

AN ABSTRACT OF THE DISSERTATION OF

Kelly Marie Burnett for the degree of Doctor of Philosophy in Fisheries Science presented on July 11, 2001. Title: Relationships Among Juvenile Anadromous Salmonids, Their Freshwater Habitat, and Landscape Characteristics Over Multiple Years and Spatial Scales in the Elk River, Oregon.

Abstract approved: Signature redacted for privacy.



Gordon H. Reeves

Research on the distribution of juvenile salmonids in streams has been dominated by studies examining small areas over short periods. However, information relevant to freshwater influences on population persistence is likely to derive from longer-term, multi-scale studies. Relationships were examined among juvenile anadromous salmonids, their freshwater habitat, and landscape characteristics throughout the Elk River, Oregon over 7 years at multiple spatial scales. Ocean-type chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), coastal cutthroat trout (*O. clarki*) and winter-run steelhead (*O. mykiss*) comprised the salmonid assemblage. Habitat selection was quantified at stream system, valley segment, and channel unit scales by selection ratios estimated with bootstrapping methods. Unconstrained valleys in tributaries and pools in the mainstem were typically selected by each species except steelhead, which often

avoided these. Valley segment types generally did not differ for characteristics routinely assessed in stream surveys. Thus, fish probably perceived other biotic or abiotic differences among valley segment types. Evidence suggested competition may have influenced selection by coho and chinook salmon. Discriminant analysis indicated that level of use by juvenile chinook salmon appeared related to valley segment type and spatial position. Unconstrained valleys, nearby valley segments, and valley segments with larger, deeper pools, containing more wood were most highly used by chinook salmon. Mean volume and maximum depth of pools were each directly related to catchment area, which explained more variation than landscape characteristics summarized at any of five spatial scales. At each scale except the most spatially extensive, wood density in valley segments was negatively related to the percent area in resistant rock types and positively related to the percent area in mature to old forests. The most variation was explained with these landscape variables summarized at an intermediate spatial scale (i.e., sub-catchment). Although spatial scales appeared similar in processes affecting wood density, finer scales omitted key source areas for wood delivery, and coarser scales included source areas less tightly coupled to wood dynamics in surveyed channels. If only 1 or 2 years of data or one spatial scale had been examined, as commonly occurs, conclusions may have differed substantially from those in this study.

Relationships Among Juvenile Anadromous Salmonids,
Their Freshwater Habitat, and Landscape Characteristics
Over Multiple Years and Spatial Scales in the Elk River, Oregon

by

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I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

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Kelly Marie Burnett

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**Relationships Among Juvenile Anadromous Salmonids,
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**CHAPTER 1
INTRODUCTION**

Stream ecosystem research has been dominated by studies examining small areas over short periods. This follows a general trend in ecology. May (1994), summarizing reviews of published ecological literature, indicated that few investigations had a spatial extent of more than 10 m or a temporal extent of more than 1 year. Analogously, for ecological studies involving Atlantic salmon (*Salmo salar*), 80% lasted less than 5 years and 75% were conducted within a single tributary (Folt et al. 1998). Limits of understanding gained at fine spatiotemporal scales have become obvious as society attempts to cope with pervasive problems involving rivers and streams such as declining water quality and quantity (e.g., Carpenter et al. 1998; Postel 2000), loss of biological diversity and integrity (e.g., Moyle and Williams 1990; Hughes and Noss 1992), and species endangerment and extinction (e.g., Frissell 1993; Ricciardi and Rasmussen 1999). Aggregating fine-scale information from disparate sources has not provided decision makers with the necessary tools to address such issues. In response, freshwater resources are now commonly incorporated into bioregional assessments (Johnson et al. 1999). Additionally, stream ecosystem researchers are expanding their scope of inquiry (Reeves et al. 1995; Thompson and Lee 2000) and applying spatial statistics (Cooper et al. 1997), concepts from landscape ecology (Dunham and Rieman 1999;

Schlosser 1995), and multi-scale analysis (Roth et al.1996; Torgersen et al. 1999; Baxter and Hauer 2000).

Analysis at multiple scales can provide critical knowledge about system function and inform management decisions. For example, fish may respond to different habitat features at different scales. Multi-scale studies can identify these habitat features, suggest their importance to fish at different times, and distinguish natural processes responsible for their creation and maintenance. Examining multiple scales allowed Labbe and Faush (2000) to elaborate a conceptual model specifying how physical processes influence habitat features that mediate biotic processes and ultimately govern the persistence of a threatened fish, the Arkansas darter (*Etheostoma cragini*), in an intermittent stream. Tracing one of several pathways in the model, high rainfall elevated stream flow at a reach scale that restored connections among habitats. This improved the likelihood of population persistence because fish could disperse from source areas in the spring. Along a second pathway, increased rainfall produced floods that excavated pools at a habitat scale. Water remained in these deep pools during subsequent low flows, permitting fish to survive when shallower habitats dried. Their conceptual model offers practical information for anticipating management impacts. For example, flood control or water withdrawal for irrigation could negate benefits from increased precipitation by disconnecting habitats and reducing the potential to form new deep-pool refugia. Analysis at only one scale would have undoubtedly missed

physical and biotic processes necessary for the darter's persistence and reduced the study's relevancy to managers.

Multi-scale analysis arises from hierarchy theory. Hierarchy theory formalizes the awareness 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—each level is limited from above by its biotic and abiotic environment and from below by its components (O'Neill 1989). Higher levels provide context; lower levels provide mechanisms (Allen and Hoekstra 1992). Frissell et al. (1986) extended hierarchy theory to streams by refining the lower levels of Warren and Liss's (1983) spatially nested hierarchy for watershed classification. Frissell et al. (1986) presented habitat classification variables and controls on process at the stream system, valley segment, reach, channel unit, and sub-unit scales.

This attention to habitat was logical given that discovering relationships between organisms and their habitats is a cornerstone of ecology. In his presidential address to the British Ecological Society, Southwood (1977) proposed the concept of habitat as a templet for ecological strategies. He stressed the role of spatial and temporal heterogeneity in determining optimal habitats for species with different

reproductive strategies and in structuring the communities that they comprise (Southwood 1977; Southwood 1988). Poff and Ward (1990) detailed the relevance of 'habitat as templet' for ecosystem recovery following disturbance in streams. The view that habitat is a key determinant of community structure and organization has been integral to many developments in stream ecology, including the river continuum (Vannote et al. 1980) and process domain (Montgomery 1999) concepts, as well as the multi-scale hierarchical framework of Frissell et al. (1986).

There is no single right scale for studying relationships between fish and their habitat. The question at hand should determine which scales are examined (Wiens 1989). Investigations targeting finer scales (i.e., channel unit (10^0 - 10^1 m) or below and <1 year) may be appropriate for many questions, such as how habitat mediates interactions between a fish and conspecifics. But, for other questions, particularly those related to freshwater habitat influences on populations of anadromous salmonids, pertinent information is more likely to derive from coarser spatial scales (i.e., watershed (10^3 - 10^4 m) or above and >10 years) (Reeves et al. 1995). Watersheds are a particularly useful spatial extent for relating a population of anadromous salmon to its habitat and a collection of watersheds for relating a meta-population to its habitat (Reeves et al. 1995). However, salmonid-habitat relationships have been infrequently explored throughout a watershed (e.g., Dolloff et al. 1994; Roper et al. 1994; Scarnecchia and Roper 2000). Such watershed studies over longer periods (i.e., one or more generations for the species of interest) are valuable but even less common (e.g., Reeves et al. 1997). Population

abundances of stream fish and factors influencing these abundances may fluctuate from year to year (Platts and Nelson 1988; Grossman et al. 1990; House 1995; Ham and Pearsons 2000). Thus, failing to account for interannual variation may limit understanding of fish-habitat relationships and the transferability of results among years.

The condition of stream habitat is largely a function of conditions in the watershed that it drains (Hynes 1975; Frissell et al. 1986; Naiman et al. 1992). Thus, a watershed perspective is often recommended for studying and managing stream systems (Doppelt et al. 1993; FEMAT 1993; NRC 1996). Direct, local effects on stream habitat of features in the riparian area are relatively well established (Osborne and Koviac 1993; Naiman et al. 2000). Less well understood and agreed upon are relationships between stream habitat and riparian characteristics accumulated upstream along a channel network (e.g., Weller et al. 1998; Jones et al. 1999) or riparian and upslope characteristics accumulated throughout a catchment (e.g., Jones and Grant 1996; Thomas and Megahan 1998; Jones and Grant 2001). Riparian and catchment characteristics have been compared across multiple spatial scales for their influences on stream ecosystems in agricultural systems. However, these influences have seldom been compared for streams in mountainous areas where silviculture was the dominant land use. Abundances of Pacific salmon and trout (*Oncorhynchus spp.*) or conditions of their freshwater habitat have been related to landscape characteristics at different spatial scales, including the local riparian area (Bilby and Ward 1991), the entire riparian

network (Botkin et al. 1995; Lunetta et al. 1997), and the catchment (e.g., Reeves et al. 1993; Dose and Roper 1994; Dunham and Rieman 1999; Thompson and Lee 2000). Although these studies offered critical insights, none directly compared relationships between stream habitat and landscape characteristics at multiple spatial scales. I am aware of only two response variables, macroinvertebrate biological integrity (Hawkins et al. 2000) and abundance of adult coho salmon (*Oncorhynchus kisutch*) (Pess et al. in review), for which relationships to riparian and catchment characteristics were compared in streams draining forested, montane regions. Analogous multi-scale assessments can identify riparian and upslope areas that help create and maintain stream habitat in forestry-dominated landscapes.

I have two primary goals in this dissertation. The first is to understand relationships between juvenile anadromous salmonids and their habitat at multiple spatial scales throughout a watershed over multiple years. And the second is to understand relationships between fish habitat and landscape characteristics summarized at multiple spatial scales. Chapter 2 addresses habitat availability for and selection by members of the juvenile anadromous salmonid assemblage in the Elk River, Oregon for each of 7 years (1988-1994). Ocean-type chinook salmon (*Oncorhynchus tshawytscha*), coho salmon (*O. kisutch*), coastal cutthroat trout (*O. clarki*), and steelhead (*O. mykiss*) comprise the salmonid assemblage. Examined spatial scales are the stream system, the valley segment, and the channel unit. Habitat selection ratios and associated confidence intervals are calculated with bootstrapping methods. Interannual patterns of habitat selection are examined in

relation to environmental factors and to fish density as an indicator of potential intra- and interspecific competition. Variation in fish habitat characteristics is described at the stream system and valley segment scales within and among years.

Chapter 3 relates the annual distribution (1988-1994) of juvenile ocean-type chinook salmon among valley segments in tributaries of the Elk River to habitat features at the valley segment and channel unit scales. Stream habitat is typically thought to be less critical to juvenile ocean-type chinook salmon than to other species of salmonids that spend more time in freshwater. Habitat characteristics may, however, be important to ocean-type chinook salmon in basins, such as the Elk River, that lack a well developed estuary and that support a population exhibiting diversity in the length of freshwater residency. If habitat features are irrelevant, I expect these to explain little of the among-valley segment variation in fish use in any single year and to be inconsistently related to fish use among years. Discriminant analysis is applied to identify valley segment and channel unit features that distinguish between valley segments that are highly used by juvenile chinook salmon and those that are not. The transferability of resulting models to other years for Elk River is assessed.

Chapter 4 seeks to explain among-valley segment variation for channel unit features in the Elk River, a forested montane system, using catchment area and landscape characteristics (i.e., lithology, topography, and land cover) summarized at five spatial scales. Channel unit features are those that help distinguish between levels of use for juvenile chinook salmon. Spatial scales are designed to differ in

the area incorporated upslope and upstream of surveyed valley segments and consist of three riparian buffer scales (i.e., corridor, sub-network, and network) and two upslope scales (i.e., sub-catchment and catchment). By comparing relationships between fish habitat and landscape characteristics at multiple spatial scales, I hope to determine which riparian and upslope areas are most tightly linked to channel unit features. Any similarities and differences among the scales should suggest key processes responsible for the relationships.

A context for this study is provided by research in the Elk River basin over the past three decades. This tradition began prior to the establishment of the State of Oregon salmon hatchery on Elk River in 1968. The hatchery was intensively supported during the first two decades by the Coastal Chinook Salmon Studies research project of the Oregon Department of Fish and Wildlife. Under the auspices of this project, information was acquired on numerous aspects of chinook salmon ecology in the Elk and other coastal Oregon rivers. Much of this was published in annual and special reports of the Oregon Department of Fish and Wildlife Research Section and is summarized in Nicholas and Hankin (1988). Data collected on ocean-type chinook salmon in Elk River included interactions among juveniles (Reimers 1968), numbers of returning hatchery and wild adults (Nicholas and Downey 1983; Hankin et al. 1993), and the spatial and temporal distribution of spawning adults (Burck and Reimers 1978). Another research project on the Elk River was initiated in the mid-1980s by a team from Oregon State University and the Pacific Northwest Research Station of the United States Forest Service. The

focus of that effort was to examine landsliding relative to rock type and land management (McHugh 1986), riparian and channel responses to hillslope erosional processes (Ryan and Grant 1991), and natural and management effects on stream temperatures (McSwain 1987). Characterizing juvenile salmonid populations and their habitats was also an objective of that project. The present study continues work on this objective.

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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

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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 (10^0 - 10^1 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 (10^3 - 10^4 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) (10^1 - 10^2 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 confidence 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

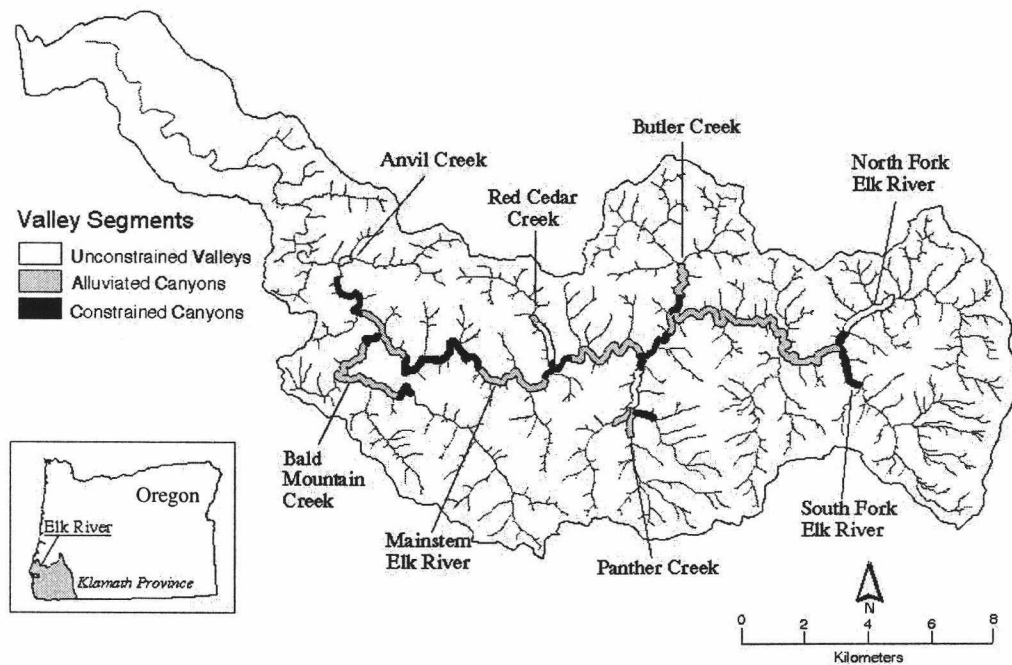


Figure 2.1. Location and map of the Elk River, Oregon with valley segments identified for anadromous fish-bearing sections of the mainstem and its tributaries.

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)

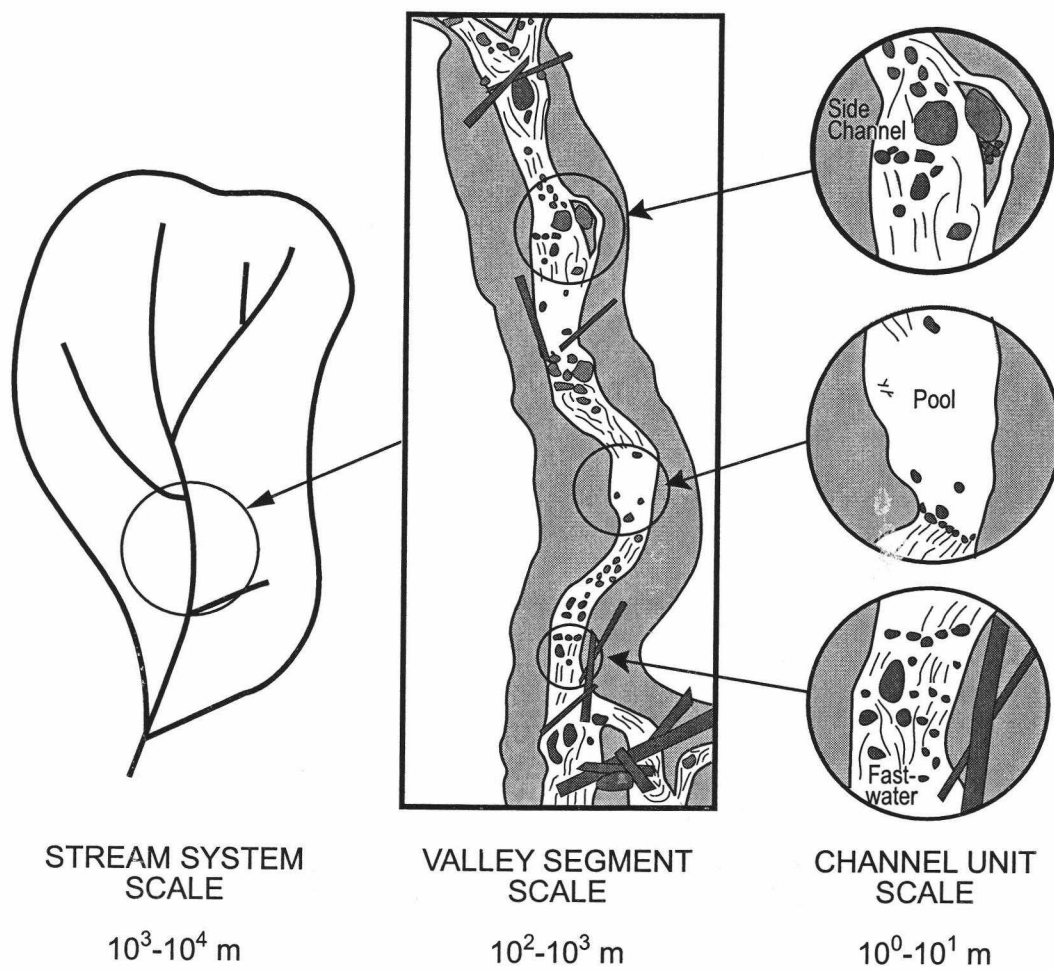


Figure 2.2. Spatial scales examined in the Elk River, Oregon. Linear spatial scale approximates units in 3rd-5th order channels (figure adapted from Frissell et al. 1986).

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).

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	4251	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)	

Table 2.1. (continued)

Valley segment	Valley segment type	Length (m)	Mean (SD) % gradient	Drainage area (ha)
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)	

(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 \cong 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 3 weeks. Data were collected for 23 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.

Each channel unit was classified by type [i.e., 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 (i.e., 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., \geq 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 10:00a.m. and 4:00p.m. 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/INFO¹ (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 obtain channel unit features of mean length (m), mean wetted width (m), mean maximum depth of pools (m); mean volume (m³); 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 m²) 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

¹The 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.

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 m².

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)

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 7 years for each species, selection functions were developed for each of the two types at the stream system scale (i.e., mainstem and tributaries); for

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 100m².

Year	Chinook salmon		Coho salmon		Cutthroat trout		Steelhead	
	mainstem	tributaries	mainstem	tributaries	mainstem	tributaries	mainstem	tributaries
1988	10.1 (1.3)	0.60 (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)

Table 2.4. Estimated stream discharge and water temperature in the Elk River, Oregon (1988-1994). Data were obtained from the USGS gauge (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).

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°)	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

each of the three types at the valley segment scale (i.e., 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 (i.e., 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):

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

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 Bonferroni 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 unit

Table 2.5. Percent of habitat area sampled for fish (p_i) 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).

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	34	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)

scale. 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 pairwise 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 confidence 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 $\alpha=0.05$. One-way ANOVA was used to compare means of channel unit features among years for each stream system type (i.e., mainstem and tributaries) and each valley segment type (i.e., unconstrained valleys, alluviated canyons, and unconstrained canyons). A Bonferroni adjustment was applied for the 21 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 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

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		1989		1990		1991		1992		1993		1994	
		Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	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†	(0.4)	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†	(0.3)	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 ¹	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	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)

†Means for year were significantly ($P \leq 0.001$) different.

*Means for year were significantly ($P \leq 0.05$) different.

¹ANOVA for among-year means comparison conducted on ranked data

²Means with the same subscript were significantly ($P \leq 0.05$ after Bonferroni adjustment for 21 comparisons) different between years.

Table 2.6. (continued)

	Stream System Type	1988		1989		1990		1991		1992		1993		1994	
		Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	SE
Pools:															
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† _b	(3.7)	31.7 _{ab}	(6.0)	14.7*	(5.1)

†Means for year were significantly ($P \leq 0.001$) different.

*Means for year were significantly ($P \leq 0.05$) different.

¹ANOVA for among-year means comparison conducted on ranked data.

²Means with the same subscript were significantly ($P \leq 0.05$ after Bonferroni adjustment for 21 comparisons) different between years.

Table 2.6. (continued)

	Stream System Type	1988		1989		1990		1991		1992		1993		1994	
		Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	SE
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 ¹ small gravel as dominant substrate	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 ($P \leq 0.001$) different.

*Means for year were significantly ($P \leq 0.05$) different.

¹ANOVA for among-year and each within-year means comparison conducted on ranked data.

²Means with the same subscript were significantly ($P \leq 0.05$ after Bonferroni adjustment for 21 comparisons) different between years.

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 (i.e., 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 (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).

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		1989		1990		1991		1992		1993		1994	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	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	89.0	(10.4)	117.5*	(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	<i>13.9²</i>	<i>(0.8)</i>	11.7	(0.4)	<i>11.7</i>	<i>(0.3)</i>	11.5	(1.3)	10.9	(0.7)	12.2	(0.7)	<i>12.8</i>	<i>(0.5)</i>
	CC	<i>12.5</i>	<i>(0.8)</i>	11.2	(0.4)	<i>10.8</i>	<i>(0.3)</i>	10.7	(1.3)	10.6	(0.7)	11.2	(0.7)	<i>11.7</i>	<i>(0.5)</i>
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	<i>703.1</i>	<i>(169.3)</i>	895.2	(180.1)	<i>731.3*</i>	<i>(80.7)</i>	567.8	(170.2)	455.6	(105.5)	634.9	(154.6)	628.1	(228.2)
	CC	<i>943.9</i>	<i>(169.3)</i>	1291.0	(180.1)	<i>1385.5*</i>	<i>(80.7)</i>	876.9	(170.2)	729.9	(105.5)	936.4	(154.6)	1150.4	(228.2)

*Means were significantly ($P \leq 0.05$) different between valley segment types for that year.

¹Means in bold and italic were significantly ($P \leq 0.05$) correlated with drainage area and were adjusted for that covariate in ANCOVA.

²Means with the same subscript were significantly ($P \leq 0.05$ after Bonferroni adjustment for 21 comparisons) different between years.

³ANOVA for among-year means comparisons conducted on ranked data.

Table 2.7. (continued)

	Valley Segment Type	1988		1989		1990		1991		1992		1993		1994	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Pools:															
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	(1.2)	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)	<i>55.6*_{de}¹</i>	(3.8)	64.2	(6.5)	76.3 _{abd}	(5.9)	75.3 _{cc}	(5.0)
	CC	72.0	(5.8)	74.3	(8.2)	78.1	(6.6)	<i>72.9*</i>	(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)

*Means were significantly ($P \leq 0.05$) different between valley segment types for that year.

¹Means in bold and italic were significantly ($P \leq 0.05$) correlated with drainage area and were adjusted for that covariate in ANCOVA.

²Means with the same subscript were significantly ($P \leq 0.05$ after Bonferroni adjustment for 21 comparisons) different between years.

³ANOVA for among-year means comparisons conducted on ranked data.

Table 2.7. (continued)

	Valley Segment Type	1988		1989		1990		1991		1992		1993		1994	
		Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
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 ³ small gravel as dominant substrate	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 ($P \leq 0.05$) different between valley segment types for that year.

¹Means in bold and italic were significantly ($P \leq 0.05$) correlated with drainage area and were adjusted for that covariate in ANCOVA.

² Means with the same subscript were significantly ($P \leq 0.05$ after Bonferroni adjustment for 21 comparisons) different between years.

³ANOVA for among-year and each within-year means comparison 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 error) 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		1989		1990		1991		1992		1993		1994	
		Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Pools:															
Mean length (m)	UV	21.6	(3.3)	25.1	(5.8)	26.4	(4.5)	20.1	(3.0)	23.4¹	(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	(0.08)	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)

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

¹Means in bold and italic were significantly ($P \leq 0.05$) correlated with drainage area and were adjusted for that covariate in ANCOVA.

²Means with the same subscript were significantly ($P \leq 0.05$ after Bonferroni adjustment for 21 comparisons) different between years.

Table 2.8. (continued)

	Valley Segment Type	1988		1989		1990		1991		1992		1993		1994	
		Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Pools:															
Mean volume (m ³)	UV	<i>57.5¹</i>	<i>(6.7)</i>	65.5	(20.4)	64.6	(20.8)	<i>48.8</i>	<i>(10.9)</i>	<i>56.2</i>	<i>(8.9)</i>	<i>53.1</i>	<i>(6.5)</i>	<i>45.3</i>	<i>(5.4)</i>
	AC	<i>49.1</i>	<i>(6.0)</i>	42.3	(15.8)	40.9	(16.1)	<i>49.6</i>	<i>(10.0)</i>	<i>57.9</i>	<i>(8.1)</i>	<i>44.1</i>	<i>(5.9)</i>	<i>40.2</i>	<i>(4.9)</i>
	CC	<i>56.6</i>	<i>(4.5)</i>	64.4	(13.4)	51.6	(12.7)	<i>46.2</i>	<i>(8.5)</i>	<i>40.0</i>	<i>(6.4)</i>	<i>38.1</i>	<i>(4.7)</i>	<i>35.5</i>	<i>(3.9)</i>
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	(3.3)	7.5	(4.0)
Frequency (no./km)	UV	16.1	(2.7)	11.7	(3.4)	15.2	(3.6)	<i>21.1</i>	<i>(3.3)</i>	18.2	(3.0)	23.7	(4.9)	<i>21.9*</i>	<i>(3.8)</i>
	AC	19.5	(2.3)	17.1	(2.7)	16.3	(2.8)	<i>18.7</i>	<i>(3.0)</i>	17.2	(2.7)	24.7	(4.4)	<i>24.1</i>	<i>(3.4)</i>
	CC	19.0 ² _a	(1.8)	16.2 _{bf}	(2.3)	20.2 _c	(2.2)	<i>22.8_d</i>	<i>(2.6)</i>	22.5 _e	(2.2)	29.0 _f	(3.5)	<i>34.6*_{abcde}</i>	<i>(2.7)</i>
%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)

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

¹Means in bold and italic were significantly ($P \leq 0.05$) correlated with drainage area and were adjusted for that covariate in ANCOVA.

²Means with the same subscript were significantly ($P \leq 0.05$ after Bonferroni adjustment for 21 comparisons) different between years.

Table 2.8. (continued)

	Valley Segment Type	1988		1989		1990		1991		1992		1993		1994	
		Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Pools:															
%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	(6.1)	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)

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

¹Means in bold and italic were significantly ($P \leq 0.05$) correlated with drainage area and were adjusted for that covariate in ANCOVA.

²Means with the same subscript were significantly ($P \leq 0.05$ after Bonferroni adjustment for 21 comparisons) different between years.

³ANOVA for among-year and each within-year means comparison was conducted on the ranked data.

Table 2.8. (continued)

	Valley Segment Type	1988		1989		1990		1991		1992		1993		1994	
		Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)	Mean	(SE)
Fastwater:															
%Area with large gravel as dominant substrate	UV	<i>12.0^l</i>	<i>(4.9)</i>	<i>22.8</i>	<i>(9.5)</i>	24.0	(6.7)	38.7	(6.9)	41.5	(8.8)	<i>30.1</i>	<i>(6.8)</i>	21.3	(9.1)
	AC	<i>6.8</i>	<i>(4.3)</i>	<i>7.7</i>	<i>(7.7)</i>	15.1	(5.2)	19.8	(6.2)	28.5	(7.9)	<i>12.3</i>	<i>(6.2)</i>	27.7	(8.2)
	CC	<i>7.5</i>	<i>(3.2)</i>	<i>19.5</i>	<i>(6.4)</i>	12.2	(4.1)	27.3	(5.2)	22.7	(6.2)	<i>9.2</i>	<i>(4.9)</i>	8.3	(6.5)
%Area with ³ small gravel as dominant substrate	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 ($P \leq 0.05$ after Bonferroni adjustment for 3 comparisons) different between valley segment types.

^lMeans in bold and italic were significantly ($P \leq 0.05$) correlated with drainage area and were adjusted for that covariate in ANCOVA.

