AN ABSTRACT OF THE DISSERTATION OF

Rebecca L. Flitcroft for the degree of Doctor of Philosophy in Fisheries Science
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Title: Regions to Streams: Spatial and Temporal Variation in Stream Occupancy
Patterns of Coho Salmon (*Oncorhynchus kisutch*) on the Oregon Coast.

Abstract approved______________________________________
Gordon H. Reeves

Aquatic ecological investigation is expanding to encompass considerations of multiple scales across large landscapes. Much of the analysis included in this work focuses specifically on coho salmon (*Oncorhynchus kisutch*) in multiple subbasins on the Oregon coast. Coho salmon were chosen for an investigation of spatial scales, network connections, and life history stages due to their broad distribution on the Oregon coast, and abundant data describing their distribution, habitat needs, behavior, and survival. Chapter 2 introduces dynamic network topology (DNT) as a framework for analysis and interpretation of aquatic obligate species. DNT is based on the premise that in-stream habitats change in form and organization over time, and native aquatic species are adapted to those changes through movement and life history diversity. Chapter 3 analyzes juvenile coho salmon density and stream network occupancy at three spatial scales (site, patch, and subbasin). The site scale analysis indicated that combining network and traditional in-stream habitat metrics (i.e., substrate and habitat juxtaposition variables) are most effective at describing juvenile coho salmon density. Patch sizes of juvenile coho salmon were defined using variograms. Variogram shape indicated that a nested spatial structure may be present in larger subbasins, indicating overlapping patterns of juvenile stream use. At the subbasin scale, stream network occupancy by juvenile coho salmon was shown to vary over time within subbasins, and appeared to increase or decrease similarly to the size of the adult spawning run. In chapter 3, two-tier Bayesian hierarchical models were applied to adult (subbasin and basin scales) and juvenile (site and subbasin scales) coho salmon in an attempt to combine spatial scales that might be influential at each life history stage. The best fitting adult model included the percent of large trees in the riparian zone at the subbasin scale with mean annual precipitation at the basin scale. The best fitting juvenile model included three variables, percent sand, stream order, and network distance to spawning habitat which mirrors the result of modeling efforts in Chapter 3. Multiple spatial scales and the framework of a stream network were informative at detecting patterns and interactions among scales and life history stages of coho salmon.

Regions to Streams: Spatial and Temporal Variation in Stream Occupancy Patterns of Coho Salmon (*Oncorhynchus kisutch*) on the Oregon Coast

by
Rebecca L. Flitcroft

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APPROVED:

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Dean of the Graduate School

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.

Rebecca L. Flitcroft, Author

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CONTRIBUTION OF AUTHORS

Dr. Gordon H. Reeves was an advisor and editor on all manuscripts included in this work. Dr. Robert E. Gresswell was an advisor and editor on Chapter 2. Dr. Lisa Ganio was an advisor, editor, statistical consultant, and statistical programmer on Chapter 3. Dr. Alix Gitelman was an advisor, editor, and statistical consultant on Chapter 4. Kelly Christianson was a GIS analyst on Chapter 4.

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Chapter 1

Stream Networks and Multiple Spatial Scales for an Analysis of Coho Salmon (*Oncorhynchus kisutch*) on the Oregon Coast

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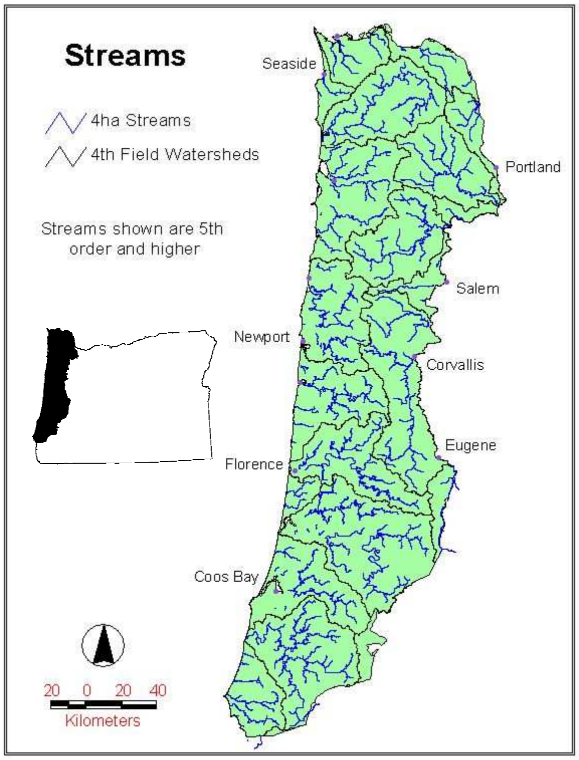
Introduction

