larger rivers, juvenile salmonids have been associated with specific physical characteristics of valley segments

or reaches. More complex reaches had higher densities of cutthroat trout and coho salmon (Rosenfeld et al. 2000), mainstem reaches with more pool area were selected by chinook salmon (Roper et al. 1994), and higher densities of older steelhead occurred in mainstem reaches with lower temperatures (Roper et al. 1994), higher gradients (Schwartz 1990), or larger substrates (Dambacher 1991).

Intraspecific competition may have influenced selection by chinook salmon for constrained canyons in the mainstem. If intraspecific competition influenced habitat selection, annual densities and selection ratios for a species should have been inversely related at densities above the carrying capacity of any truly preferred habitat type as poorer competitors chose less suitable habitat types (Fretwell and Lucas 1970). Densities in the mainstem and selection ratios of constrained canyons in the mainstem for chinook salmon were negatively related. This was the only species and the only spatial scale for which such a relationship was identified. Densities of juveniles in the Elk River basin for all salmonid species except chinook salmon in the mainstem were at or below those in other coastal Oregon basins (Schwartz 1990; Frissell 1992; Roper et al. 1994; Solazzi et al. 2000). Thus, carrying capacities of preferred habitat types were probably not routinely exceeded in any other circumstance, reducing the likelihood that intraspecific competition would markedly affect habitat selection in Elk River.

In contrast to the mainstem, valley segment types in the tributaries were often selected or avoided by juvenile salmonids. Chinook salmon selected unconstrained valleys more strongly and consistently than the other species, commonly selecting for this valley segment type over alluviated canyons and constrained canyons. Coho salmon and cutthroat trout also selected for unconstrained valleys, but only cutthroat trout routinely selected these over another type, constrained canyons. In contrast, steelhead often avoided unconstrained valleys in favor of the other two valley segment types. These findings suggested that chinook salmon and steelhead perceived physical differences between unconstrained valleys and the other valley segment types in about half of the surveyed years. Cutthroat trout seemed to differentiate unconstrained valleys from constrained canyons at a similar frequency. No species, except chinook salmon, selected alluviated canyons with a probability that typically differed significantly from the other valley segment types. This may reflect that alluviated canyons are intermediate to unconstrained valleys and constrained canyons in physical characteristics (Frissell 1992).

The geomorphic context of smaller streams has been shown to influence use by juvenile salmonids. Greater abundances were found of non-anadromous cutthroat trout in lower gradient, less constrained valley segments and of non-anadromous rainbow trout (*O. mykiss*) in higher gradient, more constrained valley segments in southwestern Washington (Cupp 1989). Although few age 1+ steelhead were observed in a low gradient reach of an Idaho stream, young-of-the-year chinook salmon were abundant (Everest and Chapman 1972). In coastal Oregon, Hicks (1989) found greater use by age 1+ steelhead of streams with steeper gradients, larger substrates, and deeper fastwater habitat and greater use by juvenile coho salmon in lower gradient, less constrained streams.

Although we identified few differences between valley segment types in channel unit features, characteristics that we did not examine may have influenced selection for unconstrained valleys. Cupp (1989) found that moderate slope bound valley segments, subsumed in unconstrained valleys in this study, were best distinguished from

other valley segment types by characteristics of the fish assemblage instead of by channel unit features. Thus, fish apparently responded to differences in physical attributes that are not routinely assessed in stream surveys. Low gradients and wide floodplains, typical of unconstrained valleys, slow water velocities and can cause gravel and wood transported from upstream to accumulate, creating an enlarged hyporheic zone (Edwards 1998) and complex channel patterns (Gregory et al. 1991). Less topographic shading and longer distances between the wetted channel and riparian vegetation allowed more sunlight to reach streams in unconstrained valleys of Elk River (Zucker 1993). These coarse-scale geomorphic features were thought to contribute to greater gross primary production and aquatic macroinvertebrate biomass (Zucker 1993), nutrient and particulate retention (Lamberti et al. 1989), protection of redds and juveniles from high flows (Gregory et al. 1991), and groundwater upwelling (Baxter and Hauer 2000) in unconstrained channels. Such conditions may have increased the suitability of unconstrained valleys in Elk River tributaries for adult spawning and juvenile rearing by chinook salmon, coho salmon, and cutthroat trout. Water velocities are lower (Gregory et al. 1991) and summer water temperatures are more variable from increased solar heating (McSwain 1987) in unconstrained valleys than in the other valley segment types. These characteristics may be less suitable for steelhead than for other salmonids (Bisson et al. 1988; Hicks 1989; Bjornn and Reiser 1991) and help explain why steelhead avoided unconstrained valleys.

Channel Unit Scale

At the channel unit scale, species varied in their selection for pools in the mainstem. Chinook salmon generally selected pools in the mainstem, perhaps as resting sites during their seaward migration. Mainstem pools either were used in proportion to their availability or were selected by coho salmon and cutthroat trout and were avoided by steelhead. These findings correspond with results from other studies that examined channel unit types selected by salmonids and are compatible with their body morphology, behavior, and ecology (e.g., Bisson et al. 1988; Roper et al. 1994; Rosenfeld and Boss 2001). For example, steelhead have cylindrical bodies and short fins that allow them to exploit fastwater habitats (Bisson et al. 1988), but chinook salmon may be better adapted to pools because they tend to occur in aggregations, are found in relatively deep water, and have laterally compressed bodies, similar to coho salmon, that should increase maneuverability in the water column (Everest and Chapman 1972; Hillman et al. 1987; Bisson et al. 1988; Roper et al. 1994).