²Means with the same subscript were significantly ($P \leq 0.05$ after Bonferroni adjustment for 21 comparisons) different between years.

³ANOVA for among-year and each within-year means comparison was conducted on the ranked data.

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 ($P \leq 0.05$) and selected for this stream system type with a higher probability than for the tributaries ($P \leq 0.1$) (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 ($P \leq 0.1$) (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 ($P \leq 0.1$) in 4 of 7 years (Fig. 2.3d).

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 ($P \leq 0.03$) in 2 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 ($P \leq 0.03$) (Fig. 2.4b).

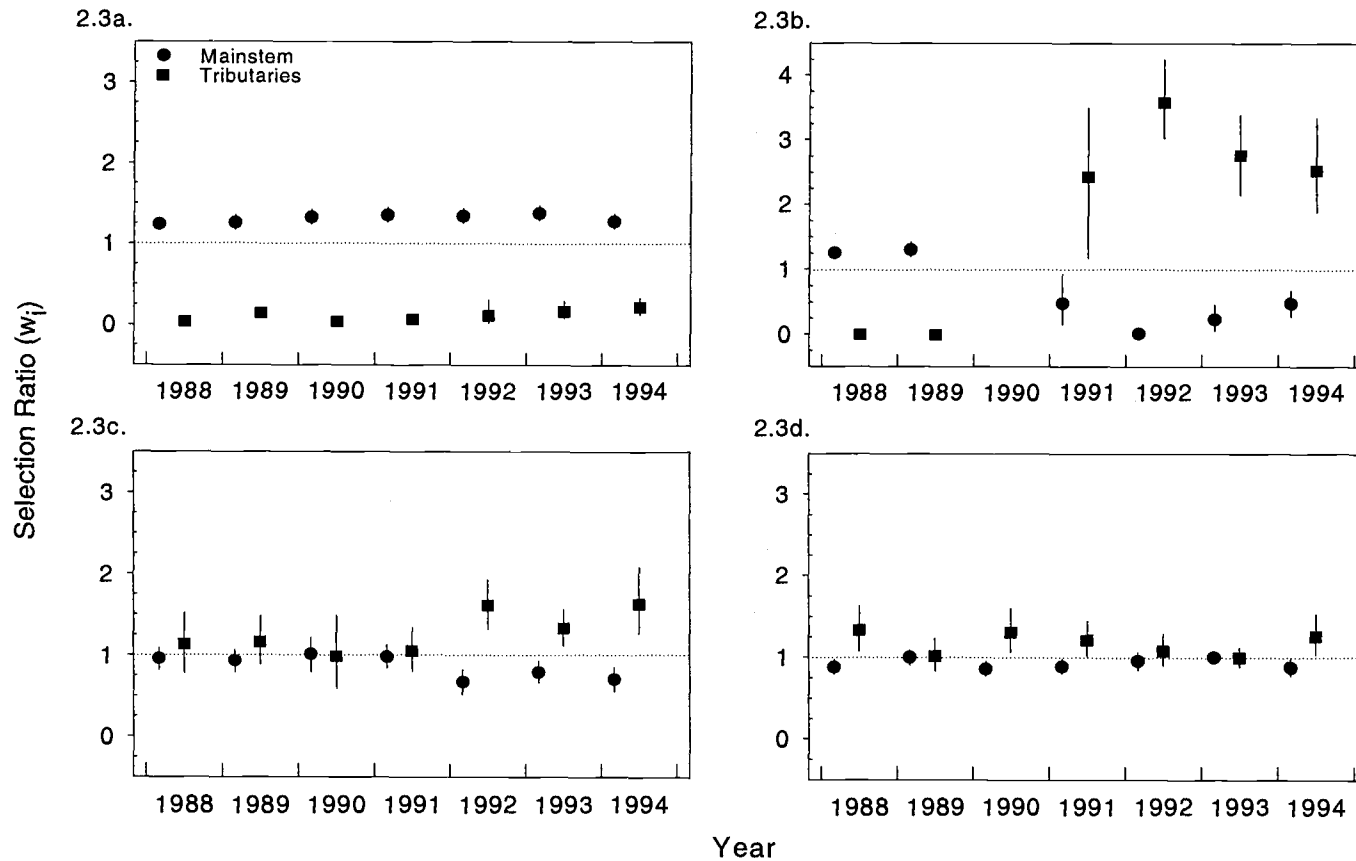
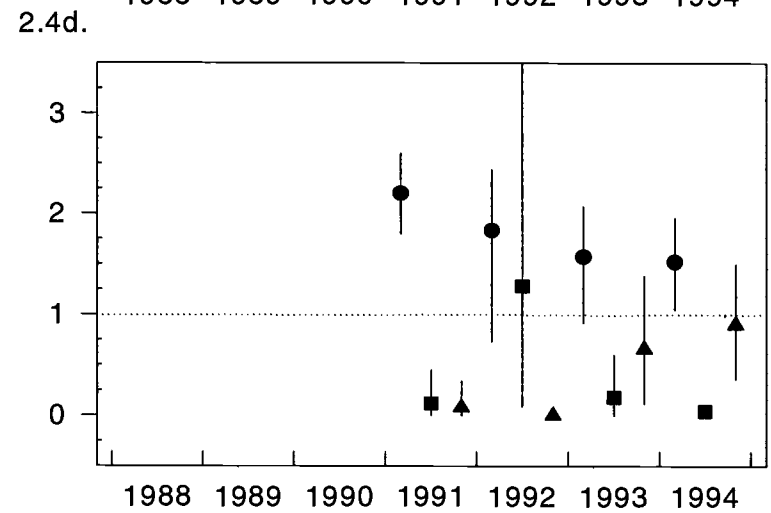
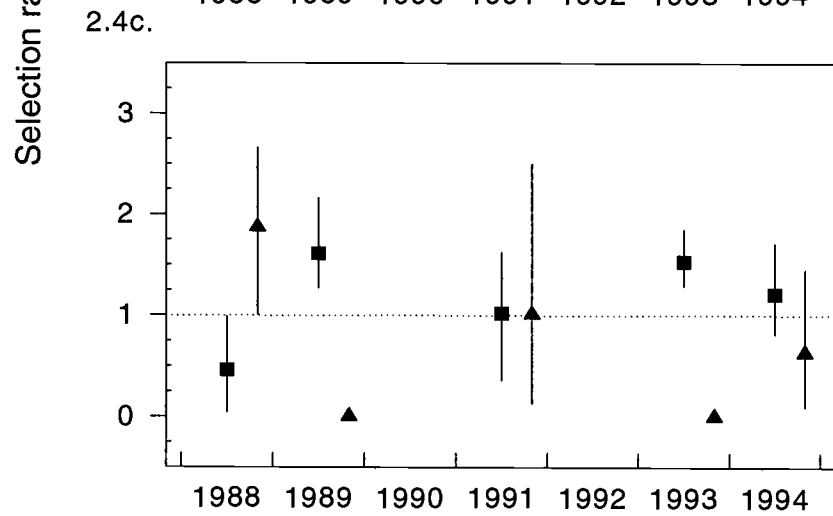
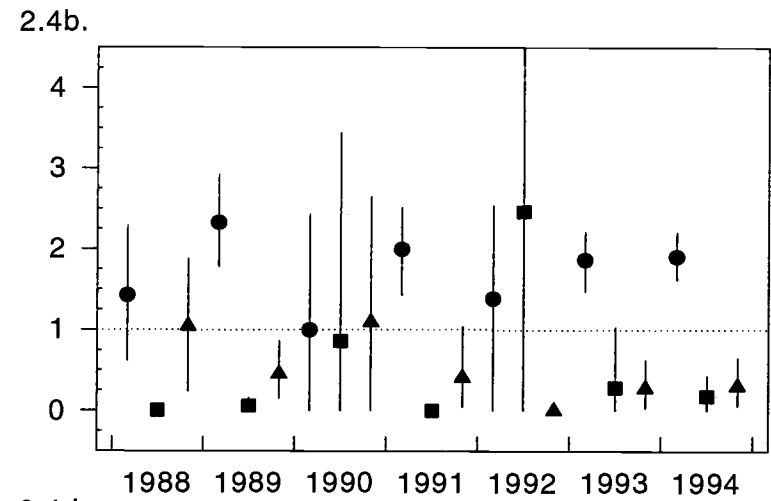
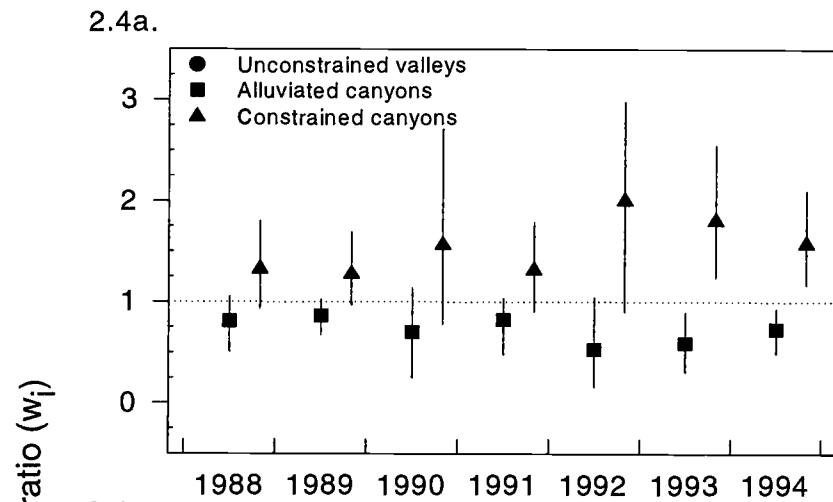
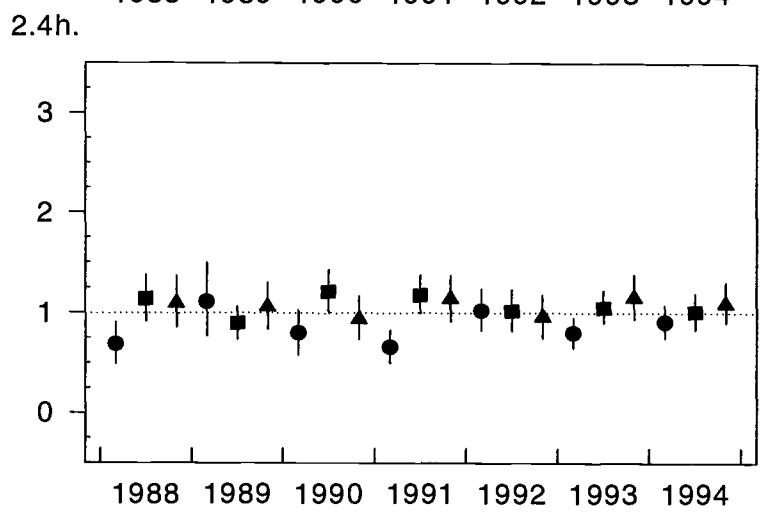
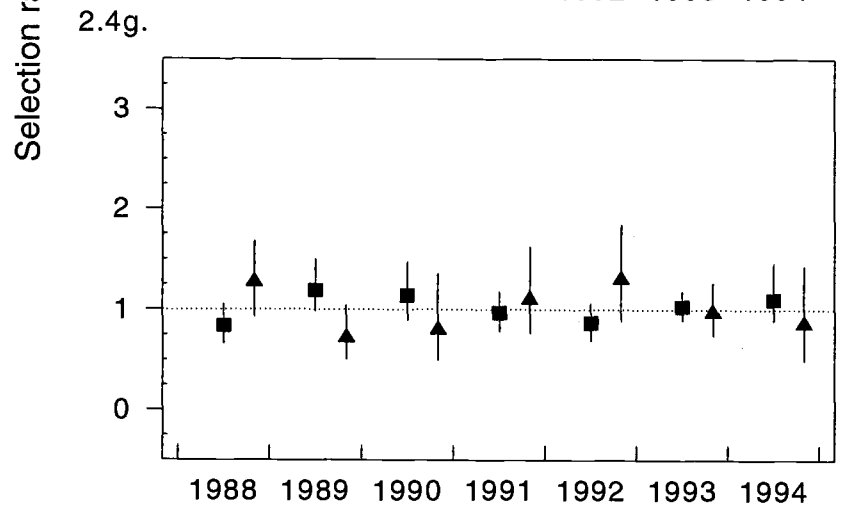
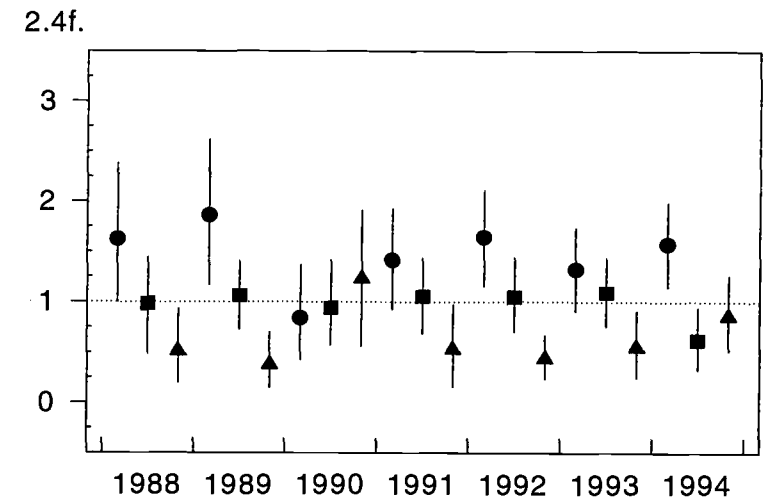
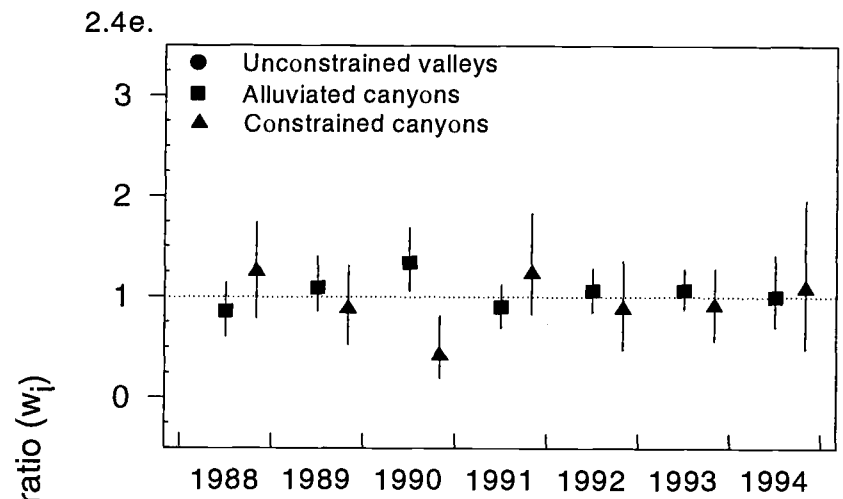


Figure 2.3. Selection ratios of juvenile salmonids for the mainstem and tributaries in Elk River, Oregon (1988-1994) for: chinook salmon (a); coho salmon (b); cutthroat trout (c); and steelhead (d). Coho salmon were not observed in the basin in 1990. A selection ratio was significant when the Bonferroni-adjusted confidence interval ($\alpha=0.1/2$) did not include one. For a given year, selection ratios were significantly different ($\alpha=0.1$) if their confidence intervals did not overlap.

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 mainstem (a) and tributaries (b); coho salmon in the mainstem (c) and tributaries (d); cutthroat trout in the mainstem (e) and tributaries (f); and steelhead in the mainstem (g) and tributaries (h). 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 ($\alpha=0.1/3$) did not include one. For a given year, selection ratios were significantly different ($\alpha=0.1/3$ Bonferroni adjusted) if their confidence intervals did not overlap.





Year

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 ($P \leq 0.03$) in 2 of the 5 years that they were observed in the mainstem (Fig. 2.4c). Coho salmon in the tributaries selected for unconstrained valleys ($P \leq 0.03$) in 1991 and 1994. This valley segment type was selected with a higher probability than alluviated canyons ($P \leq 0.03$) in 3 years and with a higher probability than constrained canyons ($P \leq 0.03$) in 2 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 1 year (1990) when alluviated canyons were selected over constrained canyons ($P \leq 0.03$) (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 ($P \leq 0.03$) in 4 years and alluviated canyons in 1 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 3 years (1988, 1991, and 1993), the probability of selecting unconstrained valleys was

less than one ($P \leq 0.03$) and less than that of selecting either of the other two valley segment types ($P \leq 0.03$) in the tributaries (Fig. 2.4h).

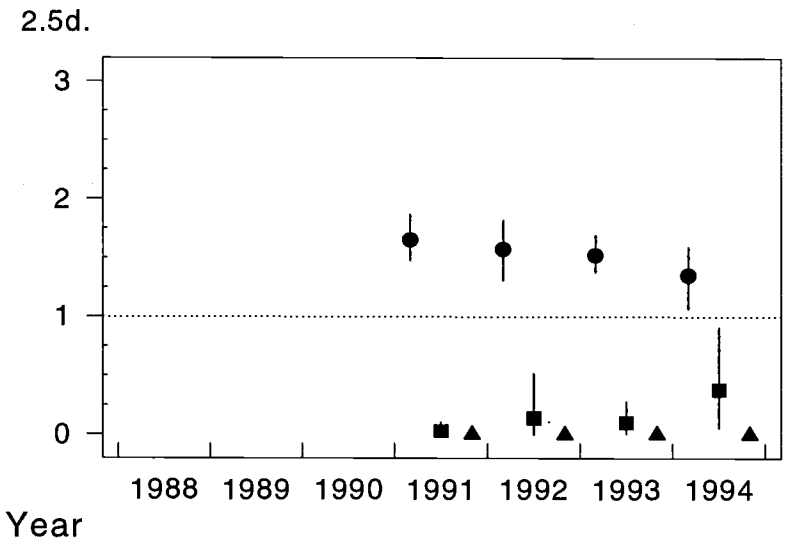
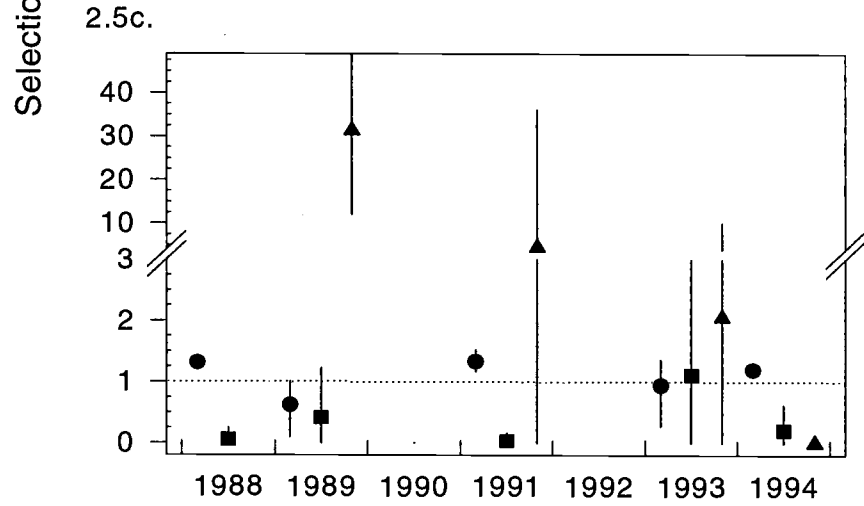
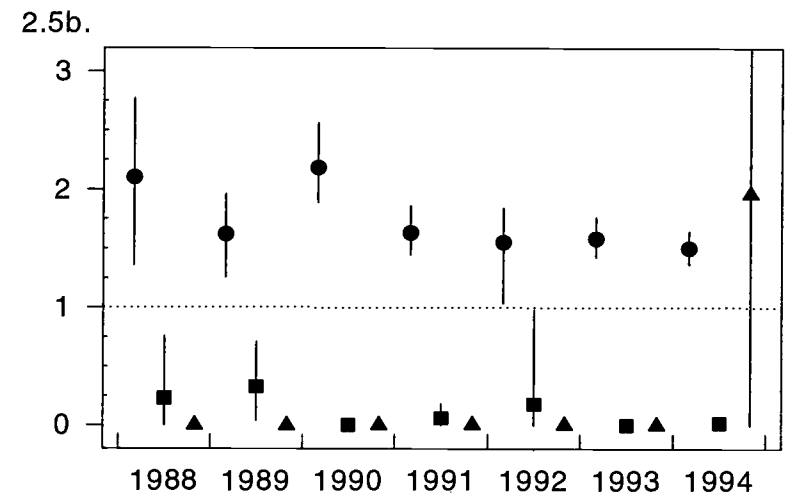
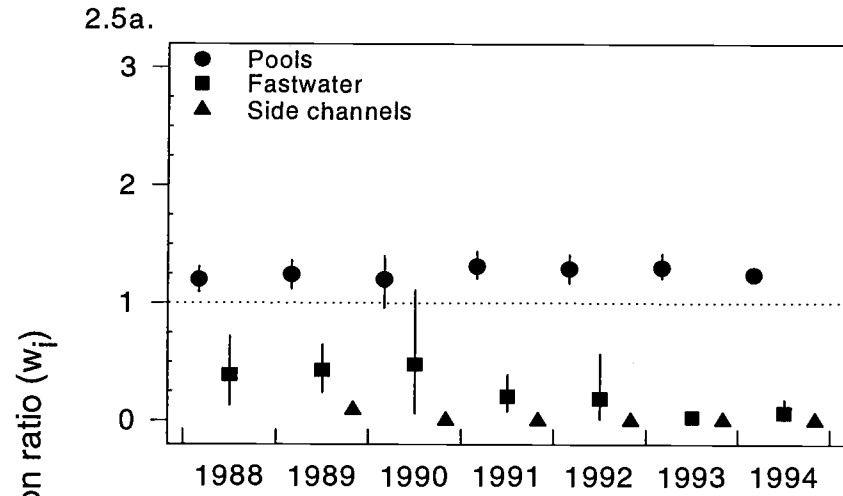
Channel unit scale

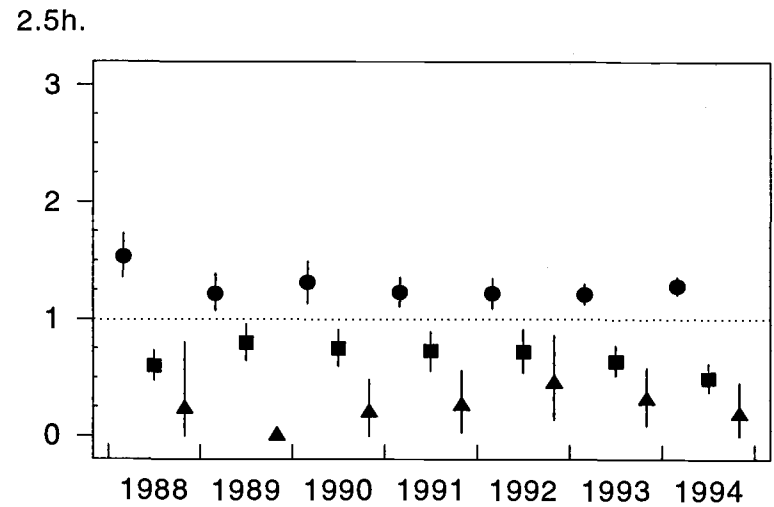
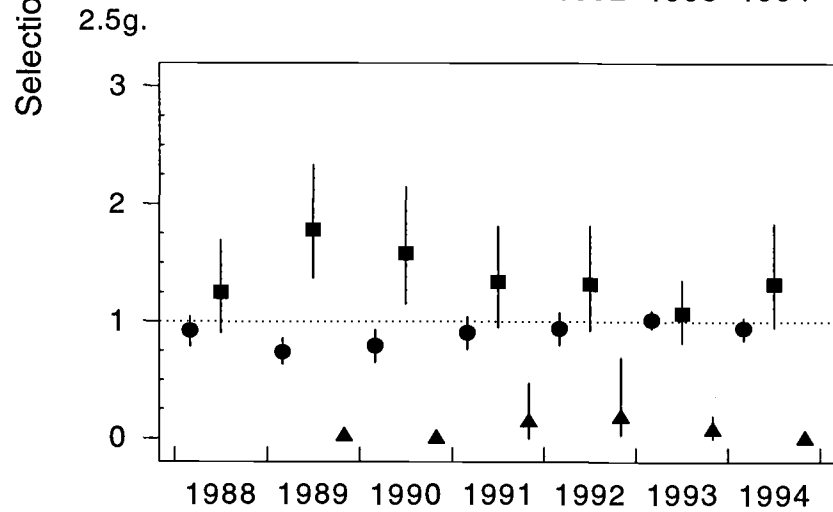
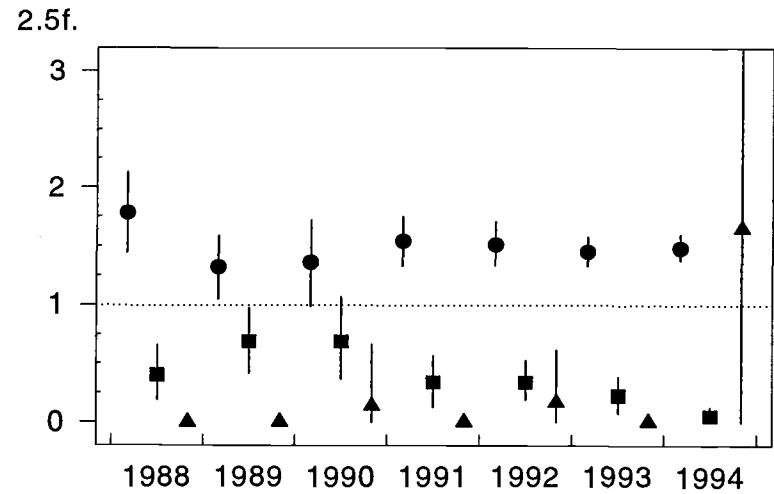
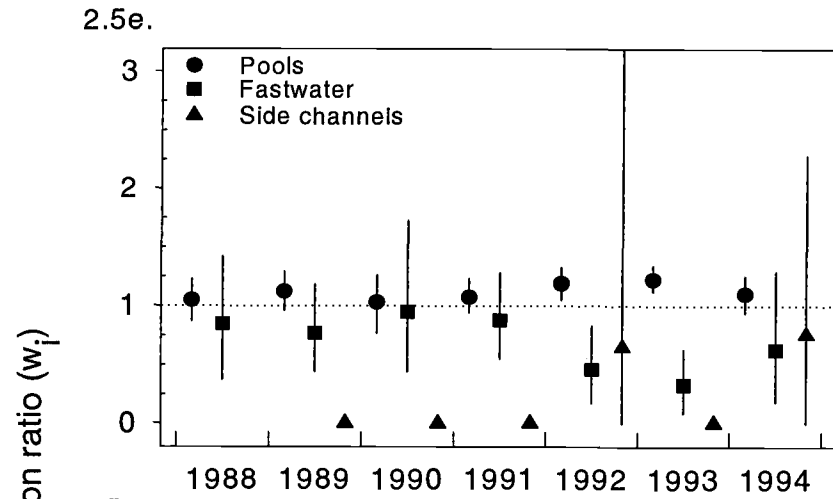
All four species selected for pools in the tributaries but selected less strongly for this channel unit type relative to fastwater in the mainstem (Fig. 2.5). Chinook salmon generally selected pools and avoided fastwater and side channels in both the mainstem and tributaries (Figs. 2.5a and b). Pools were selected ($P \leq 0.03$) and were selected with a greater probability than fastwater ($P \leq 0.03$) for all except 1 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 channel unit types were avoided in the tributaries ($P \leq 0.03$) (Fig. 2.5d). For 3 of the 5 years that coho salmon were observed in the mainstem, they selected for pools ($P \leq 0.03$) and against fastwater ($P \leq 0.03$). 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

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 mainstem (a) and tributaries (b); coho salmon in the mainstem (c) and tributaries (d); cutthroat trout in the mainstem (e) and tributaries (f); and steelhead in the mainstem (g) and tributaries (h). 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 ($\alpha=0.1/3$) did not include one. For a given year, selection ratios were significantly different ($\alpha=0.1/3$ Bonferroni adjusted) if their confidence intervals did not overlap.





usually selected over the other two channel unit types (Fig. 2.5f). Cutthroat trout selected pools with a higher probability than fastwater ($P \leq 0.03$) for only two years (1992 and 1993) in the mainstem and for all except 1 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 ($P \leq 0.03$) 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.

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

¹ns - not significant ($\alpha=0.05$).

²Regression not attempted because sample size was too small.

³Regression with the maximum daily stream flow during spring was conducted only at the stream system scale.

Table 2.9. (continued)

Species	Stream system	Valley segment		Channel unit	
		mainstem	tributaries	mainstem	tributaries
Cutthroat trout	ns ¹ 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

¹ ns - not significant ($\alpha=0.05$).

²Regression was not attempted because sample size was too small.

³Regression with the maximum daily stream flow during spring was conducted only at the stream system scale.

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 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 ramifications 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 stream system types varied among species in the Elk River basin. Chinook salmon selected the mainstem over the tributaries in each of the 7 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 were 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 1 and 2 years, respectively, and chinook salmon selected for mainstem constrained canyons in 2 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.

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Appendices

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 colluvial/competent bedrock 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)

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 100 m².