Research that meaningfully contributes to understanding patterns of occupancy for an aquatic obligate species using multiple spatial scales and a network perspective is unusual and may expand how ecologists think about aquatic organization. This dissertation focuses on juvenile and adult coho salmon (*Oncorhynchus kisutch*) in coastal Oregon streams. Patterns of occupancy by juvenile coho salmon populations in stream networks of Oregon's mid coast are explored, as are adult coho salmon populations between Astoria in the north and Cape Blanco to the south (Figure 1.1). Not only do these boundaries correspond with the area studied by the Coastal Landscape Analysis and Modeling Study (CLAMS) from which many key datasets are derived, but they correspond with coastal ecoregions that describe areas of relatively similar geology, vegetation and precipitation (Thorson et al. 2003). Coho salmon were selected for analysis in this study primarily because of their over-winter use of coastal streams, the relatively small stream size (1st–3rd-order on 1:100,000 scale maps; Strahler 1952) occupied by juveniles, and the wide distribution of migrating adults. Also, abundant data are available that document juvenile coho salmon distribution, abundance and habitat as well as adult spawning numbers and locations.

Perhaps the most important criteria for selecting coho salmon in an analysis of stream networks is that coho salmon life history, like the histories of other salmonids, is a complex example of adaptation and survival that is dependent on a diverse array of habitats. Adult and juvenile coho salmon use the stream network in different ways. Adults migrate through the stream system in search of spawning habitat and partners. Juveniles navigate the stream network in search of adequate seasonal habitats for a

Figure 1.1. Outline of streams (5th order and larger) in the CLAMS study area.



year of freshwater residency before migrating to the ocean. Each life history stage includes a variety of behaviors that are adapted to existence in a changing stream environment. I will explore the importance of habitat diversity over time for coho salmon with a network perspective that uses the complexity of a stream network for insight and investigation.

Coho Salmon Life History

Coho salmon, also known as silver salmon, range in North America between Monterey Bay, California and Point Hope, Alaska. Coho salmon are one of five species of Pacific salmon belonging to the genus *Oncorhynchus*. The other four species of Pacific salmon are pink (*O. gorbuscha*), chum (*O. keta*), sockeye (*O. nerka*) and Chinook (*O. tshawytscha*) salmon. Chinook and coho salmon are found in Oregon. The two species of anadromous trout that are also found in Oregon are steelhead (*O. mykiss*) and coastal cutthroat (*O. clarkii*). (Groot and Margolis 1991, Lichatowich 1999, Quinn 2005).

Coho salmon spawning run times vary by latitude, with adults entering rivers in Alaska in July, British Columbia in September and October and Oregon and California in November and December. However, some specific streams have migration runs of coho salmon as early as April or as late as February and March (Groot and Margolis 1991). Juvenile coho salmon in Oregon and Washington typically spend their first year in smaller streams and migrate to the ocean in the spring of their second year (Lichatowich 1999). Habitat needs for juvenile coho salmon differ between summer and winter (Nickelson et al. 1992a, Sleeper 1993, Spalding et al. 1995). Deep pools and cool water characterize summer habitat, and winter habitat is characterized by large wood and off-channel refuges such as backwaters, alcoves, secondary channels or tributaries (Quinn and Peterson 1996, Rosenfeld et al. 2000, Bell 2001, Bramblett et al. 2002).

The majority of adult coho salmon return to their natal streams to spawn. Unfortunately, research on salmon straying rates is limited. Labelle (1992) reported that approximately 4.7% of coho salmon strayed between nine streams on the coast of Vancouver Island. However, he conjectured that straying rates could be more than 40% in some streams for some years. Straying in other salmon species such as Chinook, sockeye and pink salmon and steelhead has also been documented

(Shapovalov and Taft 1954, Cooper and Mangel 1998). Quinn (2005) hypothesized that straying would be more common in species that experience greater habitat disturbance than in those with more predictable environments. In this case, straying would be an adaptation to ensure the survival of the population in inconsistent environments. This argument and the literature that documents the common incidence of straying support the assertion that metapopulation structure is possible and even likely in some populations of salmon.

Study Goals

This study seeks to accomplish three goals:

1) Develop a comprehensive framework in which to consider spatial patterns of aquatic obligate species that incorporates the physical context of a stream network.
2) Explore juvenile coho distribution at multiple spatial scales including an assessment of the usefulness of stream network orientations of habitats or spatial position in understanding juvenile stream use.
3) Incorporate multiple spatial scales into a hierarchical Bayesian model for adult and juvenile coho salmon densities.