All four species of salmonids selected pools and avoided fastwater in Elk River tributaries. Selection ratios of each species were greater for tributary pools than for mainstem pools, suggesting that, relative to fastwater, pools were of greater importance in the tributaries. Consistent with our findings, Dambacher (1991) and Roper et al. (1994) observed that larger steelhead reversed preference for pools and fastwater as stream size increased. This pattern of selection by steelhead may have been influenced by both the length of pools and the depth of fastwater. Pools were longer in the mainstem than in the tributaries. Thus, a smaller percentage of the area in mainstem pools than in tributary pools should have been favorable for steelhead trout that feed typically on macroinvertebrates drifting into the pool from upstream (Fraser 1969). Fastwater units were deeper in

the mainstem than in the tributaries and were probably deep enough to accommodate steelhead in the mainstem but not in the tributaries (Dambacher 1991). Furthermore, fastwater in the mainstem, due to steeper gradients and larger substrates, perhaps provided beneficial conditions of velocity and drift that were more abundant and evenly distributed than in relatively long mainstem pools. Our finding that selection ratios of steelhead for fastwater in the mainstem were positively related to the annual minimum daily average stream discharge also suggested depth as a factor in their selection or avoidance of fastwater.

Juvenile salmonids usually avoided side channels in the mainstem and tributaries of Elk River. Although off-channel habitats are important to rearing salmonids during winter (Cunjak 1996) and spring (Reeves et al. 1998) and juveniles were observed in Elk River side channels, it is doubtful these habitats were selected during summer low flows. Instead, fish were probably stranded in drying side channels when connections to the main channel were severed. Bisson et al. (1982) found few fish in secondary channel pools during summer, noting that these were often isolated from the main channel and had relatively high water temperatures. Coho salmon was the only species to use mainstem side channels in a proportion that exceeded availability, possibly indicating their greater use of this channel unit type earlier in the year (Swales et al. 1986; Bustard and Narver 1975).

Management Implications

A logical outcome of a multi-scale, hierarchical perspective of habitat selection is the need to understand, manage for, and protect habitat features from the landscape to the micro-habitat. Although decision makers are rarely concerned with channel units or sub-units (10^{-1}), they have been forced to rely on understanding gained at these spatial scales to plan for and manage stream ecosystems across entire regions. Knowledge that fish prefer a particular channel unit or sub-unit type engendered reductionist approaches that concentrated on that type even when it was recognized that higher level constraints were operating (Lewis et al. 1996; Rabeni and Sowa 1996; Frissell 1997). Such approaches may prevent attainment of conservation objectives. For example, our results indicated that management based on assessment or creation of pool area may negatively impact drift-feeding species, such as steelhead, particularly if habitat length or spacing issues are ignored. Fine-scale characteristics, such as large wood or pool frequency, may influence creation (Montgomery et al. 1995) or use of a particular habitat type at a coarser spatial scale. However, we think that contributions to salmonid conservation will be diminished if regional habitat strategies do not directly address coarser spatial scales. Planning for coastal basins with climatic and geologic settings similar to Elk River that manages for the proper function of unconstrained valleys and the watersheds containing them will likely help conserve chinook salmon, coho salmon, and cutthroat trout. However, a myopic focus on this valley segment type offers little advantage to steelhead. Regional conservation goals may be best advanced by simultaneously protecting and restoring the processes that create fine-scale, ephemeral features (e.g., pools) and the functions of coarse-scale, persistent geomorphic features [e.g., unconstrained valleys or streams on young glacial terraces (Benda et al. 1992)] that provide high quality habitat.

CONCLUSIONS

Our results highlight the value of multi-year studies. Temporal patterns in habitat characteristics and selection provided a context for, and reinforced our confidence in, the results for any one year. We found that means of few channel unit features varied significantly among years and that relationships between types at each scale were generally consistent. However, variation in the densities and selection ratios of most species was substantial. In many cases, if we had examined only one or two years of data, as is common in habitat selection and use studies, our conclusions may have differed substantially. These results underscore problems that may arise from developing fish-habitat relationships with data of limited temporal extent and of applying predictive habitat models that do not account for interannual variation, which for stream fish can be substantial (Platts and Nelson 1988; Grossman et al. 1990; House 1995; Ham and Pearsons 2000). With few notable exceptions (e.g., Long Term Ecological Research (LTER) program), scientific institutions are neither structured nor funded to support multi-year studies. Yet critical understanding about lotic ecosystems and long-term effects of land use may not emerge with any other approach (e.g., Hall et al. 1987; Tschaplinski 2000).

Habitats were selected by juvenile salmonids at each spatial scale examined in the Elk River basin. Pools were selected by all four species in the tributaries and by each species except steelhead in the mainstem. Relative to fastwater, all species selected less strongly for mainstem pools than for tributary pools, suggesting the heightened importance of pools in the tributaries. Unconstrained valleys were selected by chinook salmon, coho salmon, and cutthroat trout but were avoided by steelhead. However, valley segment types did not differ for most channel unit features that we examined. Thus, we think that it is important to first identify, then protect, those attributes or processes that influence selection by juvenile salmonids at the valley segment scale. Better understanding of the differences between steelhead and the other species in selection for pools in the mainstem and unconstrained valleys in the tributaries should improve habitat management and protection for all four species.

REFERENCES

Allen TFH, Hoekstra TW. 1992. Toward a unified ecology: complexity in ecological systems. Columbia University Press, New York, New York.

Angermeier PL, Winston MR. 1998. Local vs. regional influences on local diversity in stream fish communities of Virginia. Ecology 79(3): 911-927.

Armstrong JD, Grant JWA, Forsgren HL, Fausch KD, DeGraaf RM, Fleming IA, Prowse TD, Schlosser IJ. 1998. The application of science to the management of Atlantic salmon (*Salmo salar*): integration across scales. Canadian Journal of Fisheries and Aquatic Sciences 55(Suppl. 1): 303-311.

Baxter CV, Hauer FR. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). Canadian Journal of Fisheries and Aquatic Sciences 57: 1470-1481.

Benda L, Beechie TJ, Wissmar RC, Johnson A. 1992. Morphology and evolution of salmonid habitats in a recently deglaciated river basin, Washington State, USA. Canadian Journal of Fisheries and Aquatic Sciences 49: 1246-1256.

Bilby RE, Ward JW. 1991. Characteristics and function of large woody debris in streams draining old-growth, clear-cut, and second-growth for-

ests in southwestern Washington. Canadian Journal of Fisheries and Aquatic Sciences 48: 2499-2508.