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 2.3 Estimated total relative density (standard error) of juvenile salmonids in valley segment types for the tributaries of the 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 m².

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/100 m²) of juvenile salmonids in valley segments of the Elk River, OR (1988-1994).

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
	Mainstem 3	25.62	0.00	0.17	4.90
	Mainstem 4	26.93	0.02	0.19	6.06
	Mainstem 5	28.81	0.05	0.33	5.91
	Mainstem 6	12.98	0.56	0.49	2.88
	Mainstem 7	3.88	0.06	0.79	5.26
	Mainstem 8	0.67	0.00	1.77	9.95
	Mainstem 9	0.93	0.00	0.14	2.85
	Mainstem 2	34.56	0.00	0.37	6.32
1989	Mainstem 3	39.27	0.00	0.15	8.09
	Mainstem 4	46.54	0.00	0.34	6.41
	Mainstem 5	23.65	0.00	0.60	12.20
	Mainstem 6	27.88	0.00	0.38	3.04
	Mainstem 7	10.58	0.00	0.80	8.18
	Mainstem 8	6.92	0.00	0.13	7.73
	Mainstem 9	6.43	0.05	0.13	6.32
1990	Mainstem 2	6.77	0.00	0.62	14.39
	Mainstem 3	5.17	0.00	0.40	10.36
	Mainstem 4	4.96	0.00	1.58	13.10
	Mainstem 5	1.93	0.00	4.62	8.49
	Mainstem 6	2.49	0.00	0.16	0.45
	Mainstem 7	0.86	0.00	1.02	12.30
	Mainstem 8				
	Mainstem 9	0.07	0.00	0.95	5.01

Appendix 2.4. (continued)

Year	Valley Segment	Chinook salmon density	Coho salmon density	Cutthroat trout density	Steelhead density
1991	Mainstem 2	16.87	2.54	0.51	20.86
	Mainstem 3	17.24	0.10	0.55	13.32
	Mainstem 4	9.49	0.10	0.35	6.66
	Mainstem 5	11.13	2.00	0.38	12.34
	Mainstem 6	9.82	0.00	0.00	5.20
	Mainstem 7	0.43	0.00	0.55	14.97
	Mainstem 8	0.75	0.10	1.33	9.68
	Mainstem 9	0.04	0.05	0.60	4.35
	1992	Mainstem 2	4.23	0.00	0.38
Mainstem 3		2.65	0.00	0.26	18.54
Mainstem 4		0.96	0.00	0.62	13.39
Mainstem 5		0.98	0.00	1.17	17.94
Mainstem 6		0.47	0.00	0.06	1.61
Mainstem 7		0.10	0.00	0.50	10.14
Mainstem 8		0.00	0.00	0.01	6.93
Mainstem 9		0.00	0.01	0.10	2.35
1993		Mainstem 2	16.41	0.00	0.43
	Mainstem 3	6.83	0.00	0.22	6.25
	Mainstem 4	3.80	0.00	0.09	5.26
	Mainstem 5	1.69	0.00	0.12	10.61
	Mainstem 6	1.70	0.00	0.20	3.74
	Mainstem 7	2.10	0.00	0.09	11.24
	Mainstem 8	0.29	0.00	0.15	9.86
	Mainstem 9	0.28	0.27	0.34	7.12

Appendix 2.4. (continued)

Year	Valley Segment	Chinook salmon density	Coho salmon density	Cutthroat trout density	Steelhead density	
1994	Mainstem 2	6.34	0.00	0.86	12.88	
	Mainstem 3	6.12	0.02	0.08	7.24	
	Mainstem 4	8.46	0.17	0.26	6.57	
	Mainstem 5	6.51	0.61	0.30	10.06	
	Mainstem 6	1.37	1.17	0.13	3.48	
	Mainstem 7	1.97	0.53	0.15	11.48	
	Mainstem 8	0.75	0.59	0.05	14.31	
	Mainstem 9	0.88	1.01	0.20	7.88	
	1988	Bald Mountain 1	0.57	0.00	0.40	13.00
Bald Mountain 2				0.28	7.74	
Bald Mountain 3				0.00	7.64	
Butler 1		0.00	0.00	0.23	0.52	
Butler 2		0.00	0.00	0.00	0.54	
North Fork Elk 1		0.46	0.00	0.29	5.43	
North Fork Elk 2		0.05	0.00	0.53	7.10	
Panther 1		0.00	0.00	0.11	5.15	
Panther 2		0.73	0.00	0.20	2.98	
Panther 3		0.00	0.00	0.09	2.18	
W. Fork Panther		0.00	0.00	0.42	3.84	
Red Cedar 1		6.19	0.00	0.81	2.77	
Red Cedar 2		1.21	0.00	0.93	0.68	
South Fork Elk 1		0.00	0.00	0.11	5.38	
1989		Bald Mountain 1	0.00	0.00	0.40	11.94
		Bald Mountain 2			0.38	8.43
	Bald Mountain 3			0.03	1.76	
	Butler 1	0.00	0.00	0.11	2.15	
	Butler 2	0.05	0.00	0.01	1.64	

Appendix 2.4. (continued)

Year	Valley Segment	Chinook salmon density	Coho salmon density	Cutthroat trout density	Steelhead density
1989	North Fork Elk 1	3.15	0.00	0.14	7.76
	North Fork Elk 2	7.52	0.00	0.71	7.67
	Panther 1	1.78	0.00	0.00	2.63
	Panther 2	0.87	0.00	0.52	4.33
	Panther 3	0.00	0.00	0.78	3.92
	W. Fork Panther	0.28	0.00	0.09	2.11
	Red Cedar 1	2.35	0.00	0.89	0.00
	Red Cedar 2	0.75	0.00	0.53	0.64
	Red Cedar 3	0.00	0.00	0.74	0.61
	South Fork Elk 1	0.00	0.00	0.00	10.54
1990	Bald Mountain 1	0.00	0.00	5.74	15.76
	Bald Mountain 2			0.94	21.16
	Bald Mountain 3			0.00	9.14
	Butler 1	0.13	0.00	0.10	2.86
	Butler 2	0.08	0.00	0.28	4.99
	North Fork Elk 1	0.10	0.00	0.10	7.59
	North Fork Elk 2	0.01	0.00	0.21	8.97
	Panther 1	0.00	0.00	0.03	7.39
	Panther 2	0.00	0.00	1.48	9.29
	Panther 3	0.00	0.00	0.50	1.92
	E. Fork Panther	0.00	0.00	0.48	3.94
	W. Fork Panther	0.00	0.00	0.46	3.01
	Red Cedar 1	0.23	0.00	8.64	0.00
	Red Cedar 2	0.23	0.00	1.45	0.42
	Red Cedar 3	0.00	0.00	4.04	0.00
South Fork Elk 1	0.00	0.00	0.00	5.19	

Appendix 2.4. (continued)

Year	Valley Segment	Chinook salmon density	Coho salmon density	Cutthroat trout density	Steelhead density
1991	Anvil 1	0.69	14.81	0.83	5.49
	Bald Mountain 1	1.35	0.00	0.68	20.10
	Bald Mountain 2			0.48	10.68
	Bald Mountain 3			0.09	5.93
	Butler 1	0.00	0.26	0.00	5.73
	Butler 2	0.00	0.09	0.00	5.55
	North Fork Elk 1	0.08	0.00	0.46	6.20
	North Fork Elk 2	0.09	0.09	0.30	5.02
	Panther 1	0.00	0.17	0.00	3.13
	Panther 2	0.03	0.00	0.14	3.17
	Panther 3	0.00	0.20	0.28	3.96
	W. Fork Panther	0.00	0.00	0.30	4.86
	Red Cedar 1	0.31	0.00	0.00	1.99
	Red Cedar 2	1.49	0.00	0.14	3.54
	Red Cedar 3	0.00	0.00	0.21	6.47
South Fork Elk 1	0.00	0.00	0.03	8.70	
1992	Anvil 1	0.57	15.25	0.46	4.38
	Bald Mountain 1	0.00	0.00	0.40	12.94
	Bald Mountain 2			0.54	8.70
	Bald Mountain 3			0.26	5.14
	Butler 1	0.00	0.00	0.00	1.97
	Butler 2	0.00	2.48	0.69	2.89
	North Fork Elk 1	0.00	0.00	0.13	5.18
	North Fork Elk 2	0.00	0.00	0.93	8.49
	Panther 1	0.00	0.00	0.07	4.20
	Panther 2	0.00	0.00	0.14	3.99
	Panther 3	0.35	0.00	0.06	3.80
	E. Fork Panther	0.00	0.00	0.70	3.43
	W. Fork Panther	0.00	0.00	0.73	1.91

Appendix 2.4. (continued)

Year	Valley Segment	Chinook salmon density	Coho salmon density	Cutthroat trout density	Steelhead density	
1992	Red Cedar 1	0.00	0.00	0.00	0.56	
	Red Cedar 2	0.00	0.00	1.75	4.42	
	Red Cedar 3	0.00	0.00	2.04	4.16	
	South Fork Elk 1	0.00	0.00	0.22	10.09	
1993	Anvil 1	0.37	1.30	0.25	2.36	
	Bald Mountain 1	0.00	0.00	0.20	14.63	
	Bald Mountain 2			0.40	8.19	
	Bald Mountain 3			0.00	5.48	
	Butler 1	0.06	0.06	0.23	3.35	
	Butler 2	0.00	0.00	0.00	3.23	
	North Fork Elk 1	0.19	1.45	0.12	7.43	
	North Fork Elk 2	0.18	0.62	0.44	4.71	
	Panther 1	0.10	0.00	0.12	1.60	
	Panther 2	0.50	0.00	0.21	2.77	
	Panther 3	0.08	0.00	0.11	3.23	
	E. Fork Panther	0.00	0.00	0.52	2.48	
	W. Fork Panther	0.00	0.00	0.00	8.45	
	Red Cedar 1	0.00	0.00	0.00	1.48	
	Red Cedar 2	0.00	0.19	0.10	3.96	
	Red Cedar 3	0.00	0.52	0.26	6.22	
	South Fork Elk 1	0.00	0.00	0.00	7.72	
	1994	Anvil 1	0.93	6.28	1.51	6.81
		Bald Mountain 1	0.00	1.85	0.66	22.08
Bald Mountain 2				0.25	10.47	
Bald Mountain 3				0.24	6.92	
Butler 1		0.00	9.26	0.52	3.27	
Butler 2		0.13	0.15	0.18	5.04	
North Fork Elk 1		0.59	2.68	0.20	7.52	

Appendix 2.4. (continued)

Year	Valley Segment	Chinook salmon density	Coho salmon density	Cutthroat trout density	Steelhead density
	North Fork Elk 2	0.61	1.27	0.49	8.47
	Panther 1	0.56	0.00	1.27	5.56
	Panther 2	0.58	0.00	0.31	4.11
	Panther 3	0.03	0.00	0.13	2.43
	E. Fork Panther	0.00	0.00	0.33	1.31
	W. Fork Panther	0.06	0.00	0.17	3.39
	Red Cedar 1	0.00	4.08	0.00	4.30
	Red Cedar 2	0.89	11.27	0.31	4.92
	Red Cedar 3	0.20	0.29	0.05	4.59
	South Fork Elk	0.00	0.06	0.00	8.00

CHAPTER 3
VALLEY SEGMENT USE BY JUVENILE
OCEAN-TYPE CHINOOK SALMON (*Oncorhynchus tshawytscha*)
IN TRIBUTARIES OF THE ELK RIVER, OREGON (1988-1994)

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Abstract

Relationships between juvenile ocean-type chinook salmon (*Oncorhynchus tshawytscha*) and their freshwater habitats have been studied infrequently and usually at fine spatiotemporal scales. The among-valley segment distribution of juvenile ocean-type chinook salmon was examined annually (1988-1994) for tributaries of the Elk River, Oregon. Discriminant analysis indicated that level of use by juvenile chinook salmon could be explained by valley segment- and channel unit-scale characteristics in 4 of 7 years. In each of these 4 years, both valley segment type and spatial position appeared important in determining use by juvenile chinook salmon. Unconstrained valleys and valley segments located near these were more highly used by chinook salmon than valley segments of other types or in other positions. More highly used valley segments were also those with deeper pools (1988 and 1991), larger volume pools (1994), and pools with greater densities of large wood (1989). These among-year differences probably stemmed from inter-annual variation in the salmonid assemblage and, to a lesser extent, in the channel units themselves. Discriminant models were also deemed useful for classifying new observations (i.e., data collected in Elk River tributaries but for other years). Each model typically classified new observations better than random assignment as determined by the significance of the Cohen's kappa statistic. This increased confidence in the models and indicated their applicability for other years in Elk River tributaries. Results emphasize the value of examining fish and habitat

relationships over multiple years and suggest the relevance of unconstrained valleys and pool characteristics in conservation strategies for ocean-type chinook salmon.

Introduction

Prior to recent listings of chinook salmon (*Oncorhynchus tshawytscha*) under the federal Endangered Species Act, relatively little effort was directed at understanding this species' distribution and habitat use in rivers of the Pacific northwestern United States. Hicks et al. (1991) attributed an unintended bias in freshwater anadromous salmonid research toward coho salmon (*O. kisutch*), cutthroat trout (*O. clarki*), and steelhead (*O. mykiss*) to a traditional focus on small-watersheds from which chinook salmon are typically absent. This has been reinforced for ocean-type chinook salmon by the perception that freshwater habitat was of minor importance to them as juveniles (Myers et al. 1998). Juvenile ocean-type chinook salmon typically rear in streams only a few months instead of a year or more like many other salmonids, including stream-type chinook salmon (Taylor 1990; Healey 1991).

Knowledge of relationships between juveniles and their freshwater habitats may be particularly important for ocean-type chinook salmon in two situations: 1) rivers where the population exhibits diversity in the length of freshwater residency, and 2) rivers that lack a well developed estuary. Although most juvenile ocean-type chinook salmon emigrate in spring or summer after 3 to 5 months in coastal rivers, some emigrate in fall or winter (i.e., late-migrants), and others emigrate after spending up to a year in freshwater (i.e., yearlings) (Nicholas and Hankin 1988; Myers et al. 1998). Commonly, 1-13% of returning ocean-type adults emigrated from Oregon coastal rivers as yearlings (Nicholas and Hankin 1988; Myers et al.

1998). Relatively few juveniles leave freshwater after mid-summer, but these fish can be large (K.M. Burnett and G.H. Reeves, unpublished data). Thus, they may have higher smolt-to-adult survival rates than their smaller, earlier migrating counterparts due to increased marine survival as commonly found for anadromous salmonids (e.g., Henderson and Cass 1991), particularly when ocean conditions are unfavorable (Holtby et al. 1990). Later emigrating ocean-type chinook salmon tend to be older (i.e., 5-6 yrs), larger, and more fecund adults on returning to freshwater than earlier emigrating fish (Nicholas and Hankin 1988). Larger adults may have increased reproductive success under certain circumstances. For example, they may have higher likelihoods of laying eggs below the mean scour depth of bank-full flows (Montgomery et al. 1999), contributing disproportionately to recruitment in years with bed-mobilizing floods. They may also produce eggs of greater diameter and weight than smaller adults (Nicholas and Hankin 1988). Larger eggs develop into larger juveniles (Fowler 1972) that may have a competitive advantage in both fresh- and saltwater.

The condition of freshwater habitat may be critical also to ocean-type chinook salmon in rivers lacking well developed estuaries. Estuaries are key rearing areas for juvenile ocean-type chinook salmon because they may grow better here than in freshwater (Reimers 1973; Healey 1991). However, many rivers along the Pacific coast of the continental United States lack an extensive, permanent estuary or other near-shore rearing habitats for anadromous salmonids (Bottom et al. 1986; FEMAT 1993). Thus, juvenile ocean-type chinook salmon in these coastal rivers,

even those that emigrate soon after hatching, must rely heavily, and in some years solely, on freshwater habitat for growth that is sufficient to support ocean entry.

Although a longer term, watershed perspective is increasingly recommended for strategies to conserve salmonid populations (Doppelt et al. 1993; FEMAT 1993), finer spatial and shorter temporal scales have usually been targeted when examining relationships between juvenile ocean-type chinook salmon and their freshwater habitats. This situation typifies most habitat research for salmonids (Platts and Nelson 1988; Folt et al. 1998). Habitat use by juvenile ocean-type chinook salmon has been best characterized at channel unit (10^0 m) and sub-unit scales (10^{-1} m) (Lister and Genoe 1970; Johnson et al. 1992; Scarnecchia and Roper 2000). Distributions of juvenile ocean-type chinook salmon within a watershed were documented and explained qualitatively (Stein et al. 1972; Murray and Rosenau 1989; Johnson et al. 1992; Scarnecchia and Roper 2000). However, empirically-derived statistical relationships have seldom been developed for juvenile ocean-type chinook salmon and their habitat at coarser spatial scales (Schwartz 1990). In some of these watershed studies (Schwartz 1990; Scarnecchia and Roper 2000), juveniles were likely a mixture of ocean- and stream-type fish. Only one study examining habitat use by juvenile ocean-type chinook salmon included data from more than 2 years (Stein et al. 1972). Given that abundances of stream fish can vary greatly from year to year (Platts and Nelson 1988; Grossman et al. 1990; Ham and Pearsons 2000), longer-term studies are necessary to understand

interannual variability and to identify and protect habitat characteristics that are important to fish at each level of abundance.

The goal of this study was to better understand the role of freshwater rearing habitat for juvenile ocean-type chinook salmon. The Elk River was chosen as the study site because it supports an ocean-type chinook salmon population averaging 3% (range 0-18%) of returning adults each year with a yearling life history (Nicholas and Hankin 1988; Myers et al. 1998) and it has a small, ephemeral estuary that does not form in many years. Specific objectives were to: 1) explain the annual distribution (1988-1994) of juvenile ocean-type chinook salmon in tributaries of the Elk River basin using valley segment and channel unit characteristics; 2) determine how consistently specific characteristics were related to fish distribution; and 3) evaluate the transferability of results among years.

Methods

Study area

Elk River is located in southwestern Oregon, USA (Fig. 3.1). 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 provide spawning and rearing

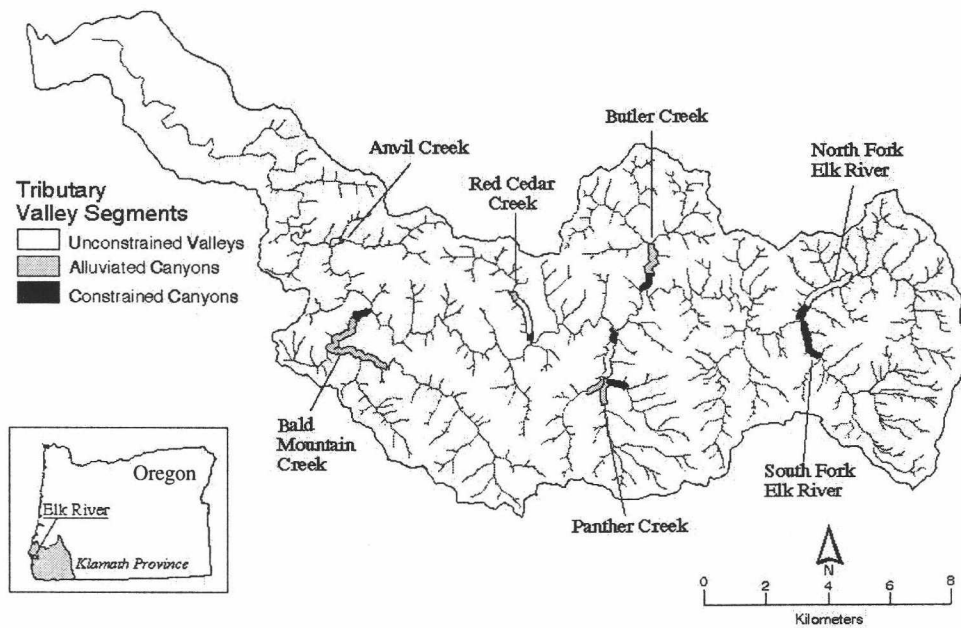


Figure 3.1. Location and map of the Elk River, Oregon with valley segments identified for anadromous fish-bearing sections of its tributaries.

habitat for native chinook salmon, coho salmon, coastal cutthroat trout, and winter-run steelhead. Chum salmon (*O. keta*) occurs with these species in the lower mainstem. All chinook salmon in Elk River are considered ocean-type fish, henceforth, they are referred to only as chinook salmon. The basin is highlighted in both state and federal strategies to protect and restore salmonids (USDA and USDI 1994; State of Oregon 1997). The study area was confined to tributaries in the upper basin (i.e., above and inclusive of Anvil Creek).

Valley segments

Valley segments encompass sections of tributaries accessible to anadromous salmonids. Accessibility was determined in the field based on the absence of

physical features thought to be barriers for adult fish migrating upstream. Surveyed tributaries were either 3rd or 4th order channels (Strahler 1957) on the 1:24,000, centerlined, routed, vector-based, digital stream coverage obtained from the Siskiyou National Forest. The UTM projection, Zone 10, Datum Nad 27 was used for the stream coverage. The type and boundaries of each valley segment were determined through field reconnaissance. Valley segments were classified as one of three types (adapted from Frissell 1992) (Table 3.1 and Fig. 3.1). Unconstrained valleys (UV) contain stream channels that are relatively low gradient (mean \pm SD; $1.5 \pm 0.9\%$) and unconfined (i.e., valley floor width $>2 \times$ active channel width). Any confinement is imposed by channel-adjacent terraces. Constrained canyons (CC) contain stream channels that are relatively high gradient (mean \pm SD; $3.1 \pm 1.5\%$) and confined by valley walls (i.e., valley floor width \approx channel width). Alluviated canyons (AC) contain stream channels that are intermediate in gradient (mean \pm SD; $2.3 \pm 0.7\%$) and confinement to those in the former two valley segment types.

The percent gradient of each valley segment was the mean percent gradient for 100 m sections comprising the segment (Table 3.1). The upstream and downstream boundaries of each valley segment were located on the digital stream layer. Distance between the boundaries was divided into 100 m sections, then the stream coverage was overlain onto the US Geological Survey (USGS) 30 m digital elevation model (DEM). The change in elevation over each 100 m section was

Table 3.1. Characteristics of tributary valley segments in the Elk River, Oregon. Valley segments are numbered starting downstream. Valley segment types are unconstrained valleys (UV), constrained canyons (CC), and alluviated canyons (AC) (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).

Valley segment	Valley segment type	Length (m)	Drainage area (ha)	Mean (SD) %gradient	Influence of valley segment type ^a		
					I _{UV}	I _{CC}	I _{AC}
Anvil Creek 1	UV	532	687	0.1 (0.1)	100	0	0
Bald Mountain Creek 1	CC	826	2715	3.1 (3.8)	0	100	42
Bald Mountain Creek 2 ^b	AC	4251	2679	2.4 (2.7)	-	-	-
Butler Creek 1	CC	763	1752	3.3 (4.3)	0	100	68
Butler Creek 2	AC	1588	1724	1.2 (1.8)	0	16	100
North Fork Elk River 1	CC	648	2456	3.3 (4.9)	80	100	0
North Fork Elk River 2	UV	2511	2303	1.6 (2.9)	100	10	0
Panther Creek 1	CC	727	2347	0.6 (0.8)	70	100	58
Panther Creek 2	UV	1697	2275	2.3 (2.0)	100	49	73
Panther Creek 3	AC	1165	929	1.9 (1.9)	30	32	100
W. Fork Panther Creek 1	AC	806	575	2.8 (2.7)	33	37	100
E. Fork Panther Creek 1	CC	888	570	1.8 (3.2)	33	100	52
Red Cedar Creek 1	CC	344	743	4.7 (3.3)	80	100	19
Red Cedar Creek 2	UV	1418	737	2.1 (1.9)	100	10	23
Red Cedar Creek 3	AC	419	565	3.3 (3.4)	39	8	100
South Fork Elk River	CC	1544	1988	5.6 (6.2)	0	100	0

^aSee text and Fig. 3.2 for description.

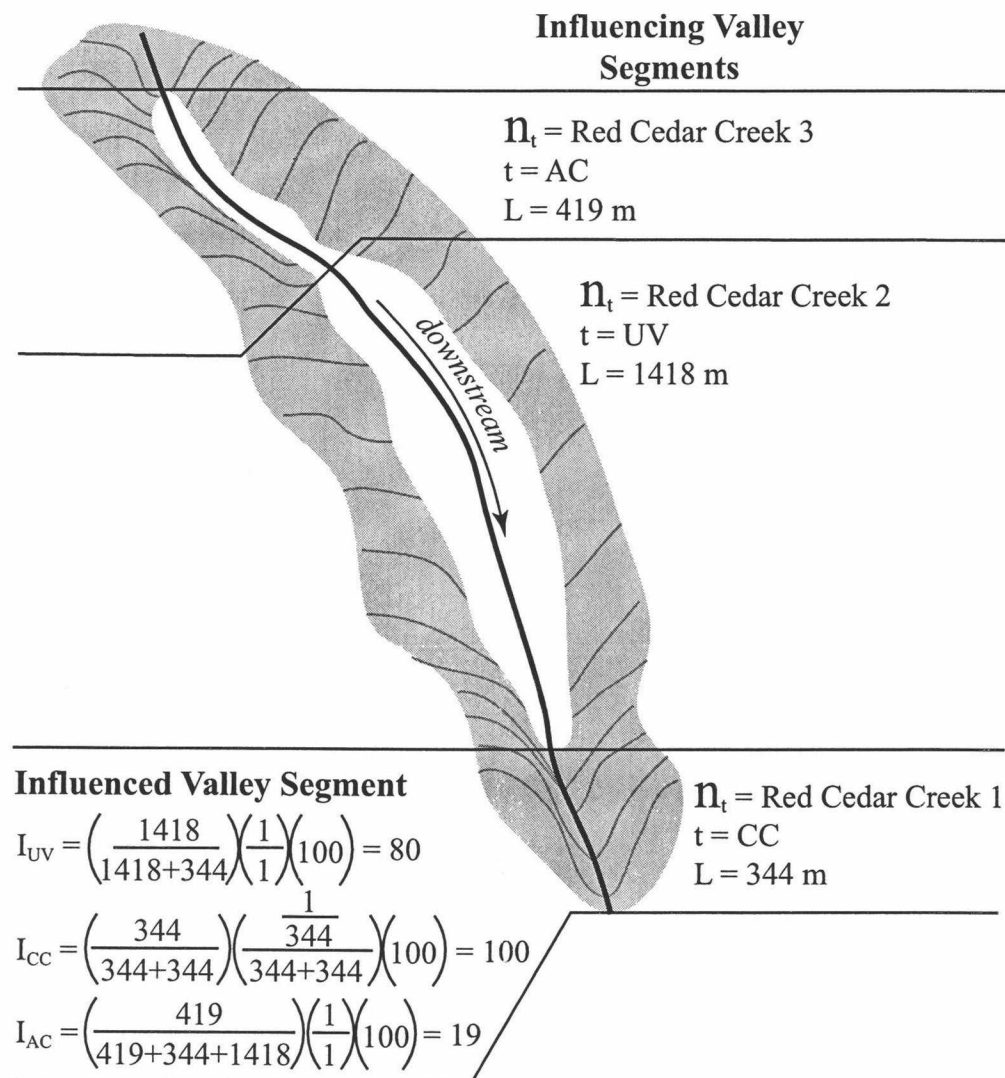
^bA barrier prohibited access by adult chinook salmon, but this valley segment was accessible to other species of anadromous salmonids so had the potential to supply marine derived nutrients. Thus, its influence on Bald Mountain Creek 1 was calculated.

determined and expressed as percent gradient. The mean and standard deviation of 100 m sections were calculated for each valley segment.

Suitability for, and use by, a terrestrial organism of a habitat patch may be affected by the patch type and by features surrounding the patch in the landscape (Weins et al. 1993). Following this rationale, we hypothesized that use of a valley segment by juvenile chinook salmon was related to the valley segment type and location relative to other valley segment types in the same tributary. Nearby valley segments may provide fish or resources (e.g., macroinvertebrate drift, dissolved nutrients, thermal buffering) or both to a particular valley segment, influencing the use of that valley segment by juvenile chinook salmon. To express the influence of valley segments of a particular type on each valley segment in a tributary, the variable, influence of valley segment type (I_t), was derived (Table 3.1 and Fig. 3.2):

$$(1) \quad I_t = \sum_{n=1}^N \left(L_{n_t} / \left(L_{n_t} + L_v + L_{b_1} + \dots + L_{b_z} \right) \right) (1/c)(100)$$

where t identified the type of influencing valley segment (i.e., unconstrained valley [UV], constrained canyon [CC], alluviated canyon [AC]); N was the number of valley segments of the influencing type in that tributary; n was the nth influencing valley segment of that type; L was the length of a valley segment; v identified the influenced valley segment; b₁ - b_z were any valley segments between the influencing and influenced valley segments; c was a weighting factor that



$$(1) \quad I_t = \sum_{n=1}^N \left(\left(\frac{L_{n_t}}{L_{n_t} + L_v + L_{b_1} + \dots + L_{b_z}} \right) (1/c)(100) \right)$$

Figure 3.2. Example to calculate the influence of each valley segment type (I_t) in Red Cedar Creek on the influenced valley segment Red Cedar Creek 1. Where t identified the type of influencing valley segment (i.e., unconstrained valley [UV], constrained canyon [CC], alluviated canyon [AC]); L was the length of a valley segment; N was the number of valley segments of the influencing type in that tributary; n was the n^{th} influencing valley segment of that type; v identified the influenced valley segment; $b_1 - b_z$ were any valley segments between the influencing and the influenced valley segments; c was a weighting factor that reflected the potential of the influencing valley segment to supply the influenced valley segment with inputs of juvenile fish and resources, $c = 1$ if the influencing valley segment had the potential to supply both classes of inputs (i.e., fish and resources), $c = 2$ if the influencing valley segment had the potential to supply only one class of inputs, and $c = L_t / L_t + L_v$ if the influencing and influenced were the same valley segment.

reflected the potential of the influencing valley segment to supply the influenced valley segment with inputs of juvenile fish and resources, $c = 1$ if the influencing valley segment had the potential to supply both classes of inputs (i.e., resources and fish), $c = 2$ if the influencing valley segment had the potential to supply only one class of inputs, and $c = L_i / L_i + L_v$ if the influencing and influenced were the same valley segment.