Network Framework: Chapter 2

I recognized the usefulness of an articulated network framework for ecological research once work on this dissertation began in earnest. I was challenged by the paucity of ecological theory and analytical tools that were focused on stream networks. While a network perspective has been explored by some researchers, much work is left to be done. For example, Gresswell et al. (2006) explored network patterns for assessment of cutthroat trout distributions. Isaak and Thurow (2006) explored patterns of Chinook redd distribution in a central Idaho basin. They found that use of the stream network increased with increasing population growth. Smith and Kraft (2005) incorporated network position variables when evaluating fish assemblages in a watershed in New York. They found that network variables, such as confluence link, provided an avenue to greater ecological understanding of the metrics that describe fish distribution. Kocik and Ferreri (1998) explored the juxtaposition of habitats and size of habitats when assessing juvenile Atlantic salmon (*Salmo salar*) growth and survival. Their model of habitat showed that understanding habitat placement and size was relevant when considering juvenile survivorship. Beyond these limited studies, little has been done to incorporate network relationships in either ecological understanding or analytical tools for exploring aquatic patterns of life in stream networks. Currently, network-based calculations of habitat relationships are absent from most current habitat interpretation or analysis.

In order to help facilitate further ecological research in streams that include a network perspective, I offer the dynamic network topology framework. This framework is meant to include the dynamic nature of stream habitats over time with the complexity of travel options unique to stream networks due to limited available directions of movement and the inherent flow of water, nutrients and inorganic matter.

Stream Networks and Scales for Juvenile Coho Salmon: Chapter 3

The context of the stream network will be explored in an attempt to further our understanding of distribution patterns of juvenile and adult coho salmon. Patterns within stream networks were identified by Gresswell et al. (2006) as an important research direction for analysis of biotic and abiotic relationships. Network distance measurements and variables that describe network position will be incorporated into the analysis of juvenile patterns of distribution. This analysis included multiple spatial scales in an attempt to explore interactions between ecological processes and fish distribution in the network. Three spatial scales will be considered: site, patch and subbasin. The site scale corresponds to local conditions and the juxtaposition of habitats within the network, and site level conditions such as substrate will be considered in an exploration of juvenile density. The patch scale encompasses the area of spatial autocorrelation of juvenile coho salmon within the stream network, and will provide a comparison of patterns of juvenile occupancy across subbasins. The subbasin scale allows for a comparison of larger patterns of juvenile occupancy with large scale environmental conditions such as precipitation and adult spawning run size.

Spatial location of stream features has been explored in assessments of fish assemblage (Megalhaes et al. 2002, Benda et al. 2004) or biotic diversity (Day et al. 1992, Wright and Li 2002) as researchers attempt to link patterns with biotic distributions. Burnett (2001) explored the use of different spatial extents over time in describing the distribution of juvenile salmonid assemblages in the Elk River Basin, Oregon. She found that both spatial and temporal extent were important in describing the observed variability in assemblage distribution. Geomorphic criteria have been used extensively to define stream reaches (Hankin and Reeves 1988, Moore et al. 1997, Rosgen 1994). Because fish habitat is associated with stream geomorphic characteristics, physical descriptions of streams have been helpful in characterizing seasonal habitat availability (Nickelson 1998, Jones and Moore 1999, Rosenfeld et al. 2000) and for use in predictions of population growth and survival (Nickelson et al. 1992b, Lichatowich et al. 1995, Quinn and Peterson 1996). Landscape features have also been used to predict fish distribution and abundance (Bradford et al. 1997, Lunetta et al. 1997, Argent et al. 2003).

Employing a network perspective when considering juvenile coho salmon abundance may allow for novel ecological interpretations of occupancy. For example, work by Chapman (1962) that identified two types of juvenile behavior was reinterpreted decades later from a different perspective (Nielsen 1992). Chapman identified territorial coho salmon and “nomads” that moved around and did not compete successfully with the territorial fish. He concluded that the “nomads” likely left the stream system and perished. Similar studies of behavior by Nielsen (1992) indicated that the non-territorial coho salmon may indeed not grow as quickly as territorial fish, but that the choice to move could be a successful life history strategy for these fish. Such a shift in interpretation of empirical observations may be possible when considering behavior and abundance within the context of the stream network.

Hierarchical Bayesian Modeling: Chapter 4

I reasoned that different spatial scales may correspond to the needs, drives, and limitations of fish at different points in their life history. For example, a large spatial scale might correspond with the dispersal of adult fish while a small spatial scale might correspond with movement patterns of small fish. I also reason that differences in spatial scales may contribute to a greater understanding of distribution patterns when hierarchically nested in an analysis that considers life history stage along with habitat needs.

Three spatial scales, site, subbasin, and basin, were used in this analysis of coho salmon. Adult coho salmon were hierarchically modeled using the subbasin and basin scales and juvenile coho were modeled with the site and subbasin scales. Two years of data were used to model adults (2001 and 2002) with only one year (2002) modeled for juvenile fish. Larger scale variables were used with adult salmon to reflect their movement potential and their spawning drive. Smaller scales were used for juveniles to reflect their limited mobility and their need to move among habitats to survive in freshwater for a year before migrating to the ocean.