Bisson PA, Nielsen JL, Palmason RA, Grove LE. 1982. A system of naming habitat types in small streams, with examples of habitat utilization by salmonids during low streamflow. In: Armantrout NB, editor. Acquisition and utilization of aquatic habitat inventory information. American Fisheries Society, Western Division, Bethesda, Maryland. p 62-73.

Bisson PA, Sullivan K, Nielsen JL. 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 TC, Reiser DW. 1991. Habitat requirements of salmonids in streams. American Fisheries Society Special Publication 19: 47-82.

Burck WA, Reimers PE. 1978. Temporal and spatial distribution of fall chinook salmon spawning in Elk River. Oregon Department of Fish and Wildlife, Information Reports (Fish) 78-3, Portland, Oregon.

Bustard DR, Narver DW. 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: 667-681.

Byrne M. 1996. California salmonid habitat inventory: a dynamic segmentation application. Proceedings of the ERSI Users Conference. May 20-24. Palm Springs, California.

Chesson J. 1978. Measuring preference in selective predation. Ecology 59: 211-215.

Cochran WG. 1977. Sampling techniques. Wiley, New York. 428 pp.

Cunjak RA. 1996. Winter habitat of selected stream fishes and potential impacts from land-use activity. Canadian Journal of Fisheries and Aquatic Sciences 53(Suppl. 1): 267-282.

Cupp CE. 1989. Identifying spatial variability of stream characteristics through classification. M.S. thesis, University of Washington, Seattle, Washington. 92 pp.

Dambacher J. 1991. Distribution, abundance, and emigration of juvenile steelhead (*Oncorhynchus mykiss*) and analysis of stream habitat in the Steamboat Creek basin, Oregon. MS thesis, Oregon State University, Corvallis, Oregon. 129 p.

Dixon PM. 1993. The bootstrap and jackknife: describing the precision of ecological indices. In: Scheiner SM, Gurevitch J, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York. p 290-318.

Dolloff CA, Flebbe PA, Owen MD. 1994. Fish habitat and fish populations in a southern Appalachian watershed before and after hurricane Hugo. Transactions of the American Fisheries Society 123: 668-678.

Doppelt B, Scurlock M, Frissell C, Karr J. 1993. Entering the watershed: a new approach to save America's river ecosystems. Island Press, Washington, DC. 462 p.

Downey TW, Susac GL, Nicholas JW. 1987. Research and development of Oregon's coastal chinook salmon stocks. Annual Progress Report, Fish Research Project, Oregon, Oregon Department of Fish and Wildlife. Portland, Oregon.

Edwards RT. 1998. The hyporheic zone. In: Naiman RJ, Bilby RE, editors. River ecology and management: lessons from the Pacific coastal ecoregion. Springer-Verlag, New York, New York. p 399-429.

Erickson WP, McDonald TL, Skinner R. 1998. Habitat selection using GIS data: a case study. Journal of Agricultural, Biological, and Environmental Statistics 3(3): 296-310.

Everest FH, Chapman DW. 1972. Habitat selection and spatial interaction by juvenile chinook salmon and steelhead trout in two Idaho streams. Journal Fisheries Research Board of Canada 29(1): 91-100.

Fausch KD. 1998. Interspecific competition and juvenile Atlantic salmon (*Salmo salar*): on testing effects and evaluating the evidence across scales. Canadian Journal of Fisheries and Aquatic Sciences 55(Suppl. 1): 218-231.

Fausch KD, Nakano S, Ishigaki K. 1994. Distribution of two congeneric charrs in streams of Hokkaido Island, Japan: considering multiple factors across scales. Oecologia 100: 1-12.

Folt CL, Nislow KH, Power ME. 1998. Implications of temporal and spa-

tial scale for Atlantic salmon (*Salmo salar*) research. Canadian Journal of Fisheries and Aquatic Sciences 55(Suppl. 1): 9-21.

Forest Ecosystem Management Assessment Team (FEMAT). 1993. Forest ecosystem management: an ecological, economic, and social assessment. Report of the Forest Ecosystem Management Assessment Team. United States Department of Agriculture, Forest Service; United States Department of the Interior [and others], Portland, Oregon. [irregular pagination].

Franklin JF, Dyrness CT. 1988. Natural vegetation of Oregon and Washington. Oregon State University Press, Corvallis, Oregon. 452 p.

Fraser FJ. 1969. Population density effects on survival and growth of juvenile coho salmon and steelhead trout in experimental stream-channels. In: Northcote TG, editor. Symposium on salmon and trout in streams: H.R. Macmillian lectures in fisheries. University of British Columbia, Vancouver, British Columbia. p 253-266.

Fretwell SD, Lucas HL. 1970. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19: 16-36.

Frissell CA, Liss WJ, Warren CE, Hurley MD. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. Environmental Management 10(2): 199-214.

Frissell CA. 1992. Cumulative effects of land-use on salmon habitat in southwest Oregon coastal streams. PhD dissertation, Oregon State University, Corvallis, Oregon. 227 p.

Frissell CA. 1997. Ecological principles. In: Williams JE, Wood CA, Dombeck MP, editors. Watershed restoration: principles and practices. American Fisheries Society, Bethesda, Maryland. p 96-115.

Glova GJ. 1986. Interaction for food and space between experimental populations of juvenile coho salmon (*Oncorhynchus kisutch*) and cutthroat trout (*Salmo clarki*) in a laboratory stream. Hydrobiolgia 131: 155-168.

Gordon ND, McMahon TA, Finlayson BL. 1992. Stream hydrology: an introduction for ecologists. John Wiley and Sons, New York, New York. 526 p.

Grant GE, Swanson FJ, Wolman MG. 1990. Pattern and origin of stepped-bed morphology in high gradient streams, Western Cascades, Oregon. Geological Society of America Bulletin 102: 340-352.

Gregory SV, Swanson FJ, McKee WA, Cummins KW. 1991. An ecosystem perspective of riparian zones. BioScience 41(8): 540-551.