The influence of a valley segment type was assumed to be greatest when the influencing and influenced were the same valley segment. In such cases, $I_i = 100$. If the type of influencing valley segment did not occur in a tributary, then $I_i = 0$. Values of I_i between these extremes tended to be greater when an influencing valley segment was longer than and closer to the influenced valley segment. These values were generally greater also when an influencing valley segment was upstream of the influenced valley segment because both classes of inputs (i.e., resources and fish) could be supplied, so a value of 1 was assigned to c , the weighting factor. When the influencing valley segment had the potential to supply only one class of inputs, a value of 2 was assigned to c . This occurred if the influencing valley segment was downstream of the influenced valley segment or was upstream of the influenced valley segment but adult chinook salmon could not access it (e.g., Bald Mountain Creek 2). I_i was not calculated when two different valley segments were of the same type. Although we recognize mainstem valley segments may supply tributary valley segments with juvenile chinook salmon, tributaries were considered independent of mainstem influences for this analysis. Examination of the 30 m DEMs indicated

that sections of stream immediately beyond the extent of anadromy in each tributary were similar to constrained canyons, but the influence of these stream sections on valley segments was not assessed

Channel unit features and juvenile chinook salmon densities

Data for channel units and juvenile chinook salmon abundance in tributaries of the Elk River basin were collected each year from 1988 to 1994. Annual data collection began in late July to mid-August and continued for approximately 3 weeks. Data were collected for 20 km of stream in 15 valley segments in each year, for an additional 0.5 km in Anvil Creek in 1991-1994, and for an additional 0.9 km in the East Fork of Panther Creek in 1990 and 1992-1994.

Each channel unit was classified by type [i.e., 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 (i.e., fines <3 mm, 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 each year for estimating chinook salmon abundance. Every 4th pool, 10th fastwater habitat, and 2nd side channel were chosen annually using an independent random start for each channel unit type in each tributary. Abundance estimates were derived from fish counted while snorkeling in these selected units (Hankin and Reeves 1988) between 10:00a.m. and 4:00p.m. 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.

Habitat and fish abundance data for each channel unit were geo-referenced to the digital stream network with Dynamic Segmentation in ARC/INFO (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. The mean relative density (number/100 m²) and its standard error for each channel unit type in a valley segment and the total relative density (number/100 m²) and its standard error across all channel unit types in a valley segment were estimated each year for juvenile chinook salmon using equations for stratified sampling (Cochran 1977).

Statistical Analysis

All statistical analyses were performed with SAS/STAT statistical software (Version 6.12, 1997, SAS Institute Inc., Cary, NC). Estimated relative densities of juvenile chinook salmon were not normally distributed because each year few or no fish were observed in many valley segments. Preliminary data analysis indicated that linear regression assumptions were unlikely to be met following any transformation. Thus, modeling fish density as a categorical variable—High or Low use—seemed appropriate and has been recommended when using estimates from uncorrected snorkel counts (Thompson and Lee 2000). Linear discriminant analysis (e.g., Wood-Smith and Buffington 1996) and logistic regression (e.g., Rieman and McIntyre 1995) are common techniques for modeling categorical data and assigning group membership. Although logistic regression is considered more flexible (i.e., can easily accommodate categorical independent variables and has no distributional assumptions) (Tabachnick and Fidell 1996), discriminant analysis may be a more efficient strategy with continuous independent variables when its assumptions are met (James and McCulloch 1990). The two approaches should yield similar results with a dichotomous dependent variable. Discriminant analysis was applied for each year to test the null hypothesis that juvenile chinook salmon use of tributary valley segments was unrelated to valley segment and channel unit features. Resulting canonical functions were used to classify valley segments as new observations (i.e., based on data for valley segment and channel unit features collected in years other than those used to develop each canonical function). Valley

segments excluded from analysis were: Bald Mountain Creek 1 for 1992 because wood data were not collected in this year; Bald Mountain Creek 2 for every year, Anvil Creek 1 for 1988-90, E. Fork Panther Creek 1 for 1988, 1989, and 1991, and Red Cedar Creek 3 for 1988 because fish data were not collected.

Developing the grouping variable

The grouping variable in discriminant analysis was juvenile chinook salmon use. Each valley segment was designated as either High or Low observed use in each year by comparing its estimated density of juvenile chinook salmon to a threshold density for that year (Tables 3.2 and 3.3). Annual threshold densities were selected to meet two objectives: 1) ensure the smallest density in the High use group was at least twice the largest density in the Low use group, and 2) produce approximately equal group sizes. The second objective was included because the effectiveness of discriminant analysis decreases as the difference between group size increases (Tabachnick and Fidell 1996). Zero was the threshold density in years that juvenile chinook salmon were observed in less than half of the valley segments (1990, 1992, and 1993). Varying the annual threshold density to reflect the range of fish densities estimated in each year, instead of using a single fixed threshold density for all years, reduced the influence of adult spawner abundance on the observed use group into which a valley segment was designated. Valley segments were initially designated into observed use groups by two measures — total relative density and the mean relative density in pools. These estimates were highly correlated for each year ($R^2 \geq 0.90$) because juvenile chinook salmon

Table 3.2. Number of valley segments in the High and Low groups for observed use by juvenile chinook salmon in tributaries of the Elk River, Oregon (1988-1994). A valley segment was designated as either High or Low observed use for each year by comparing its estimated mean density of juvenile chinook salmon in pools to the threshold density for that year.

Year	Number of tributary valley segments	Number of valley segments with observed use		Threshold density between observed juvenile chinook salmon use groups (number/100 m ²)	Estimated mean density of juvenile chinook salmon in pools (number/100 m ²)	
		High	Low		mean±SD	(range)
1988	12	6	6	0.14	2.2 ± 5.6	(0-20.0)
1989	13	7	6	1.48	3.8 ± 5.4	(0-16.0)
1990	14	6	8	0	0.2 ± 0.3	(0-0.7)
1991	14	7	7	0.14	0.8 ± 1.4	(0-4.0)
1992	14	2	12	0	0.2 ± 0.5	(0-2.0)
1993	15	7	8	0	0.2 ± 0.4	(0-1.0)
1994	15	6	9	0.89	0.7 ± 0.8	(0-3.0)

selected for and used pools in the tributaries almost exclusively (Chapter 2).

Identical observed use groups resulted from the two density measures, so only the mean relative density of juvenile chinook salmon in pools was reported (Table 3.2).

The observed use groups were applied in two ways: 1) developing canonical functions from valley segment and channel unit features; and 2) evaluating canonical functions by supplying the basis to calculate correct classification rates.

Developing canonical functions

Overfitting a discriminant model is of concern when the number of observations in the smallest group does not exceed the number of discriminating

Table 3.3. Group, High (H) or Low (L) observed use by juvenile chinook salmon, into which each valley segment was designated annually (1988-1994) for tributaries of the Elk River, Oregon. Valley segments not sampled for juvenile chinook salmon in a particular year are identified by --. Mean (standard deviation) estimated density of juvenile chinook salmon in pools for all years that the valley segment was sampled.

Valley segment	Valley segment type	1988	1989	1990	1991	1992	1993	1994	Mean (SD) estimated density of chinook salmon in pools (number/100 m ²)
Anvil 1	UV	--	--	--	H	H	H	H	1.43(0.44)
Bald Mountain 1	CC	H	L	L	H	--	L	L	0.74(1.48)
Butler 1	CC	L	L	H	L	L	H	L	0.05(0.09)
Butler 2	AC	L	L	H	L	L	L	L	0.07(0.10)
N. F. Elk River 1	CC	H	H	H	H	L	H	H	2.42(4.09)
N. F. Elk River 2	UV	H	H	H	H	L	H	H	2.68(6.10)
Panther 1	CC	L	H	L	L	L	H	H	0.73(1.51)
Panther 2	UV	H	H	L	H	L	H	H	1.09(1.08)
Panther 3	AC	L	L	L	L	H	H	L	0.22(0.44)
W. F. Panther 1	AC	L	H	L	L	L	L	L	0.36(0.83)
E. F. Panther 1	CC	--	--	L	--	L	L	L	0.00(0.00)
Red Cedar 1	CC	H	H	H	H	L	L	L	4.48(7.74)
Red Cedar 2	UV	H	H	H	H	L	L	H	2.04(1.77)
Red Cedar 3	AC	--	L	L	L	L	L	L	0.06(0.15)
S. F. Elk River 1	CC	L	L	L	L	L	L	L	0.00(0.00)

variables (Tabachnick and Fidell 1996). To avoid this, Williams and Titus (1988) suggested the number of observations in each group should equal or exceed three times the number of discriminating variables. Whereas at least six valley segments were designated into each observed use group in all years but 1992 (Tables 3.2 and

3.3), models containing no more than two variables were considered appropriate.

Canonical function development was attempted for all years except 1992.

Discriminating variables were chosen from among four valley segment features and nine channel unit features: mean percent gradient; influence of unconstrained valleys (I_{UV}), constrained canyons (I_{CC}), and alluviated canyons (I_{AC}); mean maximum depth of pools (m); mean volume of pools (m^3); mean density of wood in pools (number of pieces/100 m); percent area of pools; frequency of pools (number/km); percent area of pools with boulders as dominant substrate; percent area of pools with bedrock as dominant substrate; percent area of fastwater units with large gravel as dominant substrate, and percent area of fastwater units with cobble as dominant substrate (Table 3.4 and Appendix 3.1). These variables were screened for univariate outliers by standardizing to mean=0 and SD=1 within each use group for each year, then comparing the annual Z scores for the High and Low use groups to a standard ($Z > 2.575$, two-tailed $P \leq 0.01$) (Tabachnick and Fidell 1996). However, no data point was suspected as an outlier in any year.

Other valley segment and channel unit features were not considered in discriminant analyses for three reasons: 1) they were consistently highly correlated with variables used in stepwise discriminant analyses (e.g., mean maximum depth of pools and mean depth of pools; $r > 0.8$ in 6 of 7 years), 2) they varied little among valley segments (e.g., percent area of fastwater units with fine sediment as dominant substrate; 7-year range across all valley segments 0-5%), or 3) they were

Table 3.4. Seven-year mean (standard deviation) of channel unit features for tributary valley segments in the Elk River, Oregon (1988-1994).

Valley segment	Valley segment type	Pools:					Fastwater:				
		Mean maximum depth (m)	Mean volume (m ³)	Mean density of wood (no./100m)	%Area	Number per km	%Area with boulders as dominant substrate	%Area with bedrock as dominant substrate	%Area with large gravel as dominant substrate	%Area with cobble as dominant substrate	
Anvil 1	UV	0.84 (0.09)	21.2 (2.2)	10 (3)	41 (6)	33 (6)	21 (12)	0.0 (0.0)	40 (7)	45 (10)	
Bald Mountain 1	CC	1.51 (0.43)	75.0 (26.8)	11 (6)	41 (9)	23 (6)	9 (7)	1.8 (0.9)	16 (12)	53 (27)	
Butler 1	CC	1.06 (0.23)	70.6 (21.4)	9 (6)	58 (5)	23 (2)	8 (10)	10.2 (10.1)	14 (12)	64 (18)	
Butler 2	AC	1.06 (0.21)	67.6 (15.0)	2 (1)	56 (5)	19 (3)	1 (1)	19.7 (14.8)	23 (16)	57 (18)	
N. F. Elk River 1	CC	1.04 (0.17)	56.4 (16.2)	9 (3)	35 (13)	19 (7)	40 (30)	13.5 (24.3)	15 (21)	31 (26)	
N. F. Elk River 2	UV	1.07 (0.06)	87.5 (18.4)	22 (11)	40 (7)	14 (2)	21 (15)	1.1 (2.6)	18 (17)	48 (18)	
Panther 1	CC	0.95 (0.25)	66.1 (21.4)	6 (3)	51 (9)	21 (6)	8 (16)	26.7 (12.8)	13 (13)	52 (15)	
Panther 2	UV	1.01 (0.22)	74.0 (22.5)	4 (3)	36 (6)	13 (3)	8 (10)	3.0 (4.0)	19 (15)	60 (18)	
Panther 3	AC	0.75 (0.10)	32.7 (7.6)	9 (2)	24 (6)	14 (5)	5 (11)	0.0 (0.0)	22 (24)	52 (27)	
W. F. Panther	AC	0.55 (0.10)	10.3 (3.9)	32 (16)	19 (5)	18 (4)	12 (13)	0.7 (1.4)	17 (13)	73 (10)	

Table 3.4. (continued)

Valley segment	Valley segment type	Pools:					Fastwater:				
		Mean maximum depth (m)	Mean volume (m ³)	Mean density of wood (no./100m)	%Area	Number per km	%Area with boulders as dominant substrate	%Area with bedrock as dominant substrate	%Area with large gravel as dominant substrate	%Area with cobble as dominant substrate	
E. F. Panther	CC	0.61 (0.11)	11.8 (3.7)	20 (9)	37 (4)	39 (13)	29 (23)	1.5 (1.5)	12 (13)	50 (25)	
Red Cedar 1	CC	0.77 (0.11)	14.5 (3.7)	13 (5)	29 (13)	24 (11)	1 (4)	1.1 (1.9)	29 (13)	65 (13)	
Red Cedar 2	UV	0.75 (0.05)	18.2 (1.7)	23 (7)	32 (6)	21 (4)	6 (10)	1.9 (1.9)	40 (25)	49 (27)	
Red Cedar 3	AC	0.90 (0.09)	21.8 (2.8)	13 (10)	58 (12)	35 (7)	7 (8)	13.6 (12.3)	11 (7)	64 (21)	
S. F. Elk River 1	CC	0.99 (0.11)	36.8 (13.1)	11 (4)	30 (7)	21 (7)	48 (16)	1.8 (2.3)	8 (11)	21 (15)	

thought to be of minor importance to chinook salmon (e.g., percent area of fastwater units with small gravel as dominant substrate).

To develop canonical functions, valley segment and channel unit features were selected objectively by stepwise procedures with a tolerance level of 0.001, the SAS defaults for the partial F tests (i.e., F-to-enter and F-to-remove, $P=0.15$), and the Wilks' Lambda statistic as the selection criterion. Stepwise methods may find an adequate model but cannot guarantee the best fitting or most relevant model (James and McCulloch 1990). Thus, we also examined numerous two-variable combinations in an attempt to identify a better fitting (i.e., based on direct criteria discussed below) or more biologically meaningful model. Objective and subjective approaches lead to the same models for each year.

Relationships between a variable and a canonical function were gauged with two measures: 1) the total canonical structure matrix to determine the strength and direction of correlations, and 2) the partial F-ratio (i.e., F-to-remove) to test the significance of the decrease in discrimination if that variable was removed from the model. Each retained canonical function was evaluated directly by testing the hypothesis that group means were equal [i.e., F-statistic for the Wilks' lambda likelihood ratio ($P \leq 0.1$)] and by the squared canonical correlation (i.e., the percentage of the variation in a canonical function that was accounted for by differences in group means). Canonical functions were also evaluated indirectly by comparing results from direct and jackknife classification when data used to develop each canonical function were classified; if outcomes differed substantially

(>15%), the canonical function was considered unreliable for classifying new observations. The linear classification criterion assigned each valley segment to the group in which the generalized squared distance between it and the group centroid was the smallest. Prior probabilities were set equal to the observed use group sizes for each year. The Cohen's kappa statistic (κ) (i.e., chance-adjusted correct classification rates) (Liebetrau 1983; Titus et al. 1984) and results from testing the null hypothesis that classification by a canonical function was no better than chance assignment ($H_0: \kappa \leq 0$; $H_a: \kappa > 0$; $P > Z$; $\alpha = 0.1$) (Liebetrau 1983) were reported.

Homogeneity of group dispersions was assessed (chi-square (χ^2), $P > 0.1$) to determine appropriateness of deriving a canonical function with a pooled covariance matrix, thus permitting a linear canonical function to be used in subsequent classification. Multivariate outliers and normality of canonical scores for the High and Low use groups were evaluated by inspecting box and normal probability plots. All retained models appeared to meet assumptions for linear discriminant analysis, so results were presented for significance tests. Because our sample sizes were small, valley segments were not randomly selected, and variables describing influence of valley segment type emphasized dependence among valley segments, a randomization procedure was used also to determine significance when testing the null hypothesis that group means were equal (Manly 1998). For each year that a canonical function was developed, data on valley segment use were randomly reordered 1000 times. Discriminant analysis was repeated for each permutation of the randomized data to obtain the F-statistic for the Wilks' lambda.

The test statistic derived from the original data was compared to the distribution of F-values arising from the 1000 random allocations to determine the proportion of values that were greater. If assumptions are met, then significance levels from classical statistical tests and from randomization procedures should be similar (Manly 1998).

Among-year differences in channel unit features comprising canonical functions

To better understand how juvenile chinook salmon relate to their habitat, among-year differences were assessed for any channel unit feature that significantly discriminated between juvenile chinook salmon use groups. Year was the independent variable and channel unit feature was the dependent variable in one-way analysis of variance with post-hoc comparisons conducted using the Ryan-Einot-Gabriel-Welsch multiple range test (REGWQ), controlling overall type I error rate at $\alpha=0.1$. Means were compared for years in which canonical functions deemed useable for classifying new observations were developed. Homogeneity of variance was evaluated with Levene's test (Snedecor and Cochran 1980). The assumption of normality was assessed by examining normal probability and box plots.

Applying models to classify new observations

To validate the canonical functions, the utility for classifying new observations and consistency of results among years were assessed. Each canonical function classified valley segments into juvenile chinook salmon use

groups based on valley segment and channel unit data collected in each of the other six surveyed years. For example, the canonical function developed from 1988 data was used to classify valley segments based on valley segment and channel unit data collected in each year from 1989 to 1994. Because the observed juvenile chinook salmon use group was known for each valley segment in each year, the correct classification rate, the Cohen's kappa statistic, and the significance of the kappa statistic could be obtained and were reported.

Canonical functions were compared among and within years. For each canonical function, kappa values were averaged over the six years that new observations were classified, then the differences in mean kappa values were determined with one-way analysis of variance. Each canonical function was judged for each classified year by its kappa values, direction of misclassifications, and identity of misclassified valley segments.

Results

Valley segment use by juvenile ocean-type chinook salmon

Models with two variables and that discriminated ($P > F$ for Wilks' λ ; $P \leq 0.03$) between the High and Low use groups for juvenile chinook salmon in tributary valley segments were developed for five of six years attempted (Table 3.5). The squared canonical correlation for these models ranged from 44 to 83%. Means of the canonical scores for the High use group were positive in every year (Fig. 3.3). The valley segment variable, influence of unconstrained valleys (I_{UV}),

Table 3.5. Results of discriminant analysis to distinguish between valley segments that were highly used by juvenile chinook salmon and those that were not in tributaries of the Elk River, Oregon (1988-1994). A discriminant model that met the variable selection criteria could not be derived from 1990 data. Model development was not attempted with 1992 data. Model Wilks' λ $P > F$ were determined from a single discriminant analysis and from a randomization procedure. Standardized canonical scores (SC) were calculated as $SC = c_1 z_1 + c_2 z_2$ where c was the standardized canonical coefficient, and z was the standardized score on each discriminating variable.

Year	Discriminating variables	Wilks' λ Partial F-ratio P>F	Total canonical structure coefficient	%Squared canonical correlation	Model Wilks' λ P>F (df) [randomization P>F]	Standardized canonical coefficients
1988	Influence of unconstrained valleys	0.01	+0.86	62	0.01 (2,9)	1.33
	Mean maximum depth of pools	0.08	+0.51		[0.01]	0.79
1989	Influence of unconstrained valleys	0.0001	+0.93	82	0.0002 (2,10)	2.06
	Mean density of wood in pools	0.03	+0.42		[0.000]	0.85
1991	Influence of unconstrained valleys	0.0003	+0.81	74	0.0006 (2,11)	1.80
	Mean maximum depth of pools	0.007	+0.38		[0.000]	1.15
1993	Influence of unconstrained valleys	0.10	+0.66	44	0.03 (2,12)	0.74
	Mean volume of pools	0.04	+0.82		[0.04]	0.98
1994	Influence of unconstrained valleys	0.0001	+0.94	83	0.0001 (2,12)	2.13
	Mean volume of pools	0.02	+0.42		[0.000]	0.83

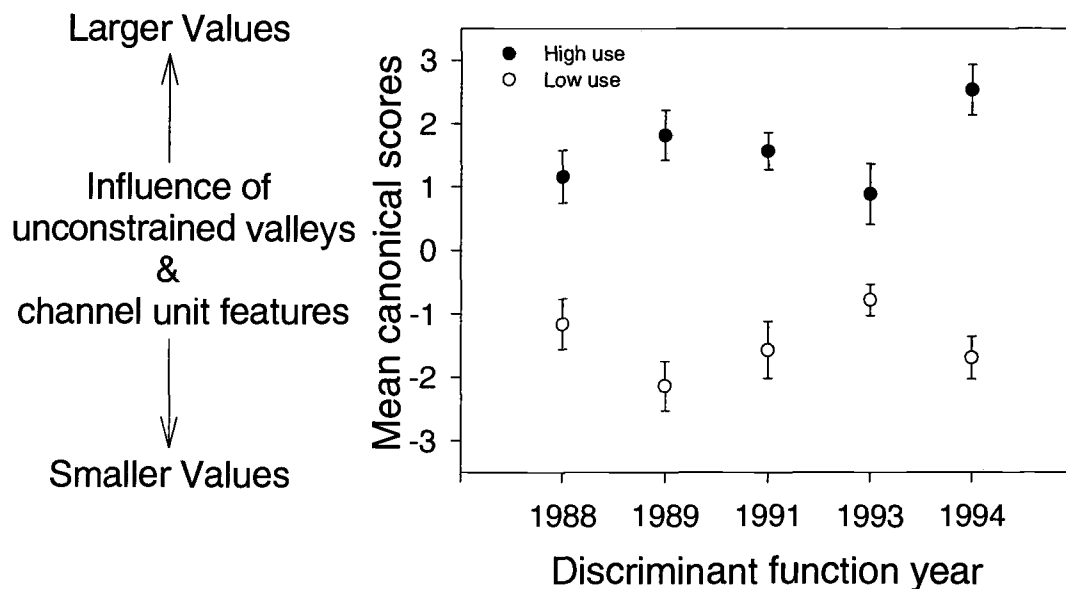


Figure 3.3. Mean and 95% confidence intervals for canonical scores when valley segments were classified into juvenile chinook salmon use groups for tributaries of the Elk River, Oregon. Canonical functions used to classify valley segments were developed with data on valley segment and channel unit features obtained in 1988, 1989, 1991, 1993, and 1994.

and one of three channel unit features, mean maximum depth of pools, mean density of wood in pools, or mean volume of pools, contributed significantly to group discrimination and were positively correlated with each canonical function and with the High use group (Table 3.5). Based on the significance of partial F-ratios and magnitude of total canonical structure coefficients, channel unit features were less significant discriminators and less correlated with the canonical function than the valley segment variable in all years except 1993.

Correct classification rates for the initial five canonical functions when classifying data used in the development of each ranged from 83 to 100% (Table 3.6). Four canonical functions yielded correct classification rates from direct

Table 3.6. Results from direct and jackknifed classification of valley segments from tributaries of the Elk River, Oregon. Canonical functions classified valley segments with the same data on valley segment and channel unit features that were used to develop each canonical function. The number of valley segments classified is n. Cohen's kappa statistic is the chance-adjusted correct classification rate [Ho: $\kappa \leq 0$ and Ha: $\kappa > 0$; $Z = \kappa - 0 / SE$ of kappa (Liebetrau 1983; Titus et al. 1984)].

Year	n	Correct classification rate	Kappa (SE)	Kappa P>Z	Jackknifed correct classification rate	Jackknifed kappa (SE)	Jackknifed kappa P>Z
1988	12	83	67 (22)	0.01	75	50 (25)	0.02
1989	13	100	100 (0)	0.0000	92	85 (15)	<0.0001
1991	14	93	86 (14)	0.0007	86	71 (19)	<0.0001
1993	15	87	73 (18)	0.003	67	32 (25)	0.09
1994	15	93	87 (13)	0.0005	93	86 (13)	<0.0001

classification of valley segments that exceeded those from the jackknife resampling procedure, indicating some instability in all but the canonical function from 1994.

Because jackknifed correct classification rates exceeded their corresponding chance-adjusted correct classification rates [i.e., Cohen's kappa values (κ)], at least one valley segment was correctly classified simply by chance in each year. Even so, valley segments were classified significantly ($P > Z$; $P \leq 0.1$) better by each canonical function than by random assignment. However, the usefulness of the canonical function from 1993 for classifying new observations was questionable given relatively unstable classification results and low jackknifed kappa values, so it was not considered further.

Of the four remaining canonical functions (1988, 1989, 1991, 1994), the highest jackknifed kappa values were for 1989 and 1994 (Table 3.6). Thus, these canonical functions performed best when classifying data used in their development. Whereas canonical functions from 1989 and 1994 were also associated with the largest squared canonical correlations, direct and indirect evaluations of canonical functions agreed (Tables 3.5 and 3.6). Similarly, the smallest kappa value and the smallest squared canonical correlation were observed for the canonical function from 1988. Significance levels of F-values for the Wilks' lambda from original parametric discriminant analyses and from randomization procedures were similar (Table 3.5). This suggested outcomes of classical statistical tests were not substantively affected by failures to meet parametric assumptions.

Among-year differences in channel unit features comprising canonical functions

The mean maximum depth of pools in valley segments did not differ significantly among three of the years that canonical functions were developed (1988, 1991, and 1994), but the means for these years were significantly (ANOVA; $F_{3,50}$; $P \leq 0.1$) less than that for 1989 (Table 3.7). Neither the mean volume of pools (ANOVA; $F_{3,50}$; $P > 0.1$) nor the mean density of wood in pools (ANOVA; $F_{3,50}$; $P > 0.1$) differed significantly among the years that canonical functions were developed.

Table 3.7. Annual mean (standard error) of selected channel unit features in tributaries of the Elk River, Oregon. Channel unit features were those that contributed significantly to discriminating between High and Low groups for juvenile chinook salmon use.

Year	Mean maximum depth of pools (m)	Mean volume of pools (m ³)	Mean density of wood in pools (number/100 m)
1988	0.91 (0.07)	54.7 (7.4)	8 (1)
1989	1.19 (0.09)	57.3 (8.9)	18 (3)
1991	0.95 (0.07)	47.9 (7.6)	13 (2)
1994	0.85 (0.04)	39.2 (5.3)	12 (3)

Applying models to classify new observations

Annual kappa values of the canonical functions ranged from approximately zero to 87% percent when classifying valley segments as new observations (i.e., based on valley segment and channel unit data from years other than those used to develop each canonical function) (Table 3.8 and Fig. 3.4). When chance-adjusted correct classification rates were averaged for years classified by each canonical function, means were between 44 and 52% and were not significantly different (ANOVA; $F_{3,20}=0.1$; $P=0.96$) (Fig. 3.4).

Although mean chance-adjusted correct classification rates did not differ, the canonical function from 1994 was least likely and that from 1989 most likely to misclassify valley segments as High use (Table 3.8). When presented with new observations, the canonical function from 1994 had the highest kappa values in three of six classified years (1989, 1990, and 1992) and matched the maximum kappa values for two other classified years (1988 and 1993). Relatively high kappa

Table 3.8. Results when valley segments from tributaries of the Elk River, Oregon were classified as new observations by canonical functions developed with data from 1988, 1989, 1991, and 1994. Each canonical function classified valley segments as new observations into either the High or Low use group for juvenile chinook salmon using data on valley segment and channel unit features that were collected in each of six other years. The number of valley segments classified in that year is n. Cohen's kappa statistic is the chance-adjusted correct classification rate [Ho: $\kappa \leq 0$ and Ha: $\kappa > 0$; $Z = \kappa - 0 / SE$ of kappa (Liebetrau 1983; Titus et al. 1984)].