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Chapter 2

Dynamic Network Topology:
Towards Developing a Stream Network Perspective

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Abstract

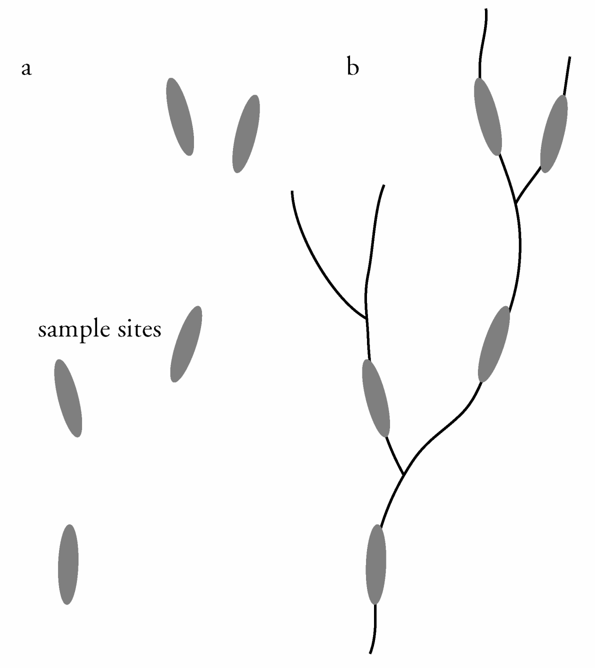
As the broader discipline of ecology embraces dynamic processes as a fundamental element of ecosystems, aquatic ecologists are working to develop theory and techniques that allow for the analysis of dynamic stream processes and communities of organisms. The stream network is the basis upon which stream habitats are organized. Natural and anthropogenic disturbances in streams alter the configuration of stream habitats seasonally, decadally, or over centuries. Native aquatic species have developed different mechanisms for coping with the dynamic nature of habitats in stream networks. However, stream network structure complicates habitat connectivity for aquatic obligate species due to limited directions of movement offered by stream channels and the inherent directionality of flow of water and other elements of the stream environment. A conceptual framework that includes the dynamic nature of streams within the context of the stream network may by useful for the study and conservation of aquatic species. Dynamic network topology is proposed as a conceptual framework that includes the location and juxtaposition of habitats in stream systems with the underlying structure of the stream network. Pacific salmon and trout are used to discuss the implications of dynamic network topology for aquatic obligate species. Ultimately, a perspective that includes the constraints and opportunities for stream species of network configurations may help in the development of analytical tools and management recommendations that benefit native species. Aquatic obligate species that reside in streams offer ecologists an opportunity to explore new ways of thinking about movement and behavior by using the stream network as a critical organizing feature describing biotic diversity.

Introduction

Ecology is an evolving science. A guiding principle in ecology has been the concept of a steady state (Wallington 2005), or climax community reached through succession (Stiling 1992). Disturbance has been viewed as a damaging disruption of systems headed for stability (Horn 1981). While the concept of instability as the normal working arrangement of ecosystems is not new (Gleason 1926, 1927), it has only been relatively recently that ecologists have begun to embrace the dynamic spatial and temporal patterns of habitats, disturbance, and organisms that are now considered a fundamental aspect of the environment (Naiman et al. 1992). This shift in philosophy has repercussions throughout ecological theory and investigation, and has been considered by some to be a paradigm change (Wallington 2005).

Several concepts and approaches to aquatic ecology are consistent with the static environment paradigm. For example, stream fishes were often investigated from the perspective of the restricted-movement paradigm (Gerking 1959), which held that adult resident fish were generally sedentary and spent the majority of their lives within short stream reaches (20-50 m). Lack of movement by resident fishes is consistent with an ecological perspective that views streams as static and unchanging. Consistent with this philosophy is the common aquatic methodological approach of sampling individual sites within a stream system, rather than entire streams (Richards and Cernera 1989, Silliman and Bertness 2002) (Figure 2.1). This sampling method assumes that fish are not using other areas thereby making sampled sites "representative" of other unsampled sites, or that movement is either uncommon, or maladaptive (Chapman 1962).

Figure 2.1. Historically, stream studies have focused on stream reaches or habitat units (a) rather than analysis of the stream network as a whole (b).