Grossman GD, Dowd JF, Crawford M. 1990. Assemblage stability in stream fishes: a review. Environmental Management 14(5): 661-671.

Hall JD, Brown GW, Lantz RL. 1987. The Alsea watershed study: a retrospective. In: Salo EO, Cundy TW, editors. Streamside management: forestry and fishery interactions. University of Washington, Seattle, Washington. p 399-416.

Ham KD, Pearsons TN. 2000. Can reduced salmonid population abundance be detected in time to limit management impacts. Canadian Journal of Fisheries and Aquatic Sciences 57: 17-24.

Hankin DG, Reeves GH. 1988. Estimating total fish abundance and total habitat area in small streams based on visual estimation methods. Canadian Journal of Fisheries and Aquatic Sciences 45: 834-844.

Hartman GF. 1965. The role of behavior in the ecology and interaction of under-yearling coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*). Journal of Fisheries Research Board of Canada 22(4): 1035-1081.

Hawkins CP, Kershner JL, Bisson PA, Bryant MD, Decker LM, Gregory SV, McCullough DA, Overton CK, Reeves GH, Steedman RJ, Young MK. 1993. A hierarchal approach to classifying stream habitat features. Fisheries 18(6): 3-12.

Healey MC. 1991. Life history of chinook salmon (*Oncorhynchus tshawytscha*). In: Groot C, Margolis L, editors. Pacific salmon life histories. UBC Press, Vancouver, British Columbia. p 311-394.

Hearn WE. 1987. Interspecific competition and habitat segregation among stream-dwelling trout and salmon: a review. Fisheries 12(5): 24-31.

Hicks BJ. 1989. The influence of geology and timber harvest on channel morphology and salmonid populations in Oregon Coast Range streams. PhD dissertation, Oregon State University, Corvallis, Oregon. 199 p.

Hillman TW, Griffith JS, Platts WS. 1987. Summer and winter habitat selection by juvenile chinook salmon in a highly sedimented Idaho stream. Transactions of the American Fisheries Society 116: 185-195.

House R. 1995. Temporal variation in abundance of an isolated population of cutthroat trout in western, Oregon, 1981-1991. North American Journal of Fisheries Management 15: 33-41.

Hunsaker CT, Levine DA. 1995. Hierarchical approaches to the study of water quality in rivers: spatial scale and terrestrial processes are important in developing models to translate research results to management practices. BioScience 45(3): 193-203.

Inman RL, Conover WJ. 1979. The use of the rank transform in regression. Technometrics 21(4): 499-509.

Ivlev VS. 1961. Experimental ecology of the feeding of fishes. Yale University Press, New Haven, Connecticut.

Jacobs J. 1974. Quantitative measurement of food selection. Oecologia 14: 413-417.

Johnson DH. 1980. The comparison of usage and availability measurements for evaluating resource preference. Ecology 61(1): 65-71.

Labbe TR, Fausch KD. 2000. Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple spatial scales. Ecological Applications 10(6): 1774-1791.

Lamberti GA, Gregory SV, Ashkenas LR, Wildman RC, Steinman AG. 1989. Influence of channel geomorphology on dissolved and particulate matter in a Cascade mountain stream. In: Abell DS, editor. Proceedings of the California riparian systems conference: protection, management and restoration for the 1990s. Gen. Tech. Rep. PSW-110. Pacific Southwest Forest and Range Experiment Station, U.S. Department of Agriculture, Forest Service, Berkeley, California. p 33-39.

Lee DC, Grant WE. 1995. A hierarchical approach to fisheries planning and modeling in the Columbia river basin. Environmental Management 19(1): 17-25.

Lewis CA, Lester NP, Bradshaw AD, Fitzgibbon JE, Fuller K, Hakanson L, Richards C. 1996. Considerations of scale in habitat conservation and restoration. Canadian Journal of Fisheries and Aquatic Sciences 53(Suppl. 1): 440-445.

Manly B, McDonald L, Thomas D. 1993. Resource selection by animals: statistical design and analysis for field studies. Chapman & Hall, London, United Kingdom. 175 p.

Manly BFJ. 1998. Randomization, bootstrap and Monte Carlo methods in biology. Chapman & Hall, London, United Kingdom. 399 p.

McHugh MH. 1986. Landslide occurrence in the Elk and Sixes River basins, southwest Oregon. MS thesis, Oregon State University, Corvallis, Oregon. 106 p.

McSwain MD. 1987. Summer stream temperature and channel characteristics of a southwestern Oregon coastal stream. MS thesis, Oregon State University, Corvallis, Oregon. 99 p.

Meehan WR, Bjornn TC. 1991. Salmonid distributions and life histories. American Fisheries Society Special Publication 19: 47-82.

Montgomery DR, Buffington JM. 1997. Channel-reach morphology in mountain drainage basins. Geological Society of America Bulletin 109(5): 596-611.

Montgomery DR, Buffington JM, Smith RD, Schmidt KM, Pess G. 1995. Pool spacing in forest channels. Water Resources Research 31(4): 1097-1105.

National Research Council (NRC). 1996. Upstream: salmon and society in the Pacific Northwest. National Academy Press, Washington, DC. 452 p.

Nehlsen W, Williams JE, Lichatowich JA. 1991. Pacific salmon at the crossroads: stocks at risk from California, Oregon, Idaho, and Washington. Fisheries 16(2): 4-21.

Nislow KH, Folt CL, Parrish DL. 1999. Favorable foraging locations for young Atlantic salmon: application to habitat and population restoration. Ecological Applications 9(3): 1085-1099.

O'Neill RV. 1989. Perspectives in hierarchy and scale. In: Roughgarten J, May RM, Levin SA, editors. Perspectives in ecological theory. Princeton University Press, Princeton, New Jersey. p 140-156.

Otis DL. 1997. Analysis of habitat selection studies with multiple patches within cover types. Journal of Wildlife Management 61(4): 1016-1022.

Platts WS, Nelson RL. 1988. Fluctuations in trout populations and their implications for land-use evaluation. North American Journal of Fisheries Management 8: 333-345.