Classified year	n	Canonical function year	% Valley segments misclassified into		% Correct classification rate	Kappa (SE)	Kappa P>Z
			Low	High			
1988	12	1989	17	17	83	67 (22)	0.001
		1991	33	17	75	50 (25)	0.02
		1994	17	17	83	67 (22)	0.001
1989	13	1988	14	33	77	53 (24)	0.01
		1991	14	33	77	53 (24)	0.01
		1994	14	0	92	85 (14)	<0.0001
1990	14	1988	33	38	64	29 (26)	0.13
		1989	33	38	64	29 (26)	0.13
		1991	33	38	64	29 (26)	0.13
		1994	33	25	71	42 (25)	0.05
1991	14	1988	0	14	93	86 (14)	<0.0001
		1989	14	29	79	57 (22)	0.005
		1994	14	14	86	71 (19)	0.001
1992	14	1988	50	58	43	-4 (24)	0.56
		1989	50	66	36	-7 (22)	0.62
		1991	50	58	43	-4 (24)	0.56
		1994	50	50	50	0 (27)	0.50

Table 3.8. (continued)

Classified year	n	Canonical function year	% Valley segments misclassified into		% Correct classification rate	Kappa (SE)	Kappa P>Z
			Low	High			
1993	15	1988	29	25	73	46 (23)	0.02
		1989	29	38	67	34 (24)	0.08
		1991	29	25	73	46 (23)	0.02
		1994	29	25	73	46 (23)	0.02
1994	15	1988	0	11	93	87 (13)	<0.0001
		1989	0	11	93	87 (13)	<0.0001
		1991	0	11	93	87 (13)	<0.0001

values for the canonical function from 1994 stemmed from fewer misclassifications into the High use group of valley segments that were typically observed in the Low use group (Table 3.9).

In general, the more years a valley segment was observed in a particular use group, the more often all four canonical functions classified it into that use group. Valley segments observed as High use in at least 3 years (Table 3.3) were classified as such more frequently by each canonical function than those observed as High use in fewer years. Each canonical function either correctly classified or misclassified into the High use group the seven valley segments that were observed as High use in at least 3 years when these were presented as new observations. The sole exception was the canonical function from 1991 that misclassified Red Cedar Creek 1 from the High into the Low use group in 1988 (Tables 3.3 and 3.9).

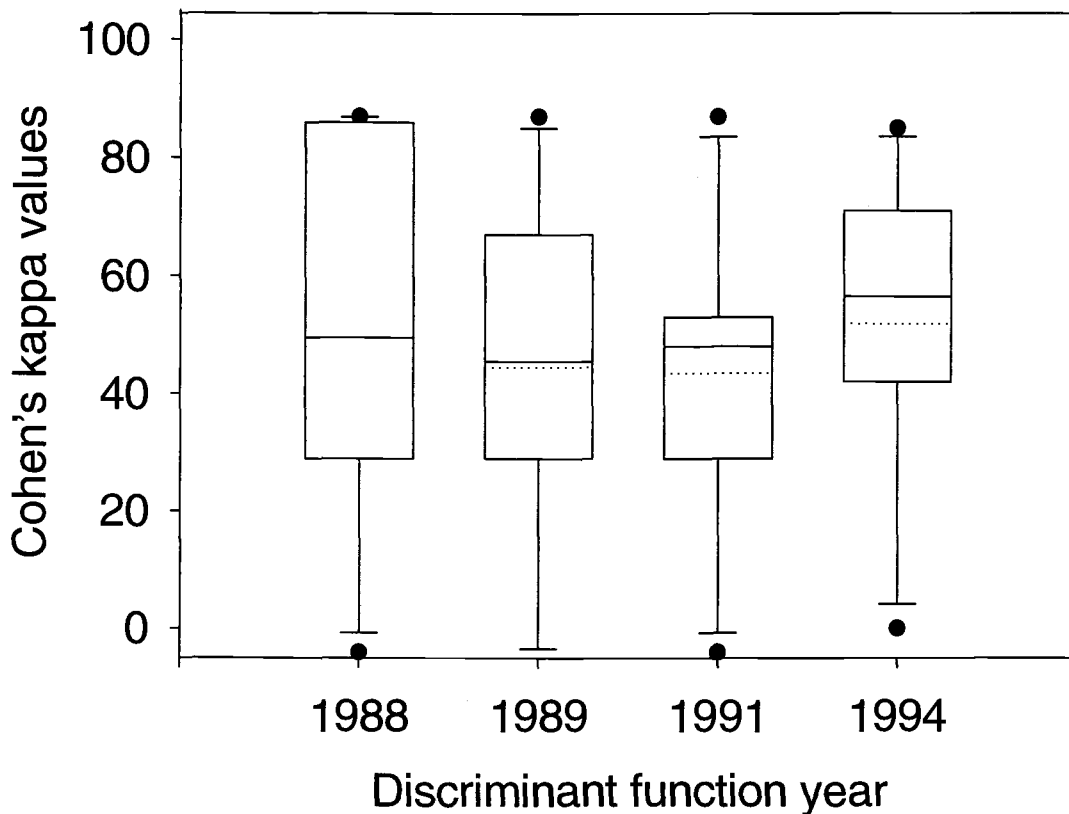


Figure 3.4. Box and whisker plots of chance-adjusted correct classification rates (i.e., Cohens's kappa values) when valley segments from tributaries of the Elk River, Oregon were classified as new observations by canonical functions developed with data from 1988, 1989, 1991, and 1994. Each canonical function classified valley segments as new observations into either the High or Low use group for juvenile chinook salmon using data on valley segment and channel unit features that were collected in each of six other years. Boxes designate the 25th and 75th percentiles, the solid line indicates the median and the dotted line the mean, whiskers denote the nearest data point within 1.5 times the inter-quartile range, and 5th and 95th percentiles are shown by disconnected points. When kappa values were averaged over all 6 years classified, mean kappa values did not differ among the canonical functions (ANOVA; $F_{3,20}=0.1$; $P=0.96$).

Table 3.9. Identity of valley segments misclassified by canonical functions for tributaries of the Elk River, Oregon (1988-1994). Canonical functions, derived from data collected in 1988, 1989, 1991, and 1994, were used to classify each valley segment into either the High or Low juvenile chinook salmon use group based on data for valley segment and channel unit features collected in that year. The observed use group was determined by comparing the annual mean estimated relative density of juvenile chinook salmon in pools for each valley segment with the threshold density for that year. Valley segments that were misclassified when the canonical function year and the classified year were the same are in parentheses.

Classified year	Misclassified valley segment	Observed High / Classified Low				Observed Low / Classified High			
		Canonical function year				Canonical function year			
		1988	1989	1991	1994	1988	1989	1991	1994
1988	Bald Mountain Creek 1	(X)	X	X	X				
	Panther Creek 1					(X)	X	X	X
	Red Cedar Creek 1			X					
1989	Bald Mountain Creek 1					X		X	
	Butler Creek 1					X		X	
	W. Fork Panther Creek 1	X		X	X				
1990	Bald Mountain Creek 1					X		X	
	Butler Creek 1	X	X	X	X				
	Butler Creek 2	X	X	X	X				
	Panther Creek 1					X	X	X	X
	Panther Creek 2					X	X	X	X
	W. Fork Panther Creek 1						X		
1991	Bald Mountain Creek 1		X		X				
	Panther Creek 1					X	X	(X)	X
	W. Fork Panther Creek 1						X		

Table 3.9. (continued)

Classified year	Misclassified valley segment	Observed High / Classified Low				Observed Low / Classified High			
		Canonical function year				Canonical function year			
		1988	1989	1991	1994	1988	1989	1991	1994
1992	North Fork Elk River 1					X	X	X	X
	North Fork Elk River 2					X	X	X	X
	Panther Creek 1					X	X	X	X
	Panther Creek 2					X	X	X	X
	Panther Creek 3	X	X	X	X				
	W. Fork Panther Creek 1						X		
	E. Fork Panther Creek 1						X		
	Red Cedar Creek 1					X	X	X	X
	Red Cedar Creek 2					X	X	X	X
	Red Cedar Creek 3					X		X	
	1993	Butler Creek 1	X	X	X	X			
Red Cedar Creek 1						X	X	X	X
Red Cedar Creek 2						X	X	X	X
Red Cedar Creek 3							X		
Panther Creek 3		X	X	X	X				
1994	Red Cedar Creek 1					X	X	X	(X)

Each of the eight valley segments that were observed as High use in fewer than 3 years (Table 3.3) were correctly classified as Low use by the canonical function from 1994 as were three of these eight valley segments (i.e., Bulter Creek 2, Panther Creek 3, and South Fork Elk River 1) by the canonical functions from 1988, 1989, and 1991. The canonical functions from 1988 and 1991 misclassified three (i.e., Bald Mountain Creek 1, Butler Creek 1, and Red Cedar Creek 3) of the eight valley segments into the High use group in at least 1 year, as did the

canonical function from 1989 (i.e., W. Fork Panther Creek 1, E. Fork Panther Creek 1, and Red Cedar Creek 3) (Tables 3.3 and 3.9).

Each canonical function misclassified at least one valley segment into the Low use group when new observations were presented, but none made this mistake with more than two valley segments in any year (Tables 3.3 and 3.9). Six of fifteen valley segments were misclassified from the High into the Low use group in at least 1 year (i.e., Bald Mountain Creek 1, Butler Creek 1 and 2; Panther Creek 3; W.F. Panther Creek; and Red Cedar Creek 1); the remaining nine valley segments were never misclassified as Low use (Table 3.9). Of the six valley segments that were incorrectly classified into the Low use group, all except Red Cedar Creek 1 were observed as High use in fewer than 3 years. With data for 1989, 1990, 1992, and 1993, all canonical functions were consistent in the number and identity of valley segments that were misclassified as Low use. Red Cedar Creek 1 in 1988 was misclassified into the Low use group by the canonical function from 1991 as was Bald Mountain Creek 1 in 1991 by the canonical function from 1994.

Discussion

Valley segment use by juvenile ocean-type chinook salmon

Juvenile ocean-type chinook salmon were usually not randomly distributed among valley segments in tributaries of the Elk River. Unconstrained valleys and adjacent downstream valley segments were more highly used by juvenile chinook salmon and more consistently classified as such by each canonical function than

valley segments of another type or in a different position. Although valley segment types may differ in channel unit features (Cupp 1989; Frissell 1992), unconstrained valleys in Elk River tributaries did not differ significantly from other valley segment types for any channel unit feature used in step-wise discriminant analyses except that the frequency of pools was significantly greater for constrained canyons than for unconstrained valleys in 1994 (Chapter 2). The importance of unconstrained valleys to juvenile chinook salmon in Elk River tributaries may, therefore, derive from characteristics not routinely assessed in fish habitat surveys. 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.

Unconstrained valleys have low gradients and wide floodplains that 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 than in constrained channels. Such conditions may have increased the suitability of unconstrained valleys in Elk River tributaries for both adult spawning and juvenile rearing by chinook salmon.

The configuration of habitat patches of similar type and juxtaposition of habitat patches of different types are commonly thought to affect the distribution and abundance of biota (Dunning et al. 1992; Wiens et al. 1993; Schlosser 1995; Hanski and Gilpin 1997). The linear nature of streams may render habitat adjacency particularly important for lotic species. Indeed, the juxtaposition of habitat types was recognized as influencing habitat value for salmon at the sub-unit (Inoue and Nakano 1999) and reach scales (Kocik and Ferreri 1998) and trout at the channel unit (D'Angelo et al. 1995; Baran et al. 1997) and landscape scales (Dunham and Rieman 1999). Similar to adult bull trout (*Salvelinus confluentus*) in the Swan River, Montana (Baxter and Hauer 2000), juvenile chinook salmon in Elk River tributaries were likely affected by both the type and spatial arrangement of valley segments. We found that valley segments near unconstrained valleys were more highly used than those farther away. At a landscape scale, certain beaver-generated patches were source areas for fish dispersal, influencing assemblage structure in adjacent streams (Schlosser 1995). Unconstrained valleys may function similarly because these are thought to be key spawning areas for chinook salmon in Elk River tributaries (Burck and Reimers 1978) and elsewhere in southwestern Oregon (Frissell 1992). Juvenile chinook salmon in excess of available habitat in unconstrained valleys may disperse to nearby valley segments. Juvenile

anadromous salmonids have been noted to disperse up- and downstream from release sites for hatchery fish (Scarnecchia and Roper 2000) and from spawning sites for wild fish (Murray and Rosenau 1989; Kocik and Ferreri 1998; Scarnecchia and Roper 2000). Unconstrained valleys may also supply downstream valley segments with key resources, such as drifting macroinvertebrate prey, that may increase habitat suitability for juvenile chinook salmon. The influence of unconstrained valleys appeared stronger and to extend farther downstream than upstream which is consistent with the interpretation that the direction of water flow affected the degree of influence.

In addition to the valley segment variable, each canonical function contained one of three channel unit features. The canonical function developed from 1994 data contained the mean volume of pools, from 1988 and 1991 data contained the mean maximum depth of pools, and from 1989 data contained the mean density of wood in pools. Juvenile chinook salmon in the Elk River used and often selected pools (Chapter 2), but neither the frequency nor percent area of pools contributed significantly to group discrimination. Reaches with more pool area did however support higher densities of juvenile spring chinook salmon in Jackson Creek, Oregon (Roper et al. 1994). The percent of surface area in pools for Jackson Creek was about half that for tributaries of the Elk River (Chapter 2) and may explain the difference between the two studies. The valley segment variable, influence of unconstrained valleys, was more significantly correlated with each canonical function and with the High juvenile chinook salmon use group than any of the

channel unit features examined for Elk River tributaries. Similarly, Watson and Hillman (1997) found that coarser-scale independent variables were more consistently and significantly related to bull trout density than finer-scale independent variables.

Differences among years in the discriminating ability of channel unit features likely derived from inter-annual variation in size and abundance of juvenile chinook salmon, in densities of other salmonid species, and to a lesser extent, in channel unit features. In years that useable canonical functions were developed, the estimated mean fork length of juvenile chinook salmon measured at a smolt trap on the Elk River was largest in 1994, intermediate in 1988 and 1991, and smallest in 1989 (K.M. Burnett and G.H. Reeves, unpublished data). Larger stream-type juvenile chinook salmon selected deeper habitats than their smaller counterparts (Everest and Chapman 1972). Correspondingly, juvenile chinook salmon in Elk River tributaries used valley segments with deeper pools more highly in years when these fish were relatively large as evidenced by canonical functions from 1988, 1991, and 1994. The mean maximum depth of pools did not differ significantly among these years, but the means for these years were significantly less than that for 1989. Because juvenile chinook salmon were smaller and pools were generally deeper, the mean maximum depth of pools appeared less important in determining valley segment use in 1989 than in other years. Deep pools can increase the abundance, diversity, and survival of juvenile salmonids by providing space for species and age classes to segregate vertically (Hartman 1965; Olson 1995), refugia

from predators or drought (Sedell et al. 1990; Labbe and Faush 2000) and cool water to help moderate summer stream temperatures (Matthews et al. 1994; Nielson et al. 1994).

Among-year differences in densities of other salmonid species may also have influenced which channel unit features were important discriminators of valley segment use. Habitats used by juvenile chinook salmon somewhat overlap those used by juvenile coho salmon (Stein et al 1972; Taylor 1991) and age 1+ steelhead (Everest and Chapman 1972; Hillman et al. 1987). However, juvenile chinook salmon sympatric with juvenile coho salmon may move into deeper water farther from shore and cover (Taylor 1991). To minimize direct interactions in 1994, the year with the greatest estimated densities of juvenile coho salmon and age 1+ steelhead in the upper basin (Chapter 2), juvenile chinook salmon in Elk River tributaries may have favored valley segments that contained pools of larger volume. This was reflected in the canonical function from 1994. The mean volume of pools did not differ significantly among years that canonical functions were developed.

Because densities of juvenile chinook salmon in the upper Elk River basin were greater in 1989 than any other studied year, valley segments that were most highly used might be expected to be those containing more wood in pools. Greater densities of territorial fish may be supported in the presence of wood due to the visual isolation it affords (Dolloff 1986). Although juvenile chinook salmon with a stream-type life history were more aggressive than those with an ocean-type life history (Taylor 1988), juvenile chinook salmon from Elk River tributaries did

display agonistic behavior and establish territories (Reimers 1968). Thus, we think that intra-specific territoriality may be heightened when juvenile chinook salmon are abundant and that valley segments with greater densities of large wood in pools may be more important during such times than when juvenile densities are lower. The mean density of wood in pools did not differ significantly among the years that canonical functions were developed. Large wood is often a conspicuous component of streams in forested basins of the Pacific Northwest, influencing many stream structures and processes that can affect fish including channel morphology and sediment transport (for recent reviews, see Maser and Sedell 1994; Bilby and Bisson 1998). The importance of large wood has been demonstrated for other anadromous (e.g., Reeves et al. 1993; Inoue and Nakano 1998) and non-anadromous salmonids (e.g., Flebbe and Dolloff 1995; Harvey et al. 1999), including stream-type juvenile chinook salmon (Swales et al. 1986).

Relevance of multiple years of study

Because juvenile chinook salmon density and habitat characteristics were estimated in each of 7 years, we had a context for interpreting discriminant analysis results for any particular year. Canonical functions were developed for 4 of the 7 years that data were collected. These four canonical functions significantly discriminated among valley segments with High and Low use by juvenile chinook salmon and had a relatively high likelihood of reliably classifying new observations. Reasons varied for the inability to develop canonical functions with data from the other 3 years; for 1992, discriminant analysis was not attempted

because only two valley segments were observed as High use; for 1990, analysis was attempted, but no variable differentiated between the High and Low use groups; and for 1993, a canonical function was developed but rejected because its reliability for classifying new observations was suspect. Multiple years of data allowed us to compare the selected canonical functions. The valley segment variable, influence of unconstrained valleys, discriminated between use groups and was positively associated with the High use group in all four years. Thus, we were reasonably certain of its significance to and consistency of relationship with juvenile chinook salmon. Channel unit features that discriminated between groups varied among years, most likely from inter-annual variation in attributes of the salmonid assemblage and, to a lesser extent, in the channel units themselves.

Had data from only one or two years been analyzed, which is typical of most studies relating fish and their freshwater habitats, quite different conclusions might have been drawn regarding the ability to discriminate among valley segments for juvenile chinook salmon use and which factors contributed to group discrimination. For example, if data from only 1990 had been analyzed, we might have erroneously concluded that juvenile ocean-type chinook salmon were typically randomly distributed in tributaries of Elk River and that freshwater habitat characteristics were uncorrelated with their use of valley segments. Because multiple years were examined, we determined instead that valley segment and channel unit features were often significantly related to the use of valley segments by juvenile ocean-type chinook salmon. Importantly, this suggested that freshwater habitat may be of

greater consequence to ocean-type chinook salmon than previously thought. Our observations are consistent with findings from other systems of substantial interannual variation in stream fish population abundance (Grossman et al. 1990; Ham and Pearsons 2000) and reinforce warnings of problems that may arise when examining fish-habitat relationships over a limited temporal extent (Platts and Nelson 1988).

Multiple years of data allowed canonical functions to be compared based on classification outcomes for each year. Valley segments were classified by canonical functions based on abiotic data collected in each of six other years. Correct classification rates could be developed for each year because the relative density of juvenile chinook salmon had been estimated. We were also able to identify inter-annual patterns in observed and classified use of valley segments. Consequently, we determined that the four canonical functions shared many desirable properties. Each canonical function correctly classified new observations for 4 of 6 years at a rate that was significantly better than chance. Generally, the more years a valley segment was observed in a particular use group, the more often each canonical function classified it into that use group. Canonical functions tended to correctly classify valley segments that were observed as High use. Although canonical functions often misclassified valley segments that were observed as Low use, this can be a valuable attribute. The annual estimated abundance of juvenile chinook salmon in Elk River tributaries was positively related to the estimated number of adults returning to spawn the previous fall (K.M. Burnett and G.H. Reeves, unpub-

lished data). Therefore, Low use of a valley segment by juvenile chinook salmon in a particular year may reflect low adult returns rather than unsuitable rearing habitat. The propensity of canonical functions to misclassify valley segments as High use would be valuable when attempting to identify valley segments with the potential to be highly used even though this potential may not be realized in every year.

Because multiple years of data were available, canonical functions were compared on their average classification performance. Mean classification rates of the four canonical functions did not differ significantly when classifying new observations. However, the canonical function from 1994 was less likely than the other three to misclassify valley segments observed as Low use which elevated its chance-adjusted correct classification rate in some years. Thus, the function from 1994 appeared better at describing the actual use of valley segments and those from 1988, 1989, and 1991 the potential for High use. The observed pattern of valley segment use by juvenile chinook salmon in 1994 may have approximated the 'average' use among years. This was supported by the finding that canonical functions from 1988, 1989, and 1991 correctly classified more observations from the 1994 data than from any other year (Table 3.8) and may explain why the canonical function from 1994 was somewhat less likely to misclassify new observations than the other canonical functions.

Management implications

If unconstrained valleys are sources of juveniles or key resources as we have suggested, then these may be practical conservation elements. Unconstrained

valleys may be termed nodal habitats in the restoration classification of Frissell (1997). Ensuring inchannel, upslope, and upstream processes necessary for their proper function may appropriately be a high priority in a regional strategy to protect and restore populations of ocean-type chinook salmon. This may also benefit other salmonids because unconstrained valleys were often selected by juvenile coho salmon and cutthroat trout (Chapter 2). Valley segments adjacent to, particularly those downstream of, unconstrained valleys may receive second priority in conserving ocean-type chinook salmon. Unconstrained valleys are relatively uncommon, persistent features that are identifiable on topographic maps or air photos and were initially mapped with this approach for southwest Oregon then field verified (Frissell 1992). Following ecological principles outlined by Frissell (1997), we propose a management framework for unconstrained valleys.

If the ultimate goal is a regional network of properly functioning unconstrained valleys, then a prudent course is to ensure those with few human impacts maintain their function and to restore function in impacted unconstrained valleys deemed critical for completing the network. Characteristics of properly functioning unconstrained valleys include that stream channels interact with floodplains by meandering and overbank flows, that relatively low sediment transport capabilities not be overwhelmed, and that water temperatures are maintained within a suitable range through hyporheic exchange and riparian shading. Unconstrained valleys tend to be low gradient, depositional zones so may

be especially susceptible to negative effects of land management (Montgomery and Buffington 1997).

After a region is mapped, each unconstrained valley can be assessed for the potential to supply habitat now and into the future then managed to meet conservation objectives. Maps of unconstrained valleys can be overlain with maps of land ownership, land use, and land cover to identify unconstrained valleys with a low probability of human impact. Because easily accessible areas downstream in a watershed were generally targeted for management first (Lichatowich 1989), minimally impacted unconstrained valleys will most likely occur on relatively remote public lands farther upstream in a watershed. After a low level of impact is confirmed, safeguarding against future anthropogenic threats and recovering any past damage is advantageous. These may often be viable management options, particularly for unconstrained valleys on public lands or for those on private lands when a common interest in conservation is established, incentives are provided, and landowners needs can be met.

Reconnecting the subset of minimally impacted unconstrained valleys that anchor the regional network is a next logical step. Restoring connections both within and among river basins is important. But the first choices for restoration may be degraded unconstrained valleys in basins with those that are relatively intact. Function will likely be restored only when natural processes that create and maintain habitat are recovered and any damaging activities can be stopped (Frissell 1997). Unconstrained valleys located downstream on larger rivers may offer the

greatest long-term benefit for conserving ocean-type chinook salmon (Lichatowich 1989; Frissell et al. 1997) but may be more difficult to incorporate into a regional strategy. For Oregon coastal rivers, the property within each downstream unconstrained valley has generally been sub-divided and is held by many different private non-industrial owners (K.M. Burnett and G.H. Reeves, unpublished data). Working with these landowners to discover ways of meeting their needs while restoring ecological function appears an especially productive approach given the value of downstream unconstrained valleys to conservation.

Although process-based links to salmonid habitat have been identified in unconstrained valleys (e.g., Baxter and Hauer 2000), much remains to be learned about how these function from the site to the region. For example, valley segments meeting the definition of unconstrained valleys (i.e., valley floor width $> 2x$ active channel width) may also include stream channels that are locally constrained by terraces. These valley segments may differ from unconstrained valleys in Elk River tributaries regarding geomorphic processes (e.g., interaction with riparian forests) and habitat characteristics (e.g., presence of large wood). Understanding potential differences and roles played by each sub-type is essential for effective management. Given such uncertainties, any regional strategy focused on, and site-specific restoration in, unconstrained valleys will profit if approached experimentally from an adaptive management framework with planned and funded monitoring and evaluation.

Channel unit features were also important to juvenile chinook salmon so may be reasonably considered in conservation strategies. Valley segment use by juvenile chinook salmon was positively related to the mean maximum depth of pools, mean density of large wood in pools, and mean volume of pools. Land management activities may reduce the depth and volume of pools (McIntosh et al. 2000) and decrease the abundance of wood in the channel (Montgomery et al. 1995). Habitat conditions are usually assessed by comparing local conditions to a suite of regional benchmarks (e.g., NMFS 1996; Reeves et al. 2001). However, relationships between any individual benchmark and fish use are not always clear. For example, juvenile chinook salmon in Elk River tributaries were observed almost exclusively in pools, but pool availability did not help distinguish between High and Low use valley segments even though the percent area of pools in these valley segments ranged from 'good' to 'poor' as defined in Reeves et al. (2001). Meeting a specific benchmark through inchannel engineering projects is unlikely to restore ecological function because the symptoms of habitat degradation rather than causes are addressed (Frissell 1997). Engineering approaches may have a role in watershed restoration by helping to secure areas in stream channels until natural processes recover and by halting and reversing the causes of degradation outside of stream channels. But as previously indicated, we believe that if the objective is restoring function throughout a watershed, then reliance on inchannel structural solutions will not be adequate because only a relatively few areas can be treated and

projects typically have a relatively short life span (Frissell 1997; Reeves et al. 1997), thus actions that protect and recover natural processes will be necessary.

Conclusions

Our results indicated that juvenile ocean-type chinook salmon were usually not randomly distributed in Elk River tributaries. Unconstrained valleys and nearby valley segments were the most consistently and highly used by these fish. One of three channel unit features also helped identify highly used valley segments but each was a less significant discriminator than the valley segment variable. Factors limiting fish abundance or production of fish may differ among years in a given basin or among basins in a given year, thus fish habitat models developed with data for a particular time or place may not successfully transfer to other times or places (Leftwich et al. 1997). Multiple years of data in this study allowed variables contained in and classification outcomes of discriminant models to be compared. We are, therefore, reasonably confident in the transferability of the developed models to other years in Elk River. However, the transferability of the models to other basins should be evaluated where data on valley segment use by juvenile ocean-type chinook salmon are available or can be obtained. To assess if unconstrained valleys function as we hypothesized will require examining a range of basins by methods such as quantifying juvenile density, juvenile movement, and resource availability in unconstrained valleys and in nearby and more distant valley segments. The greater the extent of volitional movement by juveniles within the Elk River basin, the more likely their distribution will reflect their habitat choices rather

than those of adults during homing and spawning. A data set of sufficient sample size will allow the components (i.e., distance, length, spatial position) comprising the variable, influence of unconstrained valleys, to be modeled separately and the relative importance of each to be judged. If unconstrained valleys are sources of juveniles or key resources as we have suggested, then these may be practical units for inclusion in conservation strategies for ocean-type chinook salmon.

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Appendix

Appendix 3.1. Annual estimates of channel unit features for tributary valley segments in the Elk River, OR (1988-1994).