In recent decades, aquatic ecologists have followed the general trend in ecology and have begun the shift toward a worldview that considers dynamic natural processes as integral and necessary to maintaining ecological diversity (Naiman et al. 1992). The linear (Vannote et al. 1980) or static (Frissell et al. 1986) descriptions of stream organization that have dominated aquatic investigation (Fisher 1997) do not adequately represent a philosophical perspective that focuses on interconnected and dynamic processes. More recent organizational frameworks consider entire river systems, or “riverscapes” (Fausch et al. 2002), and include disturbance as a dynamic and integrated aspect of stream communities (Benda et al. 2004).

Aquatic ecologists have begun to recognize the importance of expanding the spatiotemporal scale of consideration, particularly as focus has shifted from individuals to the restoration and preservation of entire populations, species, and ecosystems (i.e., Scott et al. 1987, Li et al. 1995, Thurow et al. 1997). By expanding the scale of analysis from sites and individuals to watersheds and populations, patterns of organisms or physical processes may be interpreted differently. For example, it is possible that the decline of anadromous Pacific salmon (*Oncorhynchus* spp.) in Oregon was not identified for several decades because spawning surveys were conducted only on the same prime spawning sites every year (Cooney and Jacobs 1995). By looking at patches of individuals in isolation from the entire population, changes in habitat and salmon abundance at larger scales were missed. While this may also be a sampling design issue, it shows that population assessments are most accurate when they include the range of conditions in which individuals of the population must survive.

As aquatic ecologists begin to consider entire systems and populations, the network architecture of streams and the effects of network patterns of habitats on the distribution, abundance, and movement of aquatic obligate species is a conceptual challenge. Stream channels are the foundation upon which habitats for aquatic species are organized, and are configured as a network of branching, interconnected tributaries. The organization of habitats within the network changes in response to a variety of environmental conditions, including disturbance (Benda et al. 1998, Nakamura et al. 2000) and discharge (Gardner et al. 2003, Poff et al. 1997). For example, during low flows, fewer stream channels will have water than at high flows. At high flows, there is generally greater connectivity within the network as water fills dry channels. With changing water levels, habitats in streams also change. Summer pools flood and become winter riffles, and dry channels fill with water becoming pools. These changes in water levels, network connectivity, and habitat types mean that the configuration of habitats for aquatic organisms also changes. Therefore, individuals must be adapted to the new habitats, or be able to move to other areas of the network. The arrangement of habitats and changes in their configuration may be an important consideration of population viability assessments of aquatic species as individuals move to find adequate habitats for survival.

Scientists have observed that stream networks are in a constant state of flux in response to changing climate conditions (seasonally, decadally, or over centuries), natural disturbances (e.g., fires and landslides) and human activities (Reeves et al. 1995). Benda et al. (2004) proposed the network dynamics hypothesis that combines the hierarchical physical structure of stream networks with dynamic disturbance processes. By combining structure and process, changes in fluvial geomorphology due to disturbances such as debris flows may be predicted. For example, Benda et al. hypothesize that tributary junctions will be a nexus for habitat diversity, because it is at junctions that material from debris flows and floods will be physically forced to halt. Debris flow material contributes the raw materials necessary for habitat creation (Benda et al. 1998, Landres et al. 1999, Reeves et al. 2002).

Patterns of deposition may be important biologically. Torgersen et al. (2004) found that periodicity of freshwater distribution patterns of coastal cutthroat trout (*O. clarki clarki*) along a mainstem stream were associated with tributary junctions. Locally, disturbances change the proximity and connection of stream habitats in the network over varying temporal and spatial scales. Close proximity of habitats necessary for different life history stages has been associated with higher fish densities and abundance (Kocik and Ferreri 1998, Flitcroft 2007). At larger scales, disturbances isolate some habitats and connect others. In coastal Oregon, Reeves et al. (1995) described the complexity of stream systems over time in response to large scale disturbances. They noted that persistence in a dynamic environment required organisms to develop behaviors (e.g., movement, life-history diversity, aestivation) adapted to change (Warren and Liss 1980). The authors posited that landscape management that mimicked the extent and frequency of natural events would be less harmful than anthropogenic disturbances for native species that are adapted to natural disturbance regimes.

Ecologists have long observed that organisms are adapted to live in their environments (Southwood 1977). It intuitively follows that native aquatic species are adapted to survive in the changing habitat configurations of stream networks. For example, different behaviors among individuals will be more or less adaptive for the population depending on stream network conditions. For instance, Quinn (2005) hypothesized that adult anadromous salmonids might stray (fail to home to natal streams to spawn) more in years characterized by disturbance of natal stream beds. Adults that stray may be more successful than those that home in years when natal spawning beds have been disturbed. Therefore, straying endures within populations of salmonids. Other behaviors present in salmonid populations that essentially spread out risk include: some precocious males return early to spawn (jacks); females leave multiple pockets of eggs in each redd (Quinn 2005); and when juvenile salmon hatch, some will move, some will stay, some juveniles will be territorial and others will be “floaters” (Nielsen 1992). The diversity of behaviors exhibited by a population of individuals reflects evolutionary adaptation to dynamic stream conditions that unpredictably favor one set of behaviors over another.