Poff NL. 1997. Landscape filters and species traits: towards mechanistic under-standing and prediction in stream ecology. Journal of the North American Benthological Society 16(2): 391-409.

Poole GC, Frissell CA, Ralph SC. 1997. In-stream habitat unit classification: inadequacies for monitoring and some consequences for management. Journal of the American Water Resources Association. 33: 879-896.

Rabeni CF, Sowa SP. 1996. Integrating biological realism into habitat restoration and conservation strategies for small streams. Canadian Journal of Fisheries and Aquatic Sciences 53(Suppl. 1): 252-259.

Reeves GH, Benda LE, Burnett KM, Bisson PA, Sedell JR. 1995. A disturbance-based ecosystem approach to maintaining and restoring fresh-water habitats of evolutionarily significant units of anadromous salmonids in the Pacific Northwest. In: Nielsen J, editor. Evolution and the aquatic ecosystem. American Fisheries Society Symposium 17, Bethesda, Maryland. p 334-349.

Reeves GH, Hohler DB, Hansen BE, Everest FH, Sedell JR, Hickman TL, Shively D. 1997. Fish habitat restoration in the Pacific Northwest: Fish Creek of Oregon. In: Williams JE, Wood CA, Dombeck MP, editors. Watershed restoration: principles and practices. American Fisheries Society, Bethesda, Maryland. p 335-359.

Reeves GH, Bisson PA, Dambacher JM. 1998. Fish communities. In: Naiman RJ, Bilby RE, editors. River ecology and management: lessons from the Pacific coastal ecoregion. Springer-Verlag, New York, New York. p 200-234.

Rodgers JF, Solazzi MF, Johnson SL, Buckman MA. 1992. Comparison of three techniques to estimate juvenile coho salmon populations in small streams. North American Journal of Fisheries Management 12: 79-86.

Roper BB, Scarnecchia DL. 1995. Observer variability in classifying habitat types in stream surveys. North American Journal of Fisheries Management 15: 49-53.

Roper BB, Scarnecchia DL, La Marr TJ. 1994. Summer distribution of and habitat use by chinook salmon and steelhead within a major basin of the South Umpqua River, Oregon. Transactions of the American Fisheries Society 123: 298-308.

Rosenberg DK, McKelvey KS. 1999. Estimation of habitat selection for central-place foraging animals. Journal of Wildlife Management 63: 1028-1038.

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

Rosenfeld JS, Boss S. 2001. Fitness consequences of habitat use for juvenile cutthroat trout: energetic costs and benefits in pools and riffles. Canadian Journal of Fisheries and Aquatic Sciences 58: 585-593.

Roth NE, Allan JD, Erickson DL. 1996. Landscape influences on stream biotic integrity assessed at multiple spatial scales. Landscape Ecology 11(3): 141-156.

Ryan SE, Grant GE. 1991. Downstream effects of timber harvesting on channel morphology in Elk River basin, Oregon. Journal of Environmental Quality 20: 60-72.

Sandercock FK. 1991. Life history of coho salmon (*Oncorhynchus kisutch*). In: Groot C, Margolis L, editors. Pacific salmon life histories. UBC Press, Vancouver, British Columbia. p 395-446.

Scarnecchia DL, Roper BB. 2000. Large-scale, differential summer habitat use of three anadromous salmonids in a large river basin in Oregon, USA. Fisheries Management and Ecology 7: 197-209.

Schwartz JS. 1990. Influence of geomorphology and landuse on distribution and abundance of salmonids in a coastal Oregon basin. MS thesis,

Oregon State University, Corvallis, Oregon. 207 p.

Snedecor GW, Cochran WG. 1980. Statistical Methods. Iowa State University Press, Ames, Iowa. 507 p.

Solazzi MF, Nickelson TE, Johnson SL, Rodgers JD. 2000. Effects of increasing winter rearing habitat on abundance of salmonids in two coastal Oregon streams. Canadian Journal of Fisheries and Aquatic Sciences 57: 906-914.

State of Oregon. 1997. Coastal salmon restoration initiative: the Oregon plan for salmon and watersheds. http://www.oregon-plan.org/.

Stein RA, Reimers PE, Hall JD. 1972. Social Interaction between juvenile coho (*Oncorhynchus kisutch*) and fall chinook salmon. (O. tshawytscha) in Sixes River, Oregon. Journal Fisheries Research Board of Canada 29(12): 1737-1748.

Strahler AN. 1957. Quantitative analysis of watershed geomorphology. Transactions of the American Geophysical Union 38: 913-920.

Swales S, Lauzier RB, Levings CD. 1986. Winter habitat preferences of juvenile salmonids in two interior rivers in British Columbia. Canadian Journal of Zoology 64: 1506-1514.

Taylor EB. 1990. Environmental correlates of life-history variation in juvenile chinook salmon, *Oncorhynchus tshawytscha* (Walbaum). Journal of Fish Biology 37: 1-17.

Thompson WL, Lee DC. 2000. Modeling relationships between landscape-level attributes and snorkel counts of chinook salmon and steelhead parr in Idaho. Canadian Journal of Fisheries and Aquatic Sciences 57: 1834-1842.

Torgersen CE, Price DM, Li HW, McIntosh BA. 1999. Multiscale thermal refugia and stream habitat associations of chinook salmon in northeastern Oregon. Ecological Applications 9(1): 301-319.

Trotter PC. 1997. Sea-run cutthroat trout: life history profile. In: Hall JD, Bisson PA, Gresswell RE, editors. Sea-run cutthroat trout: biology, management, and future conservation. Oregon Chapter of the American Fisheries Society, Corvallis. p 7-15.

Tschaplinski PJ. 2000. The effects of forest harvesting, fishing, climate variation, and ocean conditions on salmonid populations of Carnation Creek, Vancouver Island, British Columbia. In: Knudsen EE, Steward CR, MacDonald DD, Williams JE, Rieser DW, editors. Sustainable Fisheries Management: Pacific Salmon. CRC Press LLC, Boca Raton, FL. p 297-328.