Year	Valley segment	Pools:				Fastwater:				
		Mean maximum depth (m)	Mean volume (m ³)	Mean density of wood (no./100m)	%Area	Number per km	%Area with boulders as dominant substrate	%Area with bedrock as dominant substrate	%Area with large gravel as dominant substrate	%Area with cobble as dominant substrate
1991	Anvil 1	0.83	22.9	10	38	45	3	0	50	47
1992	Anvil 1	0.97	18.0	6	24	32	26	0	39	52
1993	Anvil 1	0.77	22.4	11	37	47	31	0	35	31
1994	Anvil 1	0.78	21.5	11	34	42	24	0	36	50
1988	Bald Mountain 1	1.32	97.3	6	22	45	7	1	11	69
1989	Bald Mountain 1	1.93	62.2	20	17	33	4	4	19	59
1990	Bald Mountain 1	2.02	53.9	6	20	30	22	2	30	2
1991	Bald Mountain 1	1.65	118.7	14	18	34	6	2	26	46
1993	Bald Mountain 1	1.14	64.8	12	29	48	2	1	7	72
1994	Bald Mountain 1	0.97	53.3	10	33	54	13	1	0	71
1988	Butler 1	0.78	56.3	4	24	58	12	2	14	79

Appendix 3.1. (continued)

Year	Valley segment	Pools:					Fastwater:			
		Mean maximum depth (m)	Mean volume (m ³)	Mean density of wood (no./100m)	%Area	Number per km	%Area with boulders as dominant substrate	%Area with bedrock as dominant substrate	%Area with large gravel as dominant substrate	%Area with cobble as dominant substrate
1989	Butler 1	1.51	107.9	22	20	66	27	29	0	41
1990	Butler 1	1.10	94.4	10	22	60	0	14	2	77
1991	Butler 1	0.95	64.7	10	23	58	2	17	31	53
1992	Butler 1	0.94	55.1	6	21	48	2	7	30	42
1993	Butler 1	1.01	60.6	7	26	61	14	4	12	76
1994	Butler 1	1.10	55.6	6	24	58	0	0	10	81
1988	Butler 2	0.83	61.6	1	19	56	4	22	5	83
1989	Butler 2	1.39	83.0	3	14	60	1	51	1	64
1990	Butler 2	1.26	77.1	1	18	48	0	14	18	71
1991	Butler 2	1.06	60.8	1	18	54	1	14	27	48
1992	Butler 2	0.97	87.6	1	18	51	0	16	47	30

Appendix 3.1. (continued)

Year	Valley segment	Pools:					Fastwater:			
		Mean maximum depth (m)	Mean volume (m ³)	Mean density of wood (no./100m)	%Area	Number per km	%Area with boulders as dominant substrate	%Area with bedrock as dominant substrate	%Area with large gravel as dominant substrate	%Area with cobble as dominant substrate
1993	Butler 2	0.84	48.8	1	21	58	0	16	31	48
1994	Butler 2	1.04	54.1	1	23	63	1	5	32	53
1988	N. Fork Elk 1	1.35	73.0	7	9	13	21	67	0	14
1989	N. Fork Elk 1	1.21	79.7	12	11	26	35	13	0	0
1990	N. Fork Elk 1	0.95	51.9	9	17	38	21	0	37	53
1991	N. Fork Elk 1	0.94	35.4	10	21	28	34	14	49	38
1992	N. Fork Elk 1	0.90	40.8	8	25	46	16	0	15	54
1993	N. Fork Elk 1	0.96	61.7	14	23	47	100	0	0	0
1994	N. Fork Elk 1	0.94	52.4	5	25	45	56	0	0	57
1988	N. Fork Elk 2	1.08	81.6	13	16	38	36	0	11	37
1989	N. Fork Elk 2	1.12	67.7	23	13	31	25	7	5	22

Appendix 3.1. (continued)

Year	Valley segment	Pools:					Fastwater:			
		Mean maximum depth (m)	Mean volume (m ³)	Mean density of wood (no./100m)	%Area	Number per km	%Area with boulders as dominant substrate	%Area with bedrock as dominant substrate	%Area with large gravel as dominant substrate	%Area with cobble as dominant substrate
1990	N. Fork Elk 2	1.13	125.5	17	10	40	4	0	29	64
1991	N. Fork Elk 2	1.09	82.7	16	14	35	4	1	52	42
1992	N. Fork Elk 2	1.12	83.7	21	14	46	10	0	19	77
1993	N. Fork Elk 2	0.96	93.5	21	16	49	41	0	8	53
1994	N. Fork Elk 2	1.02	78.1	45	16	44	25	0	2	43
1988	Panther 1	0.89	85.5	5	19	43	0	36	7	71
1989	Panther 1	1.51	98.4	8	15	43	10	34	20	42
1990	Panther 1	0.83	60.1	6	18	61	0	22	3	67
1991	Panther 1	0.83	49.9	7	20	48	0	9	15	50
1992	Panther 1	0.87	76.9	11	18	42	0	27	39	48
1993	Panther 1	0.89	39.1	3	33	57	43	13	9	28

Appendix 3.1. (continued)

Year	Valley segment	Pools:					Fastwater:			
		Mean maximum depth (m)	Mean volume (m ³)	Mean density of wood (no./100m)	%Area	Number per km	%Area with boulders as dominant substrate	%Area with bedrock as dominant substrate	%Area with large gravel as dominant substrate	%Area with cobble as dominant substrate
1994	Panther 1	0.86	52.7	2	28	63	0	46	0	57
1988	Panther 2	0.90	71.8	1	12	32	0	0	3	93
1989	Panther 2	1.40	111.3	4	8	34	6	0	0	47
1990	Panther 2	1.24	53.0	7	13	38	7	0	20	75
1991	Panther 2	0.99	56.6	5	12	25	5	0	22	49
1992	Panther 2	0.80	98.4	8	15	42	7	9	35	46
1993	Panther 2	0.91	69.8	2	16	41	30	5	15	52
1994	Panther 2	0.88	56.9	2	15	40	3	6	38	62
1988	Panther 3	0.69	34.2	9	19	29	0	0	0	83
1989	Panther 3	0.82	34.5	8	10	21	0	0	7	4
1990	Panther 3	0.94	28.5	9	9	18	0	0	6	71

Appendix 3.1. (continued)

Year	Valley segment	Pools:					Fastwater:			
		Mean maximum depth (m)	Mean volume (m ³)	Mean density of wood (no./100m)	%Area	Number per km	%Area with boulders as dominant substrate	%Area with bedrock as dominant substrate	%Area with large gravel as dominant substrate	%Area with cobble as dominant substrate
1991	Panther 3	0.68	22.9	10	16	23	3	0	32	53
1992	Panther 3	0.75	45.7	11	9	17	0	0	35	53
1993	Panther 3	0.75	37.1	8	14	26	29	0	3	71
1994	Panther 3	0.64	26.2	5	19	33	5	0	66	30
1988	W. Fork Panther 1	0.51	8.7	12	20	15	0	0	2	82
1989	W. Fork Panther 1	0.73	16.5	43	14	19	22	0	16	62
1990	W. Fork Panther 1	0.41	6.2	51	11	12	0	0	29	71
1991	W. Fork Panther 1	0.47	11.3	34	21	28	13	1	11	83
1992	W. Fork Panther 1	0.55	14.5	49	17	21	0	0	29	63
1993	W. Fork Panther 1	0.63	7.5	16	18	18	35	0	1	83
1994	W. Fork Panther 1	0.55	7.4	19	22	21	15	4	30	63

Appendix 3.1. (continued)

Year	Valley segment	Pools:					Fastwater:			
		Mean maximum depth (m)	Mean volume (m ³)	Mean density of wood (no./100m)	%Area	Number per km	%Area with boulders as dominant substrate	%Area with bedrock as dominant substrate	%Area with large gravel as dominant substrate	%Area with cobble as dominant substrate
1990	E. Fork Panther 1	0.46	11.4	13	25	35	24	0	0	86
1992	E. Fork Panther 1	0.66	16.3	31	35	38	11	2	23	36
1993	E. Fork Panther 1	0.72	12.1	23	39	34	63	1	3	44
1994	E. Fork Panther 1	0.61	7.4	13	55	43	18	3	23	33
1989	Red Cedar 1	0.90	11.4	20	11	11	0	0	30	70
1990	Red Cedar 1	0.69	10.4	15	27	32	0	0	16	66
1991	Red Cedar 1	0.80	18.3	12	20	30	0	0	37	80
1992	Red Cedar 1	0.94	20.3	12	15	21	0	0	52	56
1993	Red Cedar 1	0.74	15.5	12	38	46	10	5	20	42
1994	Red Cedar 1	0.72	12.7	5	38	43	0	3	31	74
1988	Red Cedar 2	0.81	19.7	13	20	34	28	0	22	69

Appendix 3.1. (continued)

Year	Valley segment	Pools:					Fastwater:			
		Mean maximum depth (m)	Mean volume (m ³)	Mean density of wood (no./100m)	%Area	Number per km	%Area with boulders as dominant substrate	%Area with bedrock as dominant substrate	%Area with large gravel as dominant substrate	%Area with cobble as dominant substrate
1989	Red Cedar 2	0.82	17.6	24	14	20	0	4	60	45
1990	Red Cedar 2	0.74	15.3	35	23	33	0	0	23	32
1991	Red Cedar 2	0.68	18.7	19	24	37	1	4	32	77
1992	Red Cedar 2	0.77	17.1	22	20	29	10	3	73	59
1993	Red Cedar 2	0.75	20.3	28	26	38	6	0	63	19
1994	Red Cedar 2	0.70	18.6	21	24	36	0	3	9	25
1988	Red Cedar 3	0.80	13.1	17	31	42	33	41	11	89
1989	Red Cedar 3	0.84	17.2	9	32	49	5	19	18	51
1990	Red Cedar 3	0.90	22.2	9	31	56	0	14	9	91
1991	Red Cedar 3	0.93	24.6	5	35	71	0	33	14	48
1992	Red Cedar 3	1.06	24.1	14	26	41	19	16	10	58

Appendix 3.1. (continued)

Year	Valley segment	Pools:					Fastwater:			
		Mean maximum depth (m)	Mean volume (m ³)	Mean density of wood (no./100m)	%Area	Number per km	%Area with boulders as dominant substrate	%Area with bedrock as dominant substrate	%Area with large gravel as dominant substrate	%Area with cobble as dominant substrate
1993	Red Cedar 3	0.90	22.8	32	46	72	14	0	17	47
1994	Red Cedar 3	0.79	19.9	8	41	61	6	0	0	89
1988	S. Fork Elk 1	1.17	63.4	9	17	27	70	4	0	7
1990	S. Fork Elk 1	0.97	43.0	12	16	25	53	0	5	6
1991	S. Fork Elk 1	0.87	27.5	8	29	38	20	0	33	16
1992	S. Fork Elk 1	0.88	25.0	15	24	31	37	0	7	41
1993	S. Fork Elk 1	1.09	35.3	16	15	23	58	5	6	38
1994	S. Fork Elk 1	0.91	33.4	12	29	41	49	0	2	31

CHAPTER 4
COMPARING RIPARIAN AND CATCHMENT-WIDE INFLUENCES
OF LANDSCAPE CHARACTERISTICS ON CHANNEL UNIT FEATURES
IN TRIBUTARIES OF THE ELK RIVER, OREGON

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Abstract

Utility of multi-scale analyses for understanding relationships between landscape characteristics and stream habitat was demonstrated for a mountainous area where forestry is the primary land use. Riparian areas could be differentiated from upslope areas for a subset of landscape characteristics when riparian areas were approximated by a fixed-width buffer then described with digital topography and forest cover from satellite imagery. Percent area in forests of medium to very large diameter trees and road density were inversely related at all spatial scales, but the proportion of variation explained increased as scale increased. Mean maximum depth and volume of pools were each directly related to catchment area which explained more variation than landscape characteristics summarized at any spatial scale. Mean density of wood in pools was inversely related to catchment area. At each spatial scale except the catchment, more among-valley segment variation in wood density was explained by an inverse relationship to percent area of sedimentary rock types and a direct relationship to percent area in forest of medium to very large diameter trees than by any other regression model of landscape characteristics or catchment area. The sub-catchment-scale model explained the greatest proportion of variation in wood density. These findings suggested that although spatial scales were similar in processes affecting wood density, finer spatial scales (i.e., corridor and sub-network scales) omitted source areas for key wood delivery processes, and coarser spatial scales (i.e., network and catchment) included source areas for processes less tightly coupled to wood dynamics in

surveyed channels. Little spatial autocorrelation was suggested in regression residuals. Multi-scale analysis can identify areas and processes most closely linked to stream habitat condition and can help design effective strategies to protect and restore stream habitats.

Introduction

Habitats for stream-dwelling species are perhaps best studied by placing them in the context of their catchment (Hynes, 1975; Frissell et al. 1986; Naiman et al. 1992). A catchment contains a mosaic of patches and interconnected networks (Pickett and White 1985; Swanson et al. 1997; Jones et al. 2000). Patches and network features have characteristics such as size, shape, type (e.g., paved roads, old growth forest, or bedrock outcrops) and location (e.g., ridge top or riparian). These landscape characteristics control the routing of energy and materials to streams and ultimately shape aquatic habitat (Swanson et al. 1998; Jones et al. 2000). The direct, local effects on streams of features in the riparian area are relatively well established (Osborne and Koviac 1993; Naiman et al. 2000). Perhaps less well understood are relationships between streams and riparian characteristics accumulated upstream along a channel network (e.g., Weller et al. 1998; Jones et al. 1999) or riparian and upslope characteristics accumulated throughout a catchment (e.g., Jones and Grant 1996; Thomas and Megahan 1998; Jones and Grant 2001).

In urbanized and agricultural systems, riparian and catchment characteristics have been compared for contributing to or moderating non-point source impacts on stream ecosystems. Conclusions in these multi-scale studies, drawn from empirically-derived statistical models, differed depending upon the response variable, location, and spatial extent examined. Certain responses were best explained by landscape characteristics summarized for the local riparian area [e.g.,

ecosystem processes (Bunn et al. 1999)]. Others were best explained by landscape characteristics summarized for the entire catchment [e.g., total fish and macro-invertebrate species richness (Harding et al. 1998)]. For water quality, landscape characteristics had more explanatory power in some studies when summarized for the riparian network (Hunsaker and Levine 1995; Johnson et al. 1997) but in others when summarized over the catchment (Omernik et al. 1981; Hunsaker and Levine 1995). Even when the same response variables (i.e., biological integrity and habitat quality) were examined in the same river basin, judgements differed about the influences of riparian and catchment conditions (Roth et al. 1996; Lammert and Allan 1999). Given such variability, it may be ill-advised to extrapolate understanding derived from multi-scale studies in urbanized and agricultural systems to forested landscapes with greater topographic relief.

Riparian and catchment-wide landscape characteristics have seldom been compared for their relationships to streams in mountainous areas where silviculture was the dominant land use. Abundances of Pacific salmon and trout (*Oncorhynchus spp.*) or conditions of their freshwater habitat have been related to land cover characteristics reflecting timber harvest (e.g., road density or percent area logged). Relationships were found with such characteristics summarized at different spatial scales, including the local riparian area (Bilby and Ward 1991), the entire riparian network (Botkin et al. 1995; Lunetta et al. 1997), and the catchment (e.g., Reeves et al. 1993; Dose and Roper 1994; Dunham and Rieman 1999; Thompson and Lee 2000). Although these studies offered valuable insights, none directly compared

relationships between stream habitat and landscape characteristics at multiple spatial scales. We are aware of only two response variables, macroinvertebrate biological integrity (Hawkins et al. 2000) and abundance of adult coho salmon (*Oncorhynchus kisutch*) (Pess et al. in review), for which relationships to riparian and catchment characteristics were compared in streams draining forested, montane regions. Analogous multi-scale assessments for stream habitat can identify riparian and upslope areas that contribute to habitat protection and restoration in forestry-dominated landscapes.

The goal of this study was to compare landscape characteristics at multiple spatial scales for their relationship to channel-unit habitat features in a basin where the main land use was forestry. Channel unit features targeted were those that helped distinguish between levels of valley-segment use by juvenile ocean-type chinook salmon (i.e., mean maximum depth of pools, mean density of large wood in pools, and mean volume of pools) (Chapter 3). Higher values of these channel unit features were observed in more highly used valley segments. These channel unit features are commonly considered relevant to freshwater habitat quality for salmonids (e.g., McIntosh et al 2000; Bilby and Bisson 1998). Specific objectives were to: 1) examine differences in landscapes characteristics among five spatial scales that varied in extent from the local riparian area to the entire catchment for valley segments in tributaries of the upper Elk River basin; 2) compare the proportion of among-valley segment variation in channel unit features that was explained by catchment area and by landscape characteristics summarized within

each spatial scale; 3) determine which variables explained the greatest proportion of variation in channel unit features by selecting from among catchment area and landscape characteristics at all five spatial scales; and 4) assess residuals from these among-scale regressions for spatial autocorrelation.

Study Area

Elk River is located in southwestern Oregon, USA (Fig. 4.1). 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. The study area was confined to tributaries in the upper basin (i.e., above and inclusive of Anvil Creek).

The climate is temperate maritime with restricted diurnal and seasonal temperature fluctuations (USDA 1998). Ninety percent of the annual precipitation arrives between September and May, principally as rainfall. Peak stream flows are flashy following 3-5 day winter rainstorms rather than associated with spring snow melt, and base flows occur between July and October. Elevation ranges from sea-level to approximately 1200 m at the easternmost drainage divide. Recent tectonic uplift produced a highly dissected terrain that is underlain by the complex geologic formations of the Klamath Mountains. Stream densities in these rock types range from 3-6 km/km² (FEMAT 1993).

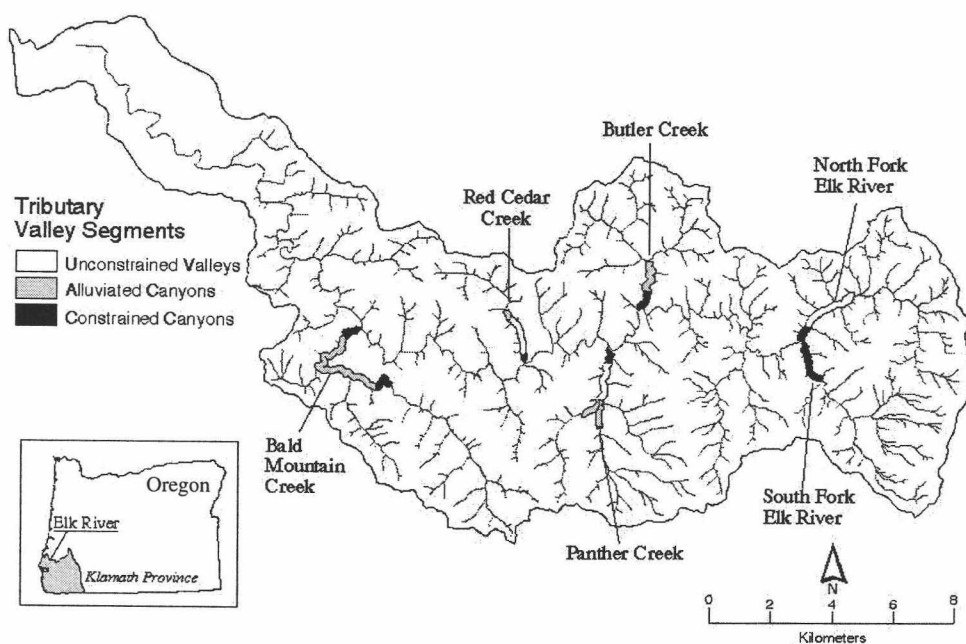


Figure 4.1. Location and map of the Elk River, Oregon with valley segments identified for anadromous fish-bearing sections of its tributaries surveyed in 1988.

Much of the study area is in mixed conifer and broadleaf forests that include tree species of Douglas fir (*Pseudotsuga menziesii*), western hemlock (*Tsuga heterophylla*), Port Orford cedar (*Chamaecyparis lawsoniana*), tanoak (*Lithocarpus densiflorus*), Pacific madrone (*Arbutus menziesii*) and California bay laurel (*Umbellularia californica*). Typical additions in riparian areas are western red cedar (*Thuja plicata*), big leaf maple (*Acer macrophyllum*), and red alder (*Alnus rubra*). Forests span early to late successional/old growth seral stages due to a disturbance regime driven by infrequent, intense wild fires and wind storms and by timber harvest (USDA 1998). The last major fire in the Elk River basin burned approximately 1.3 km² of the Butler Creek drainage in 1961. The next year a windstorm blew down approximately 2.8 km² of forest throughout the basin. Other

than these events, timber harvest has been the dominant disturbance mechanism since fire suppression began in the 1930s (USDA 1998).

Ninety percent of the study area is owned by the federal government with the majority of this managed by the US Forest Service. The remainder is in private ownership. Much of the northern and eastern drainage is in the Grassy Knob Wilderness Area, Grassy Knob Roadless Area, and Copper Mountain Roadless Area. Despite this designated federal protection, portions of two tributaries, Bald Mountain Creek and Butler Creek, do not meet beneficial uses for salmonids based on habitat and temperature concerns and have been on the federal Clean Water Act (1972) Section 303(d) list since 1994/1996.

The upper mainstem of Elk River and its tributaries provide spawning and rearing habitat for native ocean-type chinook salmon (*Oncorhynchus tshawytscha*), coho salmon, coastal cutthroat trout (*O. clarki*), and winter-run steelhead (*O. mykiss*). The basin is highlighted in both state and federal strategies for protecting and restoring salmonids (USDA and USDI 1994; State of Oregon 1997).

Methods

All GIS manipulations of digital coverages were conducted with ARC/INFO (Version 7.1, ESRI, Inc., Redlands, CA). All statistical analyses were performed with SAS/STAT statistical software (Version 6.12, 1997, SAS Institute Inc., Cary, NC).

Digital stream layer and valley segment identification

The UTM projection, Zone 10, Datum Nad 27 was used for digital coverages. A 1:24,000, centerlined, routed, vector-based, digital stream coverage, representing all perennially flowing streams within the Elk River basin, was obtained from the Siskiyou National Forest. Surveyed tributaries were either 3rd or 4th order channels (Strahler 1957) on this stream coverage.

Valley segments encompass sections of tributaries accessible by anadromous salmonids. Accessibility was determined in the field based on the absence of physical features considered to be barriers to adult fish migrating upstream. The type and boundaries of each valley segment were refined from Frissell (1992) through field reconnaissance. Valley segments were classified as one of three types (adapted from Frissell 1992) (Table 4.1 and Fig. 4.1). Unconstrained valleys (UV) contain stream channels that are relatively low gradient (mean \pm SD; $2.0 \pm 0.3\%$) and unconfined (i.e., valley width >2 x active channel width). Any confinement of the channel is imposed by terraces. Constrained canyons (CC) contain stream channels that are relatively high gradient (mean \pm SD; $3.3 \pm 1.5\%$) and confined by valley walls (i.e., valley width \cong channel width). Alluviated canyons (AC) contain stream channels that are intermediate in gradient (mean \pm SD; tributaries $2.3 \pm 0.7\%$) and confinement to those in the former two valley segment types.

Table 4.1. Characteristics of tributary valley segments in the Elk River, Oregon (1988). Numbers identifying valley segments increase in the upstream direction. Definitions of unconstrained valleys (UV), constrained canyons (CC), and alluviated canyons (AC) were adapted from Frissell (1992).

Valley segment	Type	Length (m)	Drainage area (ha)	Mean (SD) % gradient	Mean (SD) maximum depth of pools (m)	Mean (SD) volume of pools (m ³)	Mean (SD) density of wood in pools (no./100m)
Bald Mountain Creek 1	CC	826	2,715	3.1(3.8)	1.32(0.58)	97.3(97.2)	6(10)
Bald Mountain Creek 2	AC	4,251	2,679	2.4 (2.7)	0.89(0.32)	54.5(50.9)	8(16)
Bald Mountain Creek 3	CC	965	1,511	2.3(2.6)	0.94(0.35)	44.8(36.7)	9(22)
Butler Creek 1	CC	763	1,752	3.3(4.3)	0.78(0.41)	56.3(72.8)	4 (8)
Butler Creek 2	AC	1,588	1,724	1.2(1.8)	0.83(0.29)	61.6(46.9)	1 (2)
North Fork Elk River 1	CC	648	2,456	3.3(4.9)	1.35(0.38)	73.0(36.1)	7(11)
North Fork Elk River 2	UV	2,511	2,303	1.6(2.9)	1.08(0.32)	81.6(70.3)	13(16)
Panther Creek 1	CC	727	2,347	0.6(0.8)	0.89(0.47)	85.5(73.1)	5(15)
Panther Creek 2	UV	1,697	2,275	2.3(2.0)	0.90(0.34)	71.8(51.3)	1 (5)
Panther Creek 3	AC	1,165	929	1.9(1.9)	0.69(0.32)	34.2(30.2)	9(17)

Table 4.1. (continued)

Valley segment	Type	Length (m)	Drainage area (ha)	Mean (SD) % gradient	Mean (SD) maximum depth of pools (m)	Mean (SD) volume of pools (m ³)	Mean (SD) density of wood in pools (no./100m)
W. Fork Panther Creek	AC	806	575	2.8(2.7)	0.51(0.16)	8.7 (4.0)	12(23)
Red Cedar Creek 1	CC	344	743	4.7(3.3)	0.63(0.13)	13.1(12.8)	11(19)
Red Cedar Creek 2	UV	1,418	737	2.1(1.9)	0.81(0.55)	19.7(10.5)	13(20)
Red Cedar Creek 3	AC	419	565	3.3(3.4)	0.80(0.20)	13.1 (6.0)	17(26)
South Fork Elk River 1	CC	1,544	1,988	5.6(6.2)	1.17(0.44)	63.4(35.2)	9(14)

Landscape characterization

The approach for landscape characterization was to: 1) delineate analytical units for each valley segment, 2) overlay analytical units onto digital coverages of lithology, land form, and land cover, then calculate the percent area of each analytical unit occupied by each landscape characteristic, and 3) compare landscape characteristics among the five spatial scales.

Analytical units

Five analytical units, one for each spatial scale, were delineated for each valley segment. Spatial scales differed in the areas included upslope and upstream of valley segments (Fig. 4.2) and presumably in vegetative, geomorphic, and fluvial processes that may affect channel unit features. Analytical units were developed for three riparian buffer scales (i.e., corridor, sub-network, and network) and two upslope scales (i.e., sub-catchment and catchment). All buffers were based on the Riparian Reserve widths for perennial stream classes (i.e., 100 m on either side of fish-bearing channels and 50 m on either side of non-fish bearing channels) in the Northwest Forest Plan (USDA and USDI 1994). Sub-catchment and catchment boundaries were screen digitized from contour lines generated using US Geological Survey (USGS) 30 m digital elevation models (DEMs).

Corridor scale analytical units extended the length of each valley segment and included the area within a 100 m wide buffer on each side of the stream (mean \pm SD, 22 ± 19 ha) (Fig. 4.2). Channel-adjacent processes (e.g., tree mortality in riparian stands and stream-side landsliding) were assumed to dominate at the

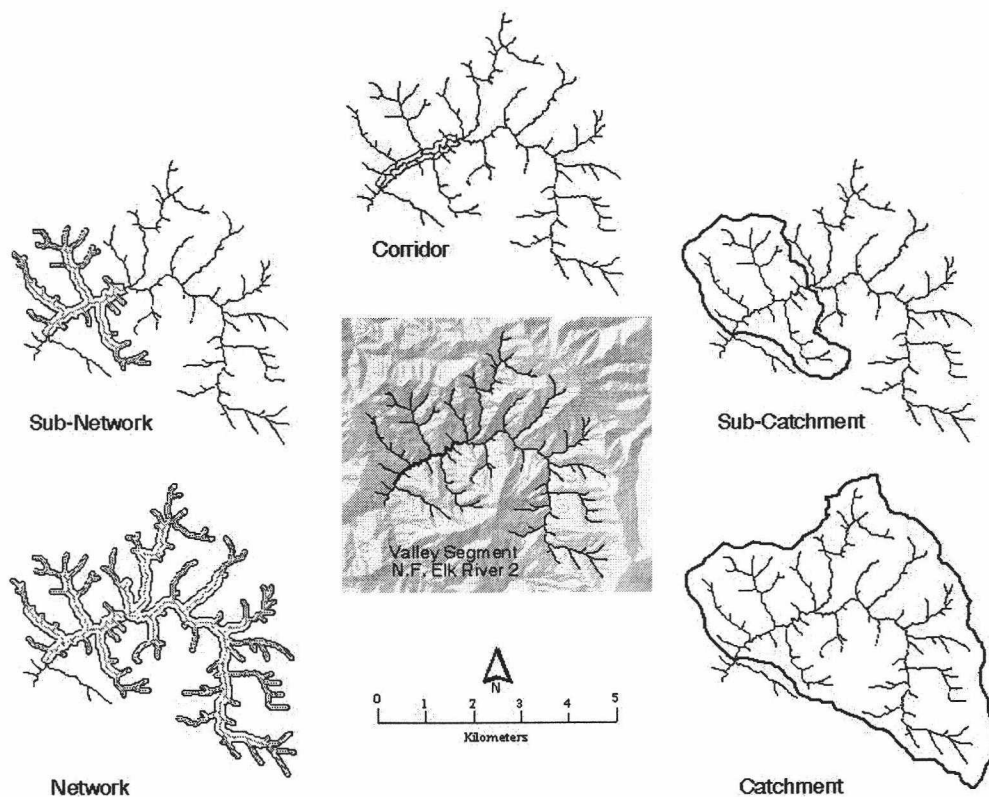


Figure 4.2. Analytical units used to summarize landscape characteristics at five spatial scales illustrated for the valley segment North Fork Elk River 2.

corridor scale. Sub-network scale analytical units encompassed those at the corridor scale plus the area within a buffer around all perennially flowing tributaries that drained directly into the valley segment from adjacent hill slopes (53 ± 82 ha) (Fig. 4.2). Debris flow processes were assumed to be added to channel-adjacent processes at the sub-network scale. Network scale analytical units included those at the sub-network scale plus the area within a buffer around all perennially flowing streams that were upstream of the valley segment (367 ± 211 ha) (Fig. 4.2). Fluvial transport processes were assumed to be added at the network scale. Sub-catchment scale analytical units contained the entire area draining into the valley segment from

adjacent hill slopes, which included unmapped stream channels capable of transporting debris flows (190 ± 299 ha) (Fig. 4.2). Non-channelized hillslope processes (e.g., surface erosion, landsliding) were assumed to be added at the sub-catchment scale. Catchment scale analytical units encompassed those at the sub-catchment scale plus the entire area upstream of the valley segment (1562 ± 820 ha) (Fig. 4.2). Fluvial transport processes were assumed to be added at the catchment scale.

Digital coverages of landscape characteristics

Classes for the lithology, land form, and land cover data layers are described in Table 4.2. The lithology coverage was generalized from the digital 1:500,000 scale Quaternary geologic map of Oregon (Walker and MacLeod 1991) by the Forest Ecosystem Management and Assessment Team (FEMAT 1993). The land form layer of percent slope was generated for the basin from USGS 30 m DEMs. Slope classes were similar to those in Lunetta et al. (1997). Road density (km/km^2) was calculated from a vector coverage of roads on all ownerships within the Elk River basin. The Siskiyou National Forest developed this coverage by augmenting the 1:24,000, 7.5 minute USGS quadrangle Digital Line Graph (DLG) with roads interpreted from Resource Orthophoto Quadrangles.