Analysis of populations of aquatic organisms could benefit by expanding the perspective of ecologists to include the complexity of spatial arrangements of habitat and movement pathways in stream networks over time. In this paper, I offer a *dynamic network topology* as a conceptual framework that encompasses the elements of network connectivity, juxtaposition of habitats, disturbance, and directionality of flow (for water, nutrients, and individual aquatic organisms) that may be critical to understanding adaptations in life history and behavior of native species. I will first describe dynamic network topology. Then in successive sections of the paper, I will discuss dynamic network topology with regard to: differences in network use depending on life history stage, the implications of spatial scale, isolation of habitats and movement of individuals, analysis of stream networks, and a hypothetical scenario that applies dynamic network topology.

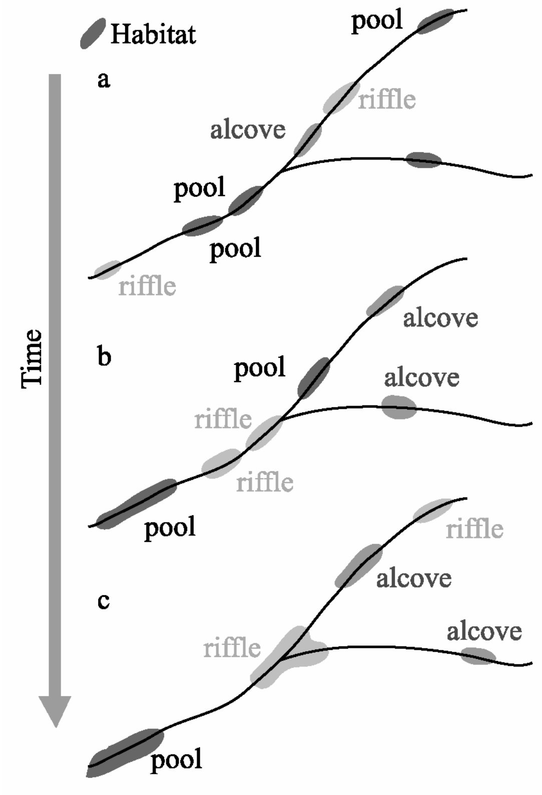
In dynamic network topology, the stream network is the template upon which habitats are arranged (topology). Resilience reflects the ability of native species to respond to the diversity and changing topology of stream network habitats that are dynamic over time. In this paper, Pacific salmon and trout (*Oncorhynchus* spp.) are generally used to explore ideas about network relationships and long-term survival because of the diversity of salmonid life history types (Pacific Fisheries Resource Conservation Council 1998), their stream occupancy, and the long history of research studying salmonid behavior and habitat needs.

Defining Dynamic Network Topology

Network topology is a universal notion that can inform assessments of population viability, habitat quality and quantity, and the interrelationship between aquatic species and the stream environment. Stream network topology principally describes the orientation and connection of habitats to one another in a stream network. However, stream habitats change over multiple spatial extents and temporal scales, and therefore, the topology of an entire stream network is in flux. Dynamic network topology, therefore, describes the orientation of habitats that change over time a stream network (Figure 2.2). The language of dynamic network topology is meant to capture the changing nature of habitats in a stream system in analysis that maintains the spatial context of the underlying physical network.

Containment of water in channels limits movement directions of organisms and abiotic elements to upstream, downstream or peripherally into the hyporheic zone (Vannote et al.1980, Fausch et al. 2002). In terrestrial systems, a habitat can connect directly to other habitats along routes extending potentially 360 degrees. In a stream system, by contrast, a habitat directly connects to other habitats along only four routes at most (upstream or downstream in a main channel, and upstream into at most two tributaries) (Figure 2.3). Further, this branching of a stream network at tributary junctions means that although two stream habitats (such as a pool and a riffle) may be near one another in two-dimensional Cartesian space, they may be very far apart in network distance space (Figure 2.4, sites 2 and 5) (Gresswell et al. 2006, Lowe et al. 2006). Aquatic organisms have few directions in which to move, and habitats may be