Turner MG, Dale VH, Gardner RH. 1989. Predicting across scales: theory development and testing. Landscape Ecology 3: 245-252.

USDA Forest Service and USDI Bureau of Land Management. 1994. Record of Decision for amendments to Forest Service and Bureau of Land Manage-ment planning documents within the range of the northern spotted owl. Portland, Oregon. 74 pp. [plus Attachment A: Standards and Guidelines].

USDA Forest Service. 1998. Elk River watershed analysis, Iteration 2. Powers Ranger District, Forest Service Pacific Northwest Region, Powers, Oregon. 176 pp.

Wiens JA. 1989. Spatial scaling in ecology. Functional Ecology 3: 385-397.

Zucker SJ. 1993. Influence of channel constraint on primary production, periphyton biomass, and macroinvertebrate biomass in streams of the Oregon Coast Range. M.S. thesis, Oregon State University, Corvallis, Oregon. 47 pp.

Appendix 2.1. Percent of total estimated area at the stream system, valley segment and channel unit scales in the Elk River, Oregon (1988-1994). Stream system types are the mainstem and tributaries. Valley segment types are unconstrained valleys (UV), alluviated canyons (AC), and constrained canyons (CC). Channel unit types are pools, fastwater (FW), and side channels (SC).

Year	% Area of basin in		% Area of mainstem in			% Area of tributaries in			% Area of mainstem in			% Area of tributaries in		
	mainstem	tributaries	UV	AC	CC	UV	AC	CC	pools	FW	SC	pools	FW	SC
1988	74	26	_	64	36	29	39	32	63	37	0	35	64	0.4
1989	72	28	_	67	33	27	43	29	58	41	0.4	34	65	0.1
1990	71	29	_	67	33	27	40	33	63	36	0.1	38	61	0.7
1991	71	29	_	65	35	30	42	28	60	39	0.4	37	62	0.9
1992	69	31	_	68	32	29	42	29	65	34	0.6	37	62	0.6
1993	68	32	_	65	35	32	39	29	76	23	0.6	43	56	1.0
1994	72	28	_	63	37	29	40	31	77	22	0.2	45	54	0.5
Mean(SD)	71(2)	29(2)		65(2)	35(2)	29(2)	41(2)	30(2)	66(8)	33(8)	0.33(0.2)	39(5)	60(5)	0.7(0.2)

Year	Valley segment type	Chinook salmon density	Coho salmon density	Cutthroat trout density	Steelhead density
1988	AC	6.57 (1.43)	0.02 (0.01)	0.30 (0.06)	3.94 (0.41)
1989	AC	13.12 (1.53)	0.03 (0.01)	0.31 (0.05)	7.66 (0.72)
1990	AC	0.93 (0.25)	0.00 (0.00)	1.52 (0.33)	7.11 (0.78)
1991	AC	3.32 (0.68)	0.33 (0.21)	0.58 (0.20)	7.98 (1.05)
1992	AC	0.41 (0.12)	0.01 (0.01)	0.35 (0.07)	7.69 (0.99)
1993	AC	1.35 (0.28)	0.18 (0.09)	0.26 (0.05)	8.33 (0.75)
1994	AC	2.07 (0.33)	0.90 (0.20)	0.21 (0.04)	8.82 (0.86)
1988	CC	18.31 (2.36)	0.14 (0.04)	0.46 (0.14)	5.90 (0.94)
1989	CC	31.91 (3.77)	0.00 (0.00)	0.35 (0.08)	6.68 (1.08)
1990	CC	5.10 (1.07)	0.00 (0.00)	1.05 (0.40)	11.61 (2.83)
1991	CC	8.72 (1.21)	0.61 (0.46)	0.67 (0.24)	10.80 (1.57)
1992	CC	1.88 (0.59)	0.00 (0.00)	0.39 (0.10)	12.15 (1.56)
1993	CC	5.58 (2.20)	0.00 (0.00)	0.20 (0.04)	7.03 (0.79)
1994	CC	5.51 (1.04)	0.34 (0.14)	0.36 (0.12)	10.19 (2.05)

Appendix 2.2. Estimated total relative density (standard error) of juvenile salmonids in valley segment types for the mainstem of the Elk River, Oregon (1988-1994). Valley segment types are alluviated canyons (AC) and constrained canyons. (CC). Density is expressed as the number of fish per 100m^2.

Appendix 2.3. Estimated total relative density (standard error) of juvenile salmonids in valley segment types for the tributaries of Elk River, Oregon (1988-1994). Valley segment types are unconstrained valleys (UV), alluviated canyons (AC), and constrained canyons (CC). Density is expressed as the number of fish per 100 m^2.

Year	Valley segment type	Chinook salmon density	Coho salmon density	Cutthroat trout density	Steelhead density
1988	UV	0.62 (0.20)	0.00 (0.00)	0.59 (0.14)	4.04 (0.54)
1989	UV	3.89 (0.84)	0.00 (0.00)	0.62 (0.13)	4.44 (0.65)
1990	UV	0.12 (0.10)	0.00 (0.00)	1.10 (0.22)	4.97 (0.69)
1991	UV	0.61 (0.15)	0.04 (0.03)	0.21 (0.05)	4.06 (0.48)
1992	UV	0.00 (0.00)	0.00 (0.00)	1.15 (0.20)	6.10 (0.50)
1993	UV	0.21 (0.05)	0.30 (0.07)	0.24 (0.04)	3.95 (0.80)
1994	UV	0.74 (0.09)	4.90 (1.05)	0.37 (0.05)	5.61 (0.39)
1988	AC	0.00 (0.00)	0.00 (0.00)	0.26 (0.07)	5.76 (0.59)
1989	AC	0.14 (0.10)	0.00 (0.00)	0.38 (0.07)	5.85 (1.12)
1990	AC	0.03 (0.03)	0.00 (0.00)	1.08 (0.22)	13.50 (4.18)
1991	AC	0.00 (0.00)	0.02 (0.01)	0.26 (0.06)	7.80 (0.61)
1992	AC	0.16 (0.10)	0.68 (0.29)	1.00 (0.25)	5.85 (0.52)
1993	AC	0.03 (0.03)	0.09 (0.05)	0.23 (0.05)	6.76 (0.59)
1994	AC	0.10 (0.04)	0.09 (0.05)	0.21 (0.06)	7.18 (0.79)
1988	CC	0.80 (0.40)	0.00 (0.00)	0.24 (0.07)	5.81 (0.63)
1989	CC	0.93 (0.24)	0.00 (0.00)	0.20 (0.06)	6.10 (0.74)
1990	CC	0.05 (0.02)	0.00 (0.00)	1.61 (0.43)	7.00 (0.81)
1991	CC	0.19 (0.10)	0.04 (0.02)	0.14 (0.05)	7.51 (0.74)
1992	CC	0.00 (0.00)	0.00 (0.00)	0.16 (0.04)	6.76 (0.74)
1993	CC	0.04 (0.02)	0.17 (0.06)	0.10 (0.04)	6.19 (0.66)
1994	CC	0.16 (0.05)	1.95 (0.39)	0.31 (0.07)	8.46 (0.59)