The forest cover layer was clipped from a coverage for western Oregon. It was developed by a regression modeling approach with spectral data from 1988 Landsat Thematic Mapper (TM) imagery and elevation data from USGS 30 m DEMs (Cohen et al. 2001). In areas such as the Elk River basin where

Table 4.2. Description of landscape characteristics for the Elk River, Oregon. All variables except road density were expressed as percent area of analytical units at each spatial scale.

Independent variable	Description
Lithology:	
Sedimentary rock types	Cretaceous - Rocky Point Formation sandstones and siltstones and Humbug Mountain Formation conglomerates
Metasedimentary rock types ¹	Jurassic - Galice Formation shales and Colebrook Formation schists
Igneous intrusive rock types ¹	Granite and diorite
Land form:	
Slope class $\leq 30\%$	
Slope class 31- 60% ¹	
Slope class $> 60\%$	
Land Cover:	
Road density	(km/km ²)
Open area and semi-closed canopy forest	$<70\%$ tree cover
Broadleaf	$>70\%$ deciduous tree and shrub cover
Mixed broadleaf/conifer and conifer forest of:	$>70\%$ of deciduous and conifer tree cover
small diameter trees ¹	≤ 25 cm diameter at breast height (dbh)
medium diameter trees	26-50 cm dbh
large diameter trees	51-75 cm dbh
very large diameter trees	>75 cm dbh
medium to very large diameter trees	>25 cm dbh

¹Classes with relatively low explanatory power that were not used in regression analyses.

forestry-related activities are the primary disturbance mechanism, age and stem diameter of forest cover reflects time since timber harvest. The greater the percent area in forests of older and larger trees the lower the percent area assumed to be affected by recent logging. With few exceptions (e.g., Botkin et al. 1995), studies relating stream and landscape characteristics in forested regions used harvest level or percent area logged (e.g., Reeves et al. 1993; Dose and Roper 1994) instead of high resolution forest cover data as was available for the Elk River basin.

Differences among spatial scales in landscape characteristics

We were interested in whether or not the five spatial scales differed with respect to landscape characteristics. Consequently, among-scale differences in variances and medians were assessed for each landscape characteristic. Among-scale differences in variances were analyzed using Levene's test of homogeneity of variance (Snedecor and Cochran 1980) on the absolute value of residuals from one-way ANOVA with scale as the independent variable. Among-scale differences in medians were evaluated using one-way ANOVA on the ranked data because parametric assumptions could not be met. Whenever an ANOVA F-test was significant ($\alpha=0.05$), post-hoc pairwise comparisons were conducted with the Ryan-Einot-Gabriel-Welsch multiple range test (REGWQ) with the overall Type I error rate of $\alpha=0.05$. Although extreme values were observed when landscape characteristics were screened for outliers, all data points were considered valid and were included in analyses.

We recognize that analytical units were not independent; analytical units at coarser scales subsumed those at finer scales (e.g., the sub-catchment scale completely encompassed the sub-network scale). Spatial dependence inherent in the design of analytical units likely reduced the actual degrees of freedom below the nominal value and inflated the probability of a type I error (Hurlbert 1984; Legendre 1993). All significance values from ANOVA and post-hoc comparisons should be evaluated with this in mind but were presented to indicate the relative strength of differences.

Regression of channel unit features with catchment area and landscape characteristics

Channel unit features

Channel unit data were collected for 20 km of stream in 15 valley segments from Elk River tributaries between July 25 and August 5, 1988. Information was obtained to derive channel unit features [i.e., mean volume of pools (m^3), mean density of wood in pools (no. pieces/100 m), and mean maximum depth of pools (m)]. These channel unit features were chosen because each helped discriminate between valley segments in Elk River tributaries for level of use by juvenile ocean-type chinook salmon (Chapter 3).

Each channel unit was classified by type [i.e., 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 for each person estimating channel unit dimensions. All estimated dimensions were multiplied by the appropriate calibration ratio, and only calibrated estimates were analyzed. Number of wood pieces (≥ 3 m long and ≥ 0.3 m diameter) were counted in each channel unit. Maximum depth of each pool was measured if ≤ 1 m and was estimated otherwise. Channel unit data were geo-referenced to the digital stream network through Dynamic Segmentation in ARC/INFO (Byrne 1996) then were summarized for each valley segment to obtain channel unit features for subsequent regression analyses.

Developing regression models

Three sets of regression models were developed to explain variation in channel unit features. First, we regressed each channel unit feature with catchment area only. Next, we attempted to develop five within-scale linear regression models for each channel unit feature by selecting from landscape characteristics at each of five spatial scales. Finally, we attempted to develop a single 'best' among-scale linear regression model for each channel unit feature by selecting from among catchment area and landscape characteristics at all spatial scales. Independent variables for within- and among-scale regression models were selected with stepwise ($P \leq 0.11$ to enter and $P \leq 0.05$ to stay in the model) and adjusted R^2 procedures. We recognize that variable selection procedures cannot guarantee the

best fitting or most relevant model unless all possible combinations are explored (James and McCulloch 1990). Thus, our criteria to determine the 'best' among-scale model was that it explained more of the variation in the dependent variable than other models we examined. Relatively few tributary valley segments ($n=15$) were available for analyses, thus we retained models with no more than two independent variables. This was a slightly more conservative criterion than the 5:1 cases to independent variables ratio of Johnston et al. (1990). The proportion of variation explained in linear regression was reported as r^2 and calculated as the coefficient of determination for one-variable models and as R^2 and calculated as the adjusted coefficient of determination for two-variable models.

Box plots and normal probability plots of regression residuals were inspected for constant variance and outliers prior to final model selection. Models were disregarded if parametric assumptions were not met following variable transformation. Reported within-scale models explained the largest proportion of variation in channel unit features and contained independent variables that were not also significantly ($P>0.05$) correlated with catchment area. This allowed the unique contribution of landscape characteristics to be assessed. For comparison, channel unit features were regressed with the same independent variables for each reported model but summarized at the other four spatial scales.

Because valley segments were not selected with a probability sampling design and were contiguous within a tributary, we assessed regression residuals from each among-scale analysis for non-random errors that might reflect spatial

autocorrelation. For all possible pairs of valley segments, stream distance and the absolute difference between regression residuals were calculated. These values were regressed to determine the proportion of the variation in the absolute difference between regression residuals explained by the stream distance between valley segments.

Results

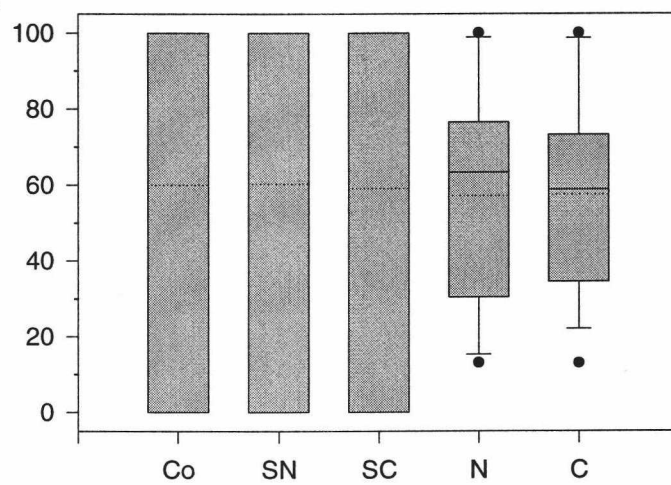
Landscape characterization

Among-scale variances differed significantly ($df = 5,84$; $P \leq 0.05$) for all but three landscape characteristics, the percent area in: 1) igneous intrusive rock types, 2) slopes $\leq 30\%$, and 3) open and semi-closed canopy forest. The smallest variance was always at either the network or catchment scales for all other landscape characteristics except the percent area in forests of small diameter trees.

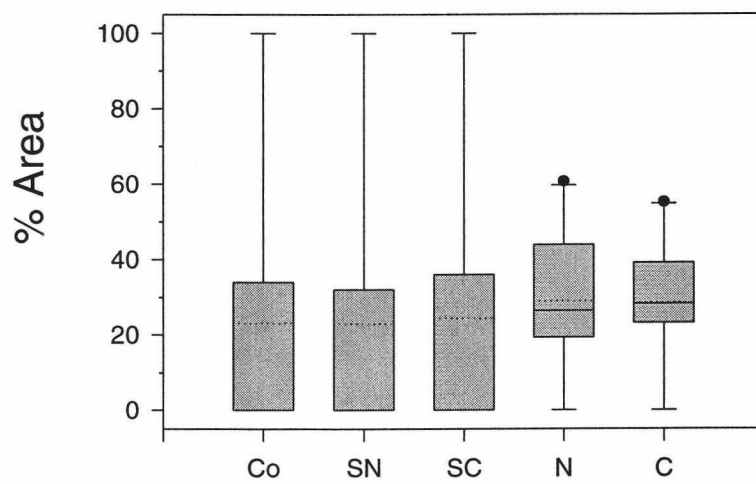
Medians differed significantly among the spatial scales for five of 14 landscape characteristics (Fig. 4.3). These were the percent area in slopes $\leq 30\%$ ($F_{4,70} = 10.0$; $P = 0.0001$) (Fig. 4.3d), broadleaf cover ($F_{4,70} = 3.6$; $P = 0.01$) (Fig. 4.3h), forests of small diameter trees ($F_{4,70} = 12.1$; $P = 0.0001$) (Fig. 4.3i), forests of medium diameter trees ($F_{4,70} = 8.5$; $P = 0.0001$) (Fig. 4.3j), and forests of very large diameter trees ($F_{4,70} = 6.4$; $P = 0.0002$) (Fig. 4.3k). Pairwise comparisons for these landscape characteristics never differed significantly ($P > 0.05$) between the corridor and sub-network scales or between the sub-catchment and catchment scales (Fig. 4.3). For variables subsequently used in regression analyses, significant pairwise

Figure 4.3. Distribution of landscape characteristics among analytical units at each of the five spatial scales in tributaries of the Elk River, Oregon. Landscape characteristics were: resistant sedimentary rock types (a); metasedimentary rock types (b); igneous intrusive rock types (c); slope class $\leq 30\%$ (d); slope class 31-60% (e); slope class $>60\%$ (f); open area and semi-closed canopy forest (g); broadleaf forest (h); mixed broadleaf/conifer and conifer forest of small diameter trees (i); mixed broadleaf/conifer and conifer forest of medium diameter trees (j); mixed broadleaf/conifer and conifer forest of large diameter trees (k); mixed broadleaf/conifer and conifer forest of very large diameter trees (l); mixed broadleaf/conifer and conifer forest of medium to very large diameter trees (m); and road density (n). Spatial scales were the corridor (Co), sub-network (SN), sub-catchment (SC), network (N), and catchment (C). Boxes designate the 25th and 75th percentiles, the solid line indicates the median and the dotted line the mean, whiskers denote the nearest data point within 1.5 times the inter-quartile range, and 5th and 95th percentiles are shown by disconnected points. Scales with significant ($P \leq 0.05$) pairwise differences between medians have the same label.

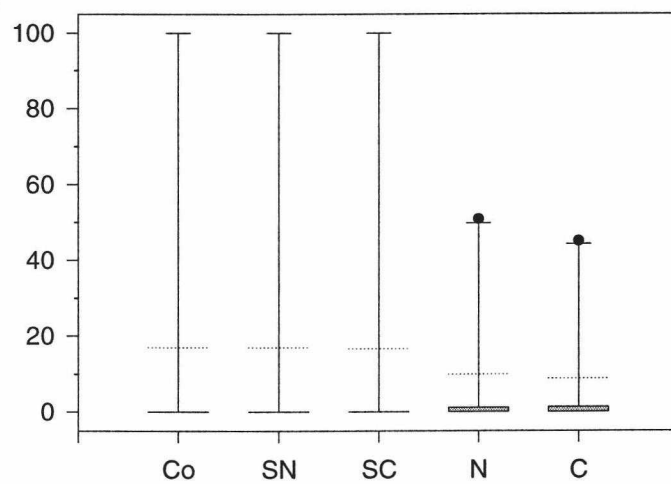
4.3a



4.3b

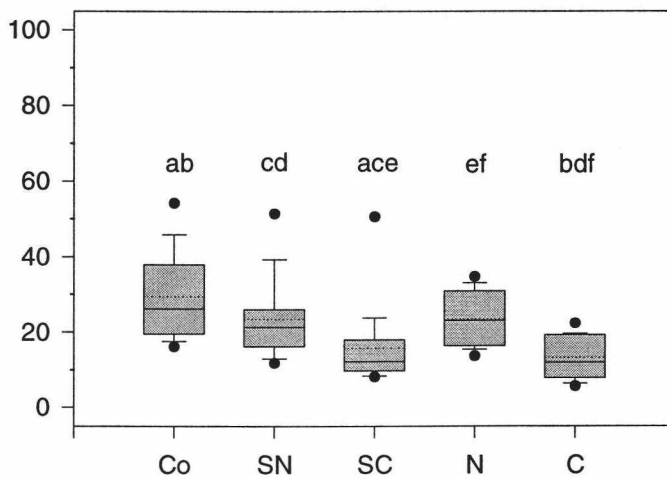


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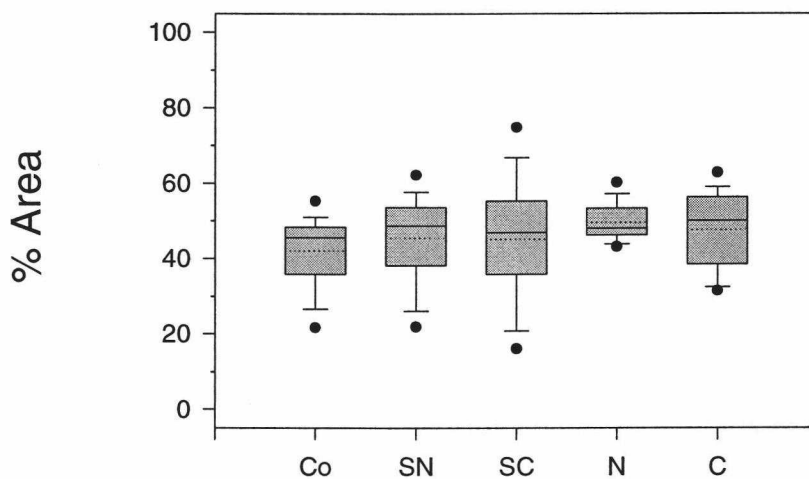


Spatial Scale

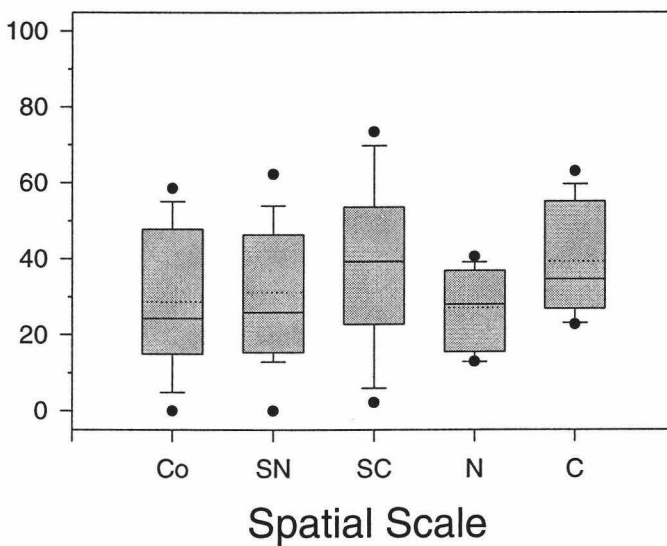
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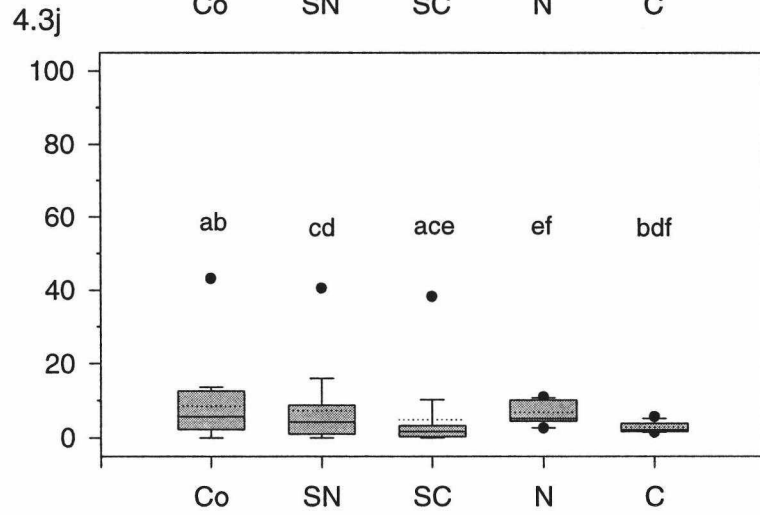
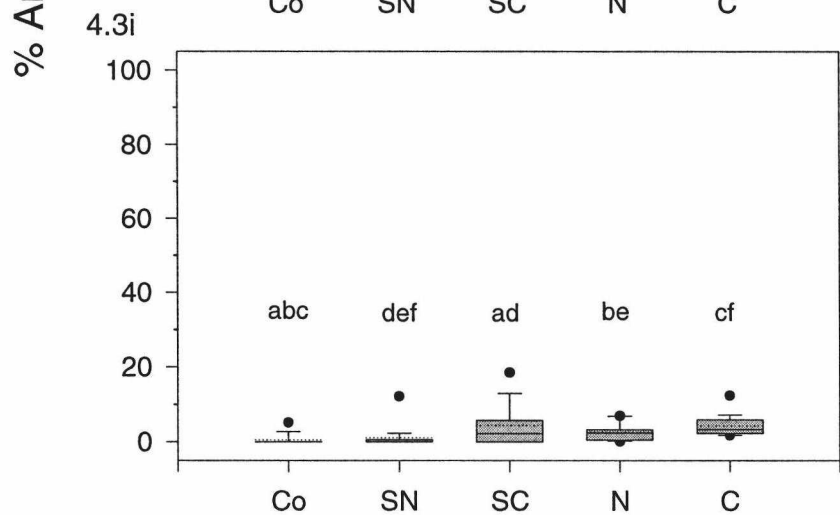
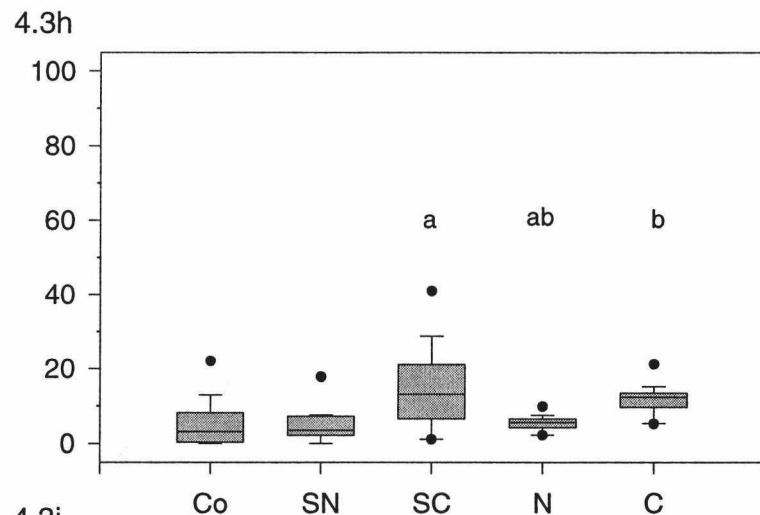
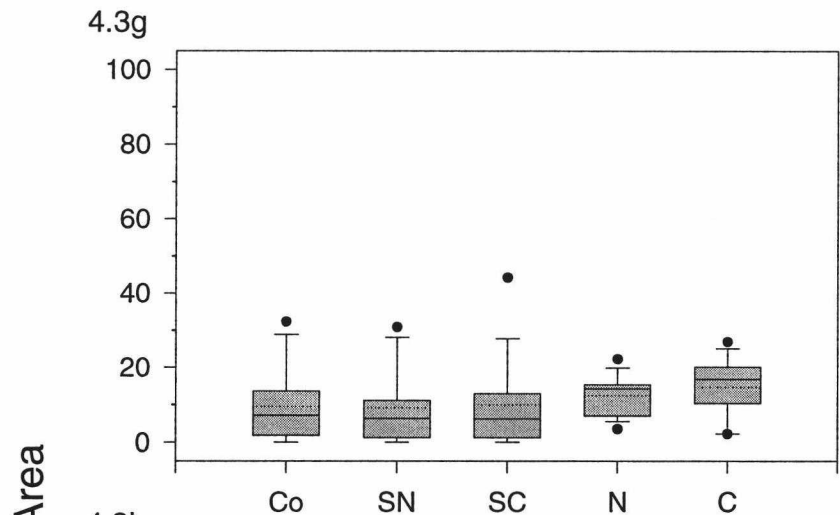


4.3e



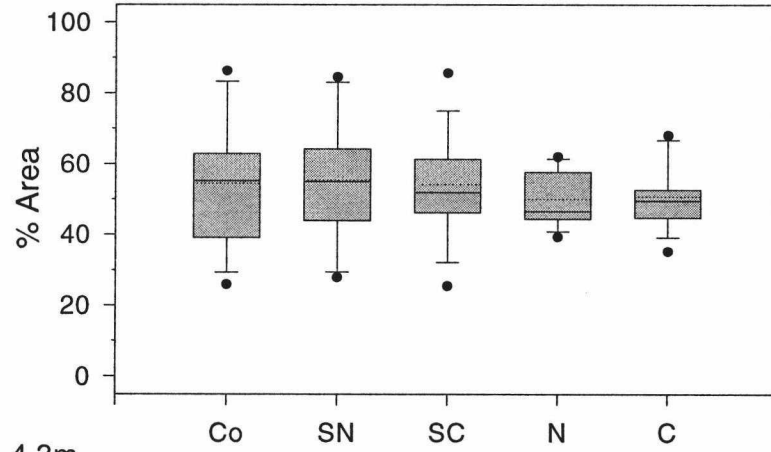
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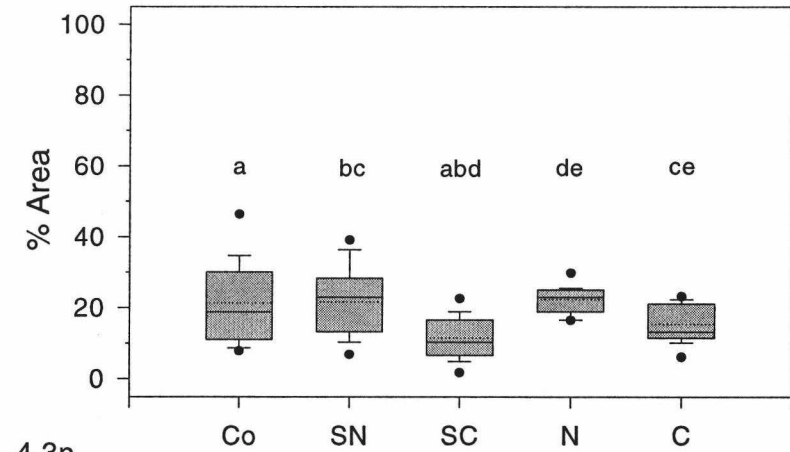


Spatial Scale

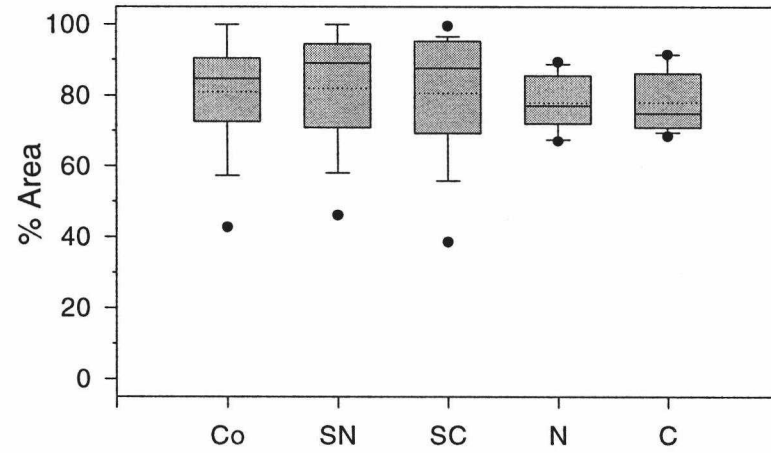
4.3k



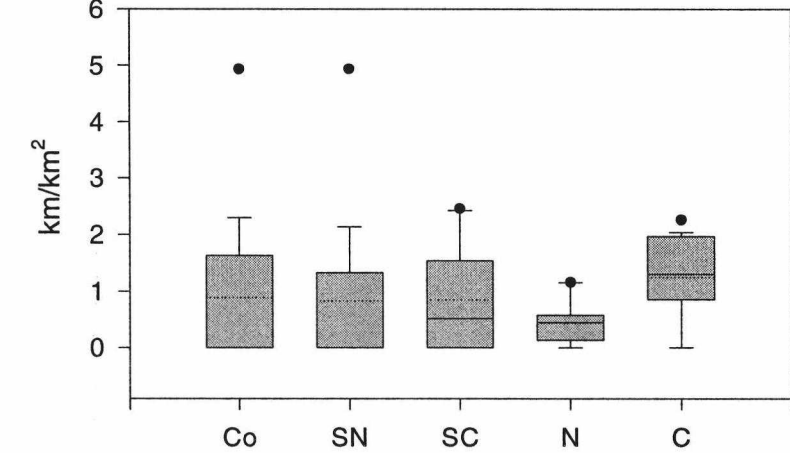
4.3l



4.3m



4.3n



Spatial Scale

comparisons were always between the upslope scales and the riparian buffer scales (i.e., corridor, sub-network, or network scales) (Fig. 4.3). As an example, for the percent area in slopes $\leq 30\%$ (Fig. 4.3d), the medians of the sub-catchment (12.2%) and the catchment (11.9%) scales, although not significantly different from each other, were significantly different ($P \leq 0.05$) from those of the corridor (26.2%), sub-network (21.3%), and network (23.1%) scales. No significant differences were observed among the riparian buffer scales for this variable.

Regression of channel unit features with catchment area and landscape characteristics

The mean maximum depth of pools and the mean volume of pools were positively related to catchment area (Table 4.3). Catchment area explained more of the valley segment-scale variation in the mean maximum depth of pools and in the mean volume of pools than any landscape characteristic summarized at any spatial scale (Table 4.3). Furthermore, no landscape characteristic was significantly ($P > 0.05$) related to either variable when considered in among-scale multiple linear regression with catchment area. Stream distance between each pair of valley segments explained only a small proportion of the variation in the absolute differences between residuals resulting from regression of catchment area with either the mean maximum depth of pools ($r^2 = 0.04$; $df = 104$; $P = 0.06$) (Fig. 4.4a) or mean volume of pools ($r^2 = 0.01$; $df = 104$; $P = 0.36$) (Fig. 4.4b).

Landscape characteristics that were most highly correlated with the mean maximum depth of pools and the mean volume of pools explained less than half the

Table 4.3. Results from linear regression to explain among-valley segment variation in channel unit features in tributaries of the Elk River, Oregon. Independent variables were catchment area and landscape characteristics summarized at five spatial scales. Direction and significance of relationships between independent and dependent variables are indicated by +/- (Prob>|t|). Models with all slope parameters significant at $\alpha=0.05$ are indicated by *. Bonferroni correction for each model results in significance at $\alpha=0.05/5=0.01$ for five spatial scales.