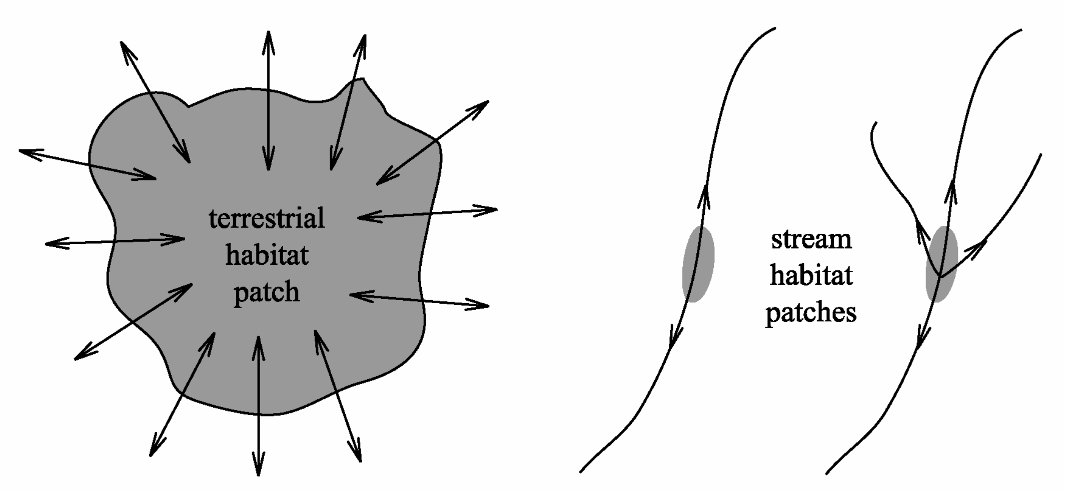
Figure 2.2. As disturbance events contribute material to streams, and as stream hydraulics reorganize substrates, the juxtaposition of stream habitats will change over time. For example, the configuration in (a) may change to configuration (b) and then to configuration (c).



far from one another in the network. Therefore, it may be difficult for aquatic species to navigate between habitats, or even find particular habitats in the stream network. Difficulty navigating the network may result in reduced survival of aquatic organisms. Analysis of habitats that neglects to consider movement paths and directions for aquatic species may misrepresent population viability.

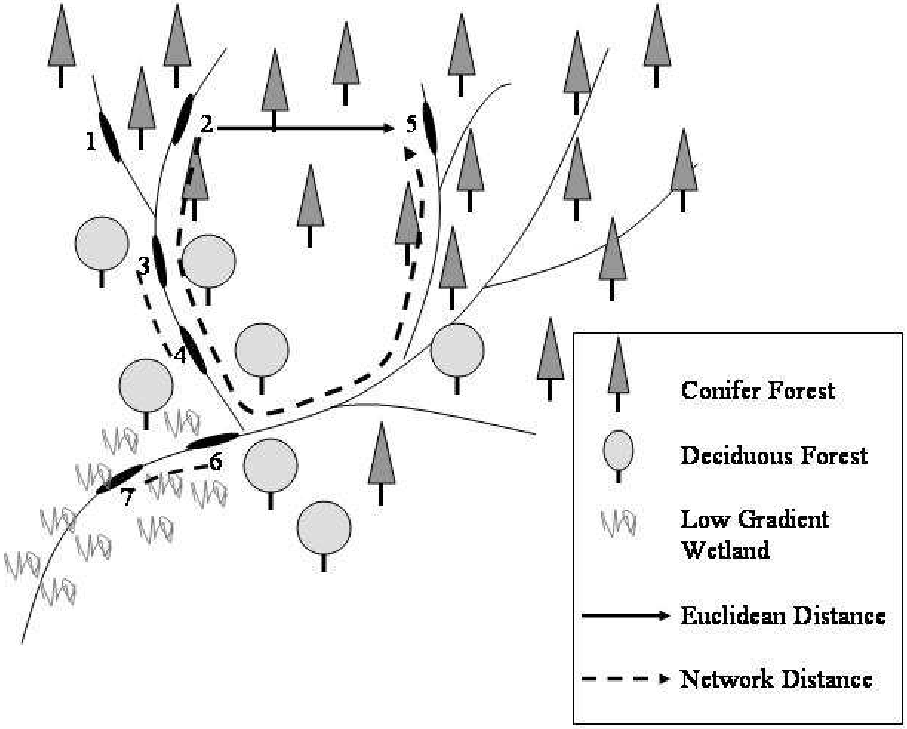
Another consideration of habitat juxtaposition in stream networks is that habitats may be far from one another in network space but have similar physical characteristics (e.g., depth, amounts of large wood, substrate composition) because

Figure 2.3. Direction and options for movement for aquatic obligate species such as fish are restricted to upstream or downstream in a stream segment or laterally into tributaries compared to species in a terrestrial system with potential routes on a 360° radius. The limited directions of movement are a fundamental organizing feature of stream networks for movement of aquatic species.



they are embedded in similar landscapes (e.g., rock type, vegetation, disturbance history, or land use) (Figure 2.4, sites 1, 2 and 5). It is also possible that stream habitats with similar physical characteristics such as substrate (Figure 2.4, sites 2 and 5) may be further from one another in network space than they will be to very dissimilar stream segments (Figure 2.4, site 2 to 4; or site 5 to 6). Therefore, network proximity between habitats does not necessarily describe habitat similarity. The juxtaposition of habitat is further complicated seasonally as water level fluctuations increase or decrease the physical connectivity among stream habitats. Therefore, the topology of habitats will change as different parts of the network are cut off or reconnected, depending on discharge (Heggenes et al. 1991). Taken together, these considerations imply that network distance can be used to orient habitats to one another, but the landscape and seasonal context is also important. Combining habitat

Figure 2.4. Network distances may reflect connectivity, but there is more to the orientation of stream segments than simply the distance between them. Sites may be close to one another using a Euclidean or “as the bird flies” distance measure, yet be far from one another using a network measurement (as in sites 2 to 5). Also, sites that are far from one another using a network distance (as in sites 2 to 5) may be more physically similar than sites that are close together (as in sites 2 to 4) because of shared underlying landscape conditions (such as vegetation, geology, elevation, and gradient).



juxtaposition with landscape conditions may allow biologists to better understand why organisms are distributed as they are. This in turn may allow for more accurate population level predictions of persistence.

Depending upon the ecological process of interest, the effective distance between two habitats in a stream network may be greater in one direction than in another, reflecting the influence of flow direction. The effect of flow will vary with life history stage and mobility of a species. For example, while two rearing habitats may be equally spaced upstream or downstream from a spawning site, a newly emerged trout alevin may be more able to move downstream with the flow of the stream than upstream and against the flow (Ottaway and Forrest 1983). As the alevin grows, movement upstream may become less difficult (Kahler et al. 2001). Thus, the strength of connection between habitats (i.e., permeability of boundaries) can vary with distance and flow direction, and may most productively be considered with respect to the mobility of individual organisms. Habitat patch size, permeability of habitat patch boundaries, and spatial isolation or connectedness of patches may be considered from a network perspective by using the framework of dynamic network topology. Dynamic network topology means that the location of habitats relative to one another is coupled with a riverscape context (i.e., geology, geomorphology, land use, disturbance history, or elevation), therefore providing an inclusive perspective for assessments of populations of aquatic species.

Life History Diversity and Dynamic Network Topology

Warren and Liss (1980) described capacity of a system as “all possible developmental states and all possible performances that a system may exhibit while still maintaining its integrity as a coherent entity.” The capacity for species to survive in a dynamic environment is embedded in the myriad behaviors and adaptations expressed as life history diversity in populations (Levin 1992). Changing habitat configurations in dynamic and easily fragmented stream environments (Fagan 2002) may have contributed to the variety of life history strategies found within and among native salmon and trout species (Rieman and Dunham 2000).

Resilient native salmon and trout must be able to persist in stream networks in which topology changes over time and across space. Much of the life history diversity among and within populations of salmon and trout focuses on movement. Dynamic network topology allows consideration of the adaptive significance of individuals that move compared to individuals that do not move. The complement of behavioral variation expressed as movement by individuals in a population may increase chances of population persistence in uncertain and dynamic stream network environments. For example, some individual trout will move great distances in their lifetime, while others will stay close to their natal pool (Heggenes et al. 1991). Both of these life history types will be most successful with different sets of environmental conditions as reflected by network juxtaposition and access to habitats. In years when adequate seasonal habitats for the trout are close to one another, both movement types will survive. In years when seasonal habitats are far apart or when disturbance makes network habitats inhospitable, the trout that moves the most may be more likely to survive than the trout that does not move.

The adaptive importance of movement behavior for survival (Levin 1992) in a dynamic stream network may warrant explorations of network topology that are species or life history stage specific. For example, the two freshwater life history stages (juvenile and spawning adult) of coho salmon (*O. kisutch*) have different mobility and life history needs that define the extent of the stream network that individuals at each life history stage will explore and occupy. Individual adult coho salmon are seeking spawning habitat and mates, and may travel among tributaries or even subbasins before spawning. Juvenile coho salmon must survive in freshwater for one year, therefore, individuals must find seasonal habitats within their natal stream system. Therefore, adults may respond to the network configuration of spawning habitats, while juvenile distribution may be associated with the juxtaposition of the several habitat types necessary for freshwater residency. These two sets of needs may overlap on a stream network, or they may not. It is possible that adults that are only seeking spawning habitat and mates would spawn in places that are not close to juvenile rearing habitat. Although the propensity of adult salmon to spawn in natal streams may compensate for this, presumably because the adult was able to rear in that site as a juvenile, this may not always be the case. Assessments of population viability that are based on instream habitat may be improved by considering the proximity between habitats necessary for each life history stage.

Networks and Spatial Scale

Changing topology has different effects at different levels of organization, from the scale of individual sites (e.g., pools) to stream reaches and entire watersheds