Appendix 2.4. Estimated total relative density (number of fish per 100 m^2) of juvenile salmonids in valley segments of the Elk River, Oregon (1988-1994).

Year	Valley segment	Chinook salmon density	Coho salmon density	Cutthroat trout density	Steelhead density	Year	Valley segment	Chinook salmon density	Coho salmon density	Cutthroat trout density	Steelhead density
1988	Mainstem 2	17.88	0.23	0.33	6.07	1993	Mainstem 4	3.80	0.00	0.09	5.26
	Mainstem 3	25.62	0.00	0.17	4.90		Mainstem 5	1.69	0.00	0.12	10.61
	Mainstem 4	26.93	0.02	0.19	6.06		Mainstem 6	1.70	0.00	0.20	3.74
	Mainstem 5	28.81	0.05	0.33	5.91		Mainstem 7	2.10	0.00	0.09	11.24
	Mainstem 6	12.98	0.56	0.49	2.88		Mainstem 8	0.29	0.00	0.15	9.86
	Mainstem 7	3.88	0.06	0.79	5.26		Mainstem 9	0.28	0.27	0.34	7.12
	Mainstem 8	0.67	0.00	1.77	9.95		Mainstem 2	6.34	0.00	0.86	12.88
	Mainstem 9	0.93	0.00	0.14	2.85		Mainstem 3	6.12	0.02	0.08	7.24
1989	Mainstem 2	34.56	0.00	0.37	6.32	1994	Mainstem 4	8.46	0.17	0.26	6.57
	Mainstem 3	39.27	0.00	0.15	8.09		Mainstem 5	6.51	0.61	0.30	10.06
	Mainstem 4	46.54	0.00	0.34	6.41		Mainstem 6	1.37	1.17	0.13	3.48
	Mainstem 5	23.65	0.00	0.60	12.20		Mainstem 7	1.97	0.53	0.15	11.48
	Mainstem 6	27.88	0.00	0.38	3.04		Mainstem 8	0.75	0.59	0.05	14.31
	Mainstem 7	10.58	0.00	0.80	8.18		Mainstem 9	0.88	1.01	0.20	7.88
	Mainstem 8	6.92	0.00	0.13	7.73		Bald Mountain 1	0.57	0.00	0.40	13.00
	Mainstem 9	6.43	0.05	0.13	6.32		Bald Mountain 2			0.28	7.74
1990	Mainstem 2	6.77	0.00	0.62	14.39	1988	Bald Mountain 3			0.00	7.64
	Mainstem 3	5.17	0.00	0.40	10.36		Butler 1	0.00	0.00	0.23	0.52
	Mainstem 4	4.96	0.00	1.58	13.10		Butler 2	0.00	0.00	0.00	0.54
	Mainstem 5	1.93	0.00	4.62	8.49		North Fork Elk 1	0.46	0.00	0.29	5.43
	Mainstem 6	2.49	0.00	0.16	0.45		North Fork Elk 2	0.05	0.00	0.53	7.10
	Mainstem 7	0.86	0.00	1.02	12.30		Panther 1	0.00	0.00	0.11	5.15
	Mainstem 8						Panther 2	0.73	0.00	0.20	2.98
	Mainstem 9	0.07	0.00	0.95	5.01		Panther 3	0.00	0.00	0.09	2.18
1991	Mainstem 2	16.87	2.54	0.51	20.86		W. Fork Panther	0.00	0.00	0.42	3.84
	Mainstem 3	17.24	0.10	0.55	13.32		Red Cedar 1	6.19	0.00	0.81	2.77
	Mainstem 4	9.49	0.10	0.35	6.66		Red Cedar 2	1.21	0.00	0.93	0.68
	Mainstem 5	11.13	2.00	0.38	12.34		South Fork Elk 1	0.00	0.00	0.11	5.38
	Mainstem 6	9.82	0.00	0.00	5.20		Bald Mountain 1	0.00	0.00	0.40	11.94
	Mainstem 7	0.43	0.00	0.55	14.97		Bald Mountain 2			0.38	8.43
	Mainstem 8	0.75	0.10	1.33	9.68	1989	Bald Mountain 3			0.03	1.76
	Mainstem 9	0.04	0.05	0.60	4.35		Butler 1	0.00	0.00	0.11	2.15
1992	Mainstem 2	4.23	0.00	0.38	16.30		Butler 2	0.05	0.00	0.01	1.64
	Mainstem 3	2.65	0.00	0.26	18.54		North Fork Elk 1	3.15	0.00	0.14	7.76
	Mainstem 4	0.96	0.00	0.62	13.39		North Fork Elk 2	7.52	0.00	0.71	7.67
	Mainstem 5	0.98	0.00	1.17	17.94		Panther 1	1.78	0.00	0.00	2.63
	Mainstem 6	0.47	0.00	0.06	1.61		Panther 2	0.87	0.00	0.52	4.33
	Mainstem 7	0.10	0.00	0.50	10.14		Panther 3	0.00	0.00	0.78	3.92
	Mainstem 8	0.00	0.00	0.01	6.93		W. Fork Panther	0.28	0.23	0.33	6.07
	Mainstem 9	0.00	0.01	0.10	2.35		Red Cedar 1	2.35	0.00	0.17	4.90
1993	Mainstem 2	16.41	0.00	0.43	0.43		Red Cedar 2	0.75	0.02	0.19	6.06
	Mainstem 3	6.83	0.00	0.22	0.22		Red Cedar 3	0.00	0.05	0.33	5.91