Model (df=14)	Corridor	Sub-network	Sub-catchment	Network	Catchment
<i>Mean maximum depth of pools vs.</i>					
Drainage area of the catchment					+(0.001)
r^2 (Prob>F)					0.57 (0.001)*
<i>Mean volume of pools vs.</i>					
Drainage area of the catchment					+(0.0001)
r^2 (Prob>F)					0.87 (0.0001)*
<i>Mean density of large wood in pools vs.</i>					
Drainage area of the catchment					-(0.02)
r^2 (Prob>F)					0.35 (0.02)*
<i>Mean density of large wood in pools vs.</i>					
% Sedimentary rock types	-(0.04)	-(0.01)	-(0.004)	-(0.04)	-(0.16)
% Forests of medium-very large diameter trees	+(0.05)	+(0.01)	+(0.003)	+(0.01)	+(0.02)
R^2 (Prob>F)	0.34 (0.03)*	0.48 (0.008)*	0.58 (0.002)*	0.41 (0.02)*	0.34 (0.03)
<i>Mean density of large wood in pools vs.</i>					
% Sedimentary rock types	-(0.08)	-(0.08)	-(0.05)	-(0.02)	-(0.18)
% Road density (km/ha)	-(0.05)	-(0.04)	-(0.06)	-(0.01)	-(0.06)
R^2 (Prob>F)	0.35 (0.03)	0.36 (0.03)	0.34 (0.03)	0.40 (0.02)*	0.22 (0.09)

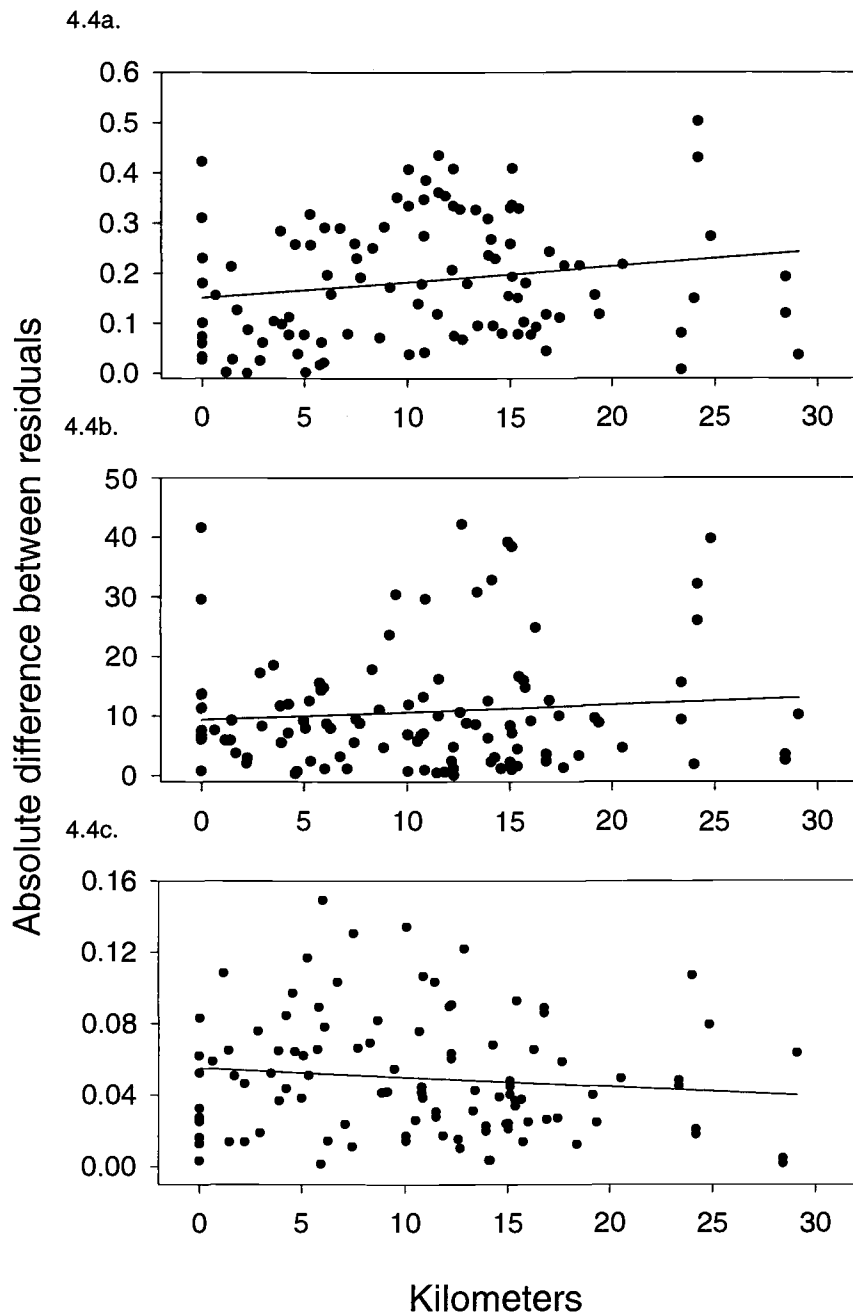


Figure 4.4. Results of linear regressions for stream distance between each pair of valley segments and the absolute difference between residuals from among-scale regressions of channel unit features with landscape characteristics for tributaries of the Elk River, Oregon. Residuals were from regression of mean maximum depth of pools with catchment area (a); mean volume of pools with catchment area (b); and mean density of large wood in pools with percent area in sedimentary rock types at the sub-catchment scale and percent area in mixed and conifer forest of medium to very large diameter trees at the sub-catchment scale (c).

variation explained by catchment area and were themselves significantly related to catchment area. For example, the mean maximum depth of pools was positively related to the percent area in broadleaf forest at the corridor scale ($r^2 = 0.29$; $df = 14$; $P = 0.04$), and the latter was positively related to catchment area ($r^2 = 0.31$; $df = 14$; $P = 0.03$).

Although the mean density of wood in pools was negatively related to catchment area, an equal or greater proportion of the variation was explained by landscape characteristics at four of the five spatial scales (Table 4.3). The mean density of wood in pools was most significantly related to the percent area of sedimentary rock types and to the percent area in forests of medium to very large diameter trees when these were summarized at each spatial scale except the catchment. With landscape characteristics summarized at the network scale, almost as much of the variation was explained by a multiple linear regression model containing the percent area in sedimentary rock types and road density (km/km^2) instead of the forest cover variable (Table 4.3). At this scale, as the density of roads increased, the percent area in forests of medium to very large diameter trees decreased ($r^2 = 0.69$, $df = 14$; $P = 0.0001$) (Fig. 4.5). These two land cover variables were negatively related also at each of the other four spatial scales ($r^2 = 0.35$ (corridor scale), $r^2 = 0.46$ (sub-network scale), $r^2 = 0.37$ (sub-catchment scale), and $r^2 = 0.85$ (catchment scale); $df = 14$; $P \leq 0.02$).

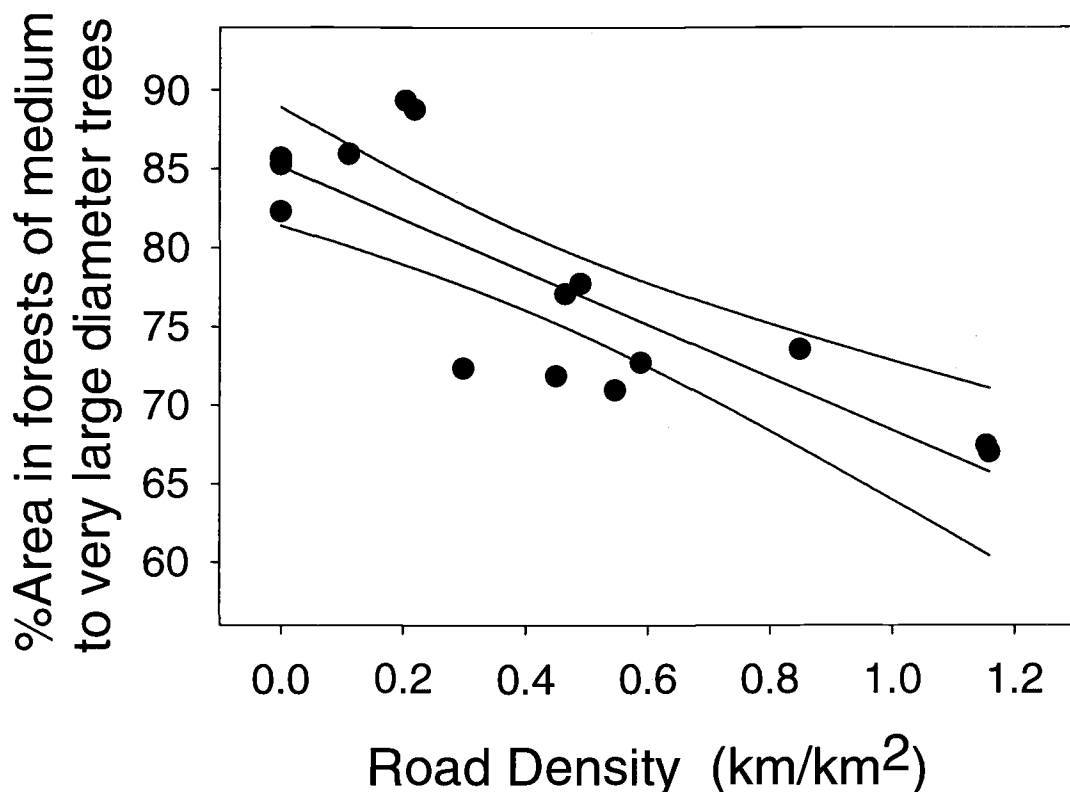


Figure 4.5. Results of linear regression between the percent area in forests of medium to very large diameter trees and road density at the sub-network scale for tributaries of the Elk River, Oregon. The linear regression line and 95% mean confidence curves are shown ($y = 85.7 - 16.7x$; $r^2 = 0.69$; $P = 0.0001$).

Both within- and among-scale variable selection resulted in the same 'best' regression model for the mean density of wood in pools. The percent area of sedimentary rock types and percent area in forests of medium to very large diameter trees explained the greatest proportion of the variation in wood density at the sub-catchment scale (Table 4.3). Stream distance between each pair of valley segments explained little of the variation in the absolute difference between residuals ($r^2 = 0.01$; $df = 104$; $P = 0.26$) (Fig. 4.4c).

Discussion

Landscape characterization

Variances differed significantly among spatial scales for the majority of landscape characteristics. The smallest variance for landscape characteristics was generally observed at either the network or catchment scale. Because the spatial resolution of landscape coverages was typically smaller than the area of analytical units, variance declined as the area of analytical units increased. This agreed with observations that variability in landscape characteristics decreases as grain or patch size increases (Forman and Godron 1986; Syms and Jones 1999).

Medians differed significantly among spatial scales for a third of the examined landscape characteristics. For landscape characteristics subsequently used in regression analyses, differences in medians were between the sub-catchment or catchment scales and one or more of the riparian buffer scales (i.e., corridor, sub-network, and network). Thus, upslope and riparian areas were distinguished when the latter was approximated with a fixed-width buffer then described by digital topography and forest cover classes from satellite imagery. Depending upon the attribute, this approach appears useful for characterizing riparian areas over broad spatial extents in forested systems. Alternatively, the actual riparian zone can be delineated in the field with vegetation, soils, and geomorphic data or estimated from aerial photography. Both are time intensive processes that limit the spatial extent reasonably addressed. If analytical units had been spatially discrete (i.e., analytical units at coarser scales had not subsumed those at finer scales), among-

scale differences may have been observed for more of the landscape characteristics. Most studies in agricultural systems that examined upslope and riparian areas over a broad region used a fixed-width buffer. Some of these found landscape characteristics in upslope and riparian areas were similar (e.g., Richards and Host 1994; Wang et. al. 1997), but others did not (e.g., Lammert and Allan 1999).

Regression of channel unit features with catchment area and landscape characteristics

Among-scale regression models explained a significant proportion of the variation in the three channel unit features (i.e., mean maximum depth of pools, mean volume of pools, and mean density of large wood in pools). Residuals from these regressions suggested little evidence of spatial autocorrelation, so we did not attempt to remove or account for spatial structure in regression models (Cliff and Ord 1973; Legendre 1993). However, relatively small sample size may have hampered our ability to identify spatial autocorrelation. We are aware of no ideal technique to assess spatial dependence for stream networks when using relatively few coarse-grained analytical units that differ in size and spacing. Consequently, we adapted an approach that assesses the degree of relationship for geographic distances between all pairs of locations and corresponding differences between values of variables at those locations (Legendre and Fortin 1989). Geographic distances are usually calculated with x-y coordinates (e.g., Hinch et al. 1994), but we chose stream distance to better reflect potential connectivity between valley segments.

Catchment area explained more among-valley segment variation in the mean maximum depth of pools and the mean volume of pools than landscape characteristics at any of the five spatial scales. Catchment area is related to stream power through its direct influence on stream discharge. Streams with higher discharge generally have greater stream power, an index of the ability to transport materials (e.g., sediment and wood), and tend to be deeper and wider than those with lower discharge (Gordon et al. 1992). Accordingly, the mean maximum depth and volume of pools in Elk River tributaries increased as catchment area increased. Pool attributes have been negatively related to level of timber harvest (e.g., Bilby and Ward 1991; Wood-Smith and Buffington 1996). However, the forestry-related land cover variables we examined explained a smaller proportion of the variation in mean maximum depth and volume of pools than catchment area. For streams in the Midwestern US, catchment area had greater explanatory power than land cover variables for parameters describing channel cross sectional diameter (Richards et al. 1996).

The mean density of wood in pools was also negatively related to catchment area which is consistent with the increased ability of larger streams to transport wood. A similar relationship was found in other forestry-dominated systems (Bilby and Ward 1991; Montgomery et al. 1995), but not in an agricultural system (Richards et al. 1996). As the intensity and duration of human-caused disturbance increases along the continuum from silvicultural to agricultural to urban landscapes, the presence of wood in the channel may be determined more by wood availability

than by fluvial transport processes. Wood density and an indicator of stream discharge, bank-full stream width, were related in areas with few human impacts (e.g., Bilby and Ward 1989). The utility of this relationship was recognized for determining if wood density at another site was similar to that expected for a 'natural' stream of the same size. Additionally, regression parameters or proportion of variation explained by the relationship may be useful benchmarks for assessing if wood dynamics at broader spatial scales are operating naturally [i.e., within natural variability (Landres et al. 1999)]. Deviations from such benchmarks may indicate that anthropogenic disturbances have disrupted wood dynamics and constrained variability of inchannel wood over an entire catchment or region.

Landscape characteristics generally explained as much or more of the variation in the density of large wood in pools than catchment area. The mean density of wood in pools was positively related to the percent area in forests of medium to very large diameter trees at all except the catchment scale. Age or stem diameter of forest cover reflects time since timber harvest in areas such as the Elk River basin where forestry-related activities currently dominate the disturbance regime. The greater the percent area in forests of medium to very large diameter trees, the lesser the percent area assumed to have been affected by recent timber harvest. Thus, our regression results using forest cover data corroborate findings wherein frequency of large wood in streams was negatively related to forest management (Bilby and Ward 1991; Reeves et al. 1993; Montgomery et al. 1995; Wood-Smith and Buffington 1996; Lee et al. 1997). Because land cover variables

had more explanatory power for the mean density of wood in pools than for the mean maximum depth and volume of pools, large wood metrics may be more sensitive at detecting forestry influences in south coastal basins than variables describing pool geometry.

In addition to the forest cover variable, the mean density of wood in pools was negatively related to the percent area of sedimentary rock types. Large wood is delivered to salmonid-bearing streams in forested, montane basins by chronic channel-adjacent processes such as bank erosion and by episodic hillslope processes such as landsliding (Bilby and Bisson 1998). Less mass wasting debris reached streams of the Elk River basin in sedimentary rock types than in either igneous-intrusive or metasedimentary rock types (McHugh 1986). Additionally, meta-sedimentary rock types experienced more mass wasting on lower slopes under intact forest than the other rock types (McHugh 1986). These considerations may in part account for the negative relationship we found between wood density and sedimentary rock types.

Linear regression explained a greater proportion of the variation in the mean density of large wood in pools when landscape characteristics were summarized at the sub-catchment scale than at finer or coarser spatial scales. The relatively low proportion of variation explained at the corridor scale suggested that wood was delivered from sources in addition to those immediately adjacent to surveyed valley segments. Approximately half the volume of wood in mainstem Cummins Creek, an Oregon Coast Range wilderness stream, was delivered from upslope sources,

primarily by debris flows through lower order tributaries (McGarry 1994).

Although debris flows may be more prevalent in Oregon Coast Range and Cascade Mountains river basins, debris flows in the Elk River basin do deliver to higher order channels (Ryan and Grant 1991). The sub-network scale included many of the lower order tributaries capable of delivering debris flow-transported wood to surveyed valley segments. Perhaps as a result, explanatory power was greater at the sub-network than at the corridor scale. More variation was explained by regression at the sub-catchment scale than at the sub-network scale. Analytical units at the sub-catchment scale encompassed unmapped lower order tributaries and upslope areas capable of delivering wood from unchanneled hillslope processes. As spatial extent expanded upstream beyond the sub-catchment scale, the proportion of variation explained by landscape characteristics decreased. This suggested that regression relationships at the network and catchment scales were less reflective of processes influencing wood dynamics. We did not determine the distance upstream that explanatory power began to decline. Identification of any such upstream threshold may help in comparing the importance of fluvial transport and other wood delivery processes and, therefore, in designing riparian protection.

With landscape characteristics summarized at the network scale, an approximately equal proportion of variation in the mean density of wood in pools was explained by substituting road density (km/km^2) for the forest cover variable in regression with percent area of sedimentary rock types. Road density and the percent area in forests of medium to very large diameter trees were negatively

correlated at all five spatial scales. The degree of correlation increased with increasing spatial extent, suggesting that roads and forest disturbances were not always sited together. Similar to our findings, percent area harvested and road density were highly correlated with each other and were almost equally correlated with a channel response variable, change in stream width, for catchments in the South Umpqua River basin (Dose and Roper 1994).

Although road density and forest cover can be highly correlated, one or the other variable may have more explanatory power for a particular response (Bradford and Irvine 2000) or at a particular spatial scale, as we found. Roads and timber removal share effects on some of the processes that shape stream ecosystems (e.g., increasing landsliding or surface runoff rates) but not all (e.g., increasing direct solar radiation) (Hicks et al. 1991) and may differ in the quality, timing, or magnitude of those effects shared (e.g., Jones and Grant 1996; Jones 2000). Roads may have intercepted debris flows that would have otherwise delivered wood to streams (Jones et al. 2000). However, the mean density of wood in pools was probably more influenced by decreasing the amount of wood available for delivery to Elk River tributaries through timber removal. This was suggested by two findings: 1) valley segment variation in the mean density of wood in pools was better explained by the regression model containing the forest cover variable at each scale than by the corresponding model containing road density; and 2) the only significant relationship to road density was at the network scale, which was one of the two spatial scales that road density and the forest cover variable were most

strongly related. Before concluding that conditions of aquatic habitat or biota are unrelated to silvicultural activities, examining relationships with both forest cover and road density appears prudent, particularly when these are summarized at finer spatial scales. Additionally, primary influences may be indicated by determining if a response variable is related to road density or forest cover or both and at what scales.

Summary and Conclusions

The utility of multi-scale analysis for understanding relationships between landscape characteristics and stream habitat was demonstrated for a mountainous area where forestry is the primary land use. At each spatial scale except the catchment, the percent area in sedimentary rock types and the percent area in forests of medium to very large diameter trees explained more variation in the mean density of wood in pools than any other regression model. These findings suggested that similar processes were operating at these spatial scales to affect wood density and that having larger, older trees on the hillslope was important to providing large wood in the channel. The greatest proportion of variation in the mean density of wood in pools was explained with landscape characteristics summarized at the sub-catchment scale. Source areas for important processes were probably not fully encompassed at finer scales, but at coarser scales, source areas were included that were less connected to large wood dynamics in surveyed channels. In contrast to the mean density of wood in pools, mean maximum depth and volume of pools were each directly related to catchment area, which explained more variation than

landscape characteristics at any spatial scale. Exploring relationships at multiple spatial scales can identify riparian and upslope areas that are most tightly linked to aquatic habitat. Among-scale similarities and differences in relationships can suggest key processes responsible for those relationships. Understanding gained from multi-scale studies can help choose analysis or modeling units for bio-regional assessments of aquatic systems. Such understanding can also be directly applied when designing land management strategies to reduce impacts on, or supply habitat elements to, streams.

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CHAPTER 5 SUMMARY AND CONCLUSIONS

This study illustrated the value of multiple year and multiple spatial scale analyses for understanding relationships among juvenile anadromous salmonids, their freshwater habitat, and landscape characteristics. Chapters 2 and 3 highlighted the relevancy of multi-year habitat selection and use studies. Interannual patterns provided a context for, and reinforced confidence in, results from any one year. Among-year differences in selection ratios for juvenile salmonids lead to consideration of factors that may have influenced habitat selection and use, such as environmental conditions and competition (Chapter 2). Multiple years of data allowed determination of how frequently the level of use by juvenile ocean-type chinook salmon was differentiated using valley segment and channel unit features (Chapter 3). Additionally, the specific features most correlated with valley segment use and the transferability of results could be compared among years.

In many cases, if only one or two years of data had been examined, as is common in habitat selection and use studies, conclusions may have differed substantially from those in this study. For example, I might have erroneously concluded that juvenile ocean-type chinook salmon were generally randomly distributed in Elk River tributaries and that their use of valley segments was unrelated to freshwater habitat features. Instead, because multiple years were examined, it was clear that valley segment and channel unit features could often distinguish among valley segments for level of use by juvenile chinook salmon

(Chapter 3). Observations in this study were congruent with findings from other systems of substantial inter-annual variation in stream fish population abundance (Grossman et al. 1990; Ham and Pearsons 2000) and reinforced warnings of problems that may arise when examining fish-habitat relationships over a limited temporal extent (Platts and Nelson 1988). With few notable exceptions (e.g., Long Term Ecological Research (LTER) program), scientific institutions are neither structured nor funded to support longer-term studies. However, critical understanding about stream ecosystems and potential for long-term, land-use effects may not emerge with any other approach (e.g., Hall et al. 1987; Tschaplinski 2000).

Analyses at multiple spatial scales within the Elk River basin also provided valuable insights. First, members of the juvenile anadromous salmonid assemblage selected habitat types at multiple spatial scales (Chapter 2). Second, the distribution of juvenile ocean-type chinook salmon was routinely influenced by both valley segment- and channel unit-scale features (Chapter 3). And third, multi-scale analysis identified riparian and upslope areas most tightly linked to stream habitat condition and suggested processes responsible for observed patterns (Chapter 4).

Habitat selection and use by juvenile salmonids were influenced by characteristics at the stream system and valley segment scales (Chapters 2 and 3). Ocean-type chinook salmon always selected for the mainstem, coastal cutthroat trout and steelhead selected for the tributaries or were randomly distributed at the stream system scale, and coho salmon selected for the mainstem in some years but

for tributaries in others (Chapter 2). Although juvenile salmonids appeared not to differentiate between the two valley segment types in the mainstem, unconstrained valleys in the tributaries were either selected or avoided by all four species.

Chinook salmon, coho salmon, and cutthroat trout often selected unconstrained valleys, but steelhead often avoided these (Chapter 2). Additionally, the influence of unconstrained valleys was the most statistically significant variable distinguishing between valley segments that were highly used by juvenile chinook salmon and those that were not (Chapter 3).

The importance of unconstrained valleys to juvenile salmonids in Elk River tributaries may derive from characteristics not routinely measured in fish habitat surveys. Unconstrained valleys rarely differed statistically from other valley segment types for any examined channel unit feature (e.g., mean maximum depth of pools; mean density of wood in pools; frequency of pools) (Chapter 2).

Unconstrained valleys may, however, support relatively high levels of primary production and aquatic macroinvertebrate biomass (Zucker 1993), nutrient and particulate retention (Lamberti et al. 1989), and groundwater upwelling (Edwards 1998; Baxter and Hauer 2000) that should increase their suitability to spawning adults and rearing juveniles for each salmonid species. On the other hand, water velocities are typically lower (Gregory et al. 1991) and summer water temperatures can be more variable from increased solar heating (McSwain 1987) in unconstrained valleys than in other valley segment types. These characteristics may be less suitable for steelhead than the other salmonids (Bisson et al. 1988; Hicks

1989; Bjornn and Reiser 1991) and help explain why steelhead avoided unconstrained valleys.

Habitat selection and use by juvenile salmonids were also influenced by characteristics at the channel unit scale (Chapters 2 and 3). Pools were selected by all species in the tributaries and by each species except steelhead in the mainstem (Chapter 2). Relative to fastwater, all four species selected less strongly for mainstem pools than for tributary pools, suggesting the heightened importance of pools in the tributaries. Although juvenile ocean-type chinook salmon in the Elk River used and often selected pools, neither the frequency nor percent area of pools helped distinguish between valley segments that were highly used by this species and those that were not (Chapter 3). Three other channel unit features, mean maximum depth of pools, mean density of large wood in pools, and mean volume of pools, were however, significantly related to level of use by juvenile chinook salmon (Chapter 3). Obtaining a better understanding of the differences between steelhead and the other salmonids in selection for pools in the mainstem and unconstrained valleys in the tributaries should improve habitat management and protection for all four species.

The assumption that animals choose resources at multiple spatial scales often structures habitat selection studies in terrestrial systems (e.g., Johnson 1980; Orians and Wittenberger 1991). Poff (1997) proposed a multi-scale conceptual model of stream systems wherein the presence of a species at a specific location is a consequence of its traits matching landscape filters in a series that progresses from

the watershed to the micro-habitat. Results suggesting that juvenile salmonids selected and used habitat features at the three examined spatial scales in Elk River are consistent with these views (Chapters 2 and 3). A logical outcome of a multi-scale perspective of selection is the need to understand, manage, and protect habitat features from the landscape to the micro-habitat. Regional conservation goals for salmonids may be best advanced by simultaneously protecting and restoring the processes that create fine-scale, ephemeral features (e.g., deep pools) and the functions of coarse-scale, persistent geomorphic features (e.g., unconstrained valleys) that are important to fish.

A multi-scale perspective may be useful also for understanding relationships between landscape characteristics and channel unit features that are important to juvenile salmonids (Chapter 4). At each spatial scale except the catchment, the density of wood in pools was negatively related to the percent area in resistant sedimentary rock types and positively related to the percent area in mature to old forest. The sub-catchment-scale model explained the greatest proportion of variation in wood density. These findings suggested that although spatial scales were similar in processes affecting wood density, finer spatial scales (i.e., corridor and sub-network scales) omitted source areas for key wood delivery processes, and the coarser spatial scales (i.e., network and catchment) included source areas for processes less tightly coupled to wood dynamics in surveyed channels. Exploring relationships at multiple spatial scales can identify riparian and upslope areas that

are most tightly linked to aquatic habitat. Among-scale similarities and differences in relationships can suggest key processes responsible for those relationships.

Spatial position of valley segments may have influenced their use by juvenile salmonids. Although the spatial arrangement of habitat patches is commonly thought to affect the distribution and abundance of biota (Dunning et al. 1992; Wiens et al. 1993; Schlosser 1995; Hanski and Gilpin 1997), this has only recently been considered for trout (D'Angelo et al. 1995; Baran et al. 1997; Baxter and Hauer 2000) and salmon (Kocik and Ferreri 1998; Inoue and Nakano 1999). Valley segments near unconstrained valleys in Elk River tributaries were more highly used by juvenile chinook salmon than those farther away (Chapter 3). Unconstrained valleys may be key spawning areas for chinook salmon (Burck and Reimers 1978; Frissell 1992) from which juveniles in excess of available habitat may disperse. Unconstrained valleys may also supply downstream valley segments with key resources, such as drifting macroinvertebrate prey, that may increase habitat suitability for juvenile chinook salmon. Exploring the assumptions underlying the composite variable, influence of unconstrained valleys, is an important next step. Such research might include determining if unconstrained valleys are sources of juvenile fish, key resources or both; how location in the stream network affects the influence of an unconstrained valley on another valley segment; and which attributes or processes fish perceive when selecting a valley segment.

Methods for characterizing spatial association in stream networks are not widely available. Spatial dependence in terrestrial systems has been quantified by point and surface pattern analyses (Isaaks and Srivastava 1989; Legendre and Fortin 1989; Legendre 1993; Carroll and Pearson 2000). In the few published geostatistical analyses of streams, the phenomenon of interest was expressed as fine-scale patches in the stream (Cooper et al. 1997), coarse-scale patches in the landscape (Dunham and Rieman 1999) or points in a reach (Geist et al. 2000). Methods for line pattern analysis are available and appropriate to describe spatial dependence in networks (Legendre and Fortin 1989), however I found no applications for terrestrial or stream ecosystems. Most methods to describe spatial dependence are ill suited to the study of rivers when relatively few coarse-grained analytical units that differ in length and spacing, such as valley segments, are used. For example, a dataset much larger than that available at the valley segment scale for Elk River tributaries, 30-50 pairs of locations for each distance class or spatial lag, would have been required for semivariogram analysis (Rossi et al. 1992). Such considerations influenced my decision to apply parametric methods in assessing spatial relationships between fish and their habitat (Chapter 3) and in relating channel unit features to landscape characteristics (Chapter 4). Implications of violating the independence assumptions were evaluated with randomization procedures for discriminant analyses (Chapter 3) and with plots of stream distances versus absolute differences between residuals for linear regression analyses (Chapter 4). Results suggested that parametric tests of significance were only

marginally affected by spatial dependence. However, I was not entirely satisfied with either approach. Advancing techniques to analyze spatial dependence in streams appears to be an interesting, beneficial, and timely direction of study.

Because all valley segments used as units of analysis were taken from the Elk River and its tributaries, rather than from a more spatially extensive population, the scope of direct statistical inference is the Elk River basin. However through less formal schemes of inference (Shrader-Frechette and McCoy 1993), understanding derived from this long-term case study should have relevance to basins with similar climatic, geologic, and biotic characteristics. Few coastal Oregon basins are as diverse as the Elk River in this suite of characteristics. Thus, when taken in its entirety, the Elk River may directly represent a relatively limited area. On the other hand, this diversity of characteristics may broaden the applicability of findings from Elk River beyond the south coast to a wider variety of basins. Case studies, such as the Alsea Watershed Study or that conducted at Carnation Creek, BC have been invaluable in their contributions to advancing understanding of stream ecosystems and effects of watershed management on salmonids (Hall et al. 1987; Tschaplinski 2000). I recognize the many constraints of a case study such as this but suggest that these results be considered for their value in suggesting testable hypotheses (Conquest and Ralph 1998), in developing techniques applicable in broader-scale assessments of aquatic resources, and in augmenting a growing body of knowledge regarding relationships between juvenile salmonids and their freshwater habitat at multiple spatial scales over time.

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