Appendix 2.4. (continued)

Year	Valley segment	Chinook salmon density	Coho salmon density	Cutthroat trout density	Steelhead density	Year	Valley segment	Chinook salmon density	Coho salmon density	Cutthroat trout density	Steelhead density
1989	South Fork Elk 1	0.00	0.00	0.00	10.54	1992	Panther 2	0.00	0.00	0.14	3.99
1990	Bald Mountain 1	0.00	0.00	5.74	15.76		Panther 3	0.35	0.00	0.06	3.80
	Bald Mountain 2		0.00	0.94	21.16		E. Fork Panther	0.00	0.00	0.70	3.43
	Bald Mountain 3		0.00	0.00	9.14		W. Fork Panther	0.00	0.00	0.73	1.91
	Butler 1	0.13	0.00	0.10	2.86		Red Cedar 1	0.00	0.00	0.00	0.56
	Butler 2	0.08	0.00	0.28	4.99		Red Cedar 2	0.00	0.00	1.75	4.42
	North Fork Elk 1	0.10	0.00	0.10	7.59		Red Cedar 3	0.00	0.00	2.04	4.16
	North Fork Elk 2	0.01	0.00	0.21	8.97		South Fork Elk 1	0.00	0.00	0.22	10.09
	Panther 1	0.00	0.00	0.03	7.39	1993	Anvil 1	0.37	1.30	0.25	2.36
	Panther 2	0.00	0.00	1.48	9.29		Bald Mountain 1	0.00	0.00	0.20	14.63
	Panther 3	0.00	0.00	0.50	1.92		Bald Mountain 2			0.40	8.19
	E. Fork Panther	0.00	0.00	0.48	3.94		Bald Mountain 3			0.00	5.48
	W. Fork Panther	0.00	0.00	0.46	3.01		Butler 1	0.06	0.06	0.23	3.35
	Red Cedar 1	0.23	0.00	8.64	0.00		Butler 2	0.00	0.00	0.00	3.23
	Red Cedar 2	0.23	0.00	1.45	0.42		North Fork Elk 1	0.19	1.45	0.12	7.43
	Red Cedar 3	0.00	0.00	4.04	0.00		North Fork Elk 2	0.18	0.62	0.44	4.71
	South Fork Elk 1	0.00	0.00	0.00	5.19		Panther 1	0.10	0.00	0.12	1.60
1991	Anvil 1	0.69	14.81	0.83	5.49		Panther 2	0.50	0.00	0.21	2.77
	Bald Mountain 1	1.35	0.00	0.68	20.10		Panther 3	0.08	0.00	0.11	3.23
	Bald Mountain 2			0.48	10.68		E. Fork Panther	0.00	0.00	0.52	2.48
	Bald Mountain 3			0.09	5.93		W. Fork Panther	0.00	0.00	0.00	8.45
	Butler 1	0.00	0.26	0.00	5.73		Red Cedar 1	0.00	0.00	0.00	1.48
	Butler 2	0.00	0.09	0.00	5.55		Red Cedar 2	0.00	0.19	0.10	3.96
	North Fork Elk 1	0.08	0.00	0.46	6.20		Red Cedar 3	0.00	0.52	0.26	6.22
	North Fork Elk 2	0.09	0.09	0.30	5.02		South Fork Elk 1	0.00	0.00	0.00	7.72
	Panther 1	0.00	0.17	0.00	3.13	1994	Anvil 1	0.93	6.28	1.51	6.81
	Panther 2	0.03	0.00	0.14	3.17		Bald Mountain 1	0.00	1.85	0.66	22.08
	Panther 3	0.00	0.20	0.28	3.96		Bald Mountain 2			0.25	10.47
	W. Fork Panther	0.00	0.00	0.30	4.86		Bald Mountain 3			0.24	6.92
	Red Cedar 1	0.31	0.00	0.00	1.99		Butler 1	0.00	9.26	0.52	3.27
	Red Cedar 2	1.49	0.00	0.14	3.54		Butler 2	0.13	0.15	0.18	5.04
	Red Cedar 3	0.00	0.00	0.21	6.47		North Fork Elk 1	0.59	2.68	0.20	7.52
	South Fork Elk 1	0.00	0.00	0.03	8.70		North Fork Elk 2	0.61	1.27	0.49	8.47
1992	Anvil 1	0.57	15.25	0.46	4.38		Panther 1	0.56	0.00	1.27	5.56
	Bald Mountain 1	0.00	0.00	0.40	12.94		Panther 2	0.58	0.00	0.31	4.11
	Bald Mountain 2			0.54	8.70		Panther 3	0.03	0.00	0.13	2.43
	Bald Mountain 3			0.26	5.14		E. Fork Panther	0.00	0.00	0.33	1.31
	Butler 1	0.00	0.00	0.00	1.97		W. Fork Panther	0.06	0.00	0.17	3.39
	Butler 2	0.00	2.48	0.69	2.89		Red Cedar 1	0.00	4.08	0.00	4.30
	North Fork Elk 1	0.00	0.00	0.13	5.18		Red Cedar 2	0.89	11.27	0.31	4.92
	North Fork Elk 2	0.00	0.00	0.93	8.49		Red Cedar 3	0.20	0.29	0.05	4.59
	Panther 1	0.00	0.00	0.07	4.20		South Fork Elk 1	0.00	0.06	0.00	8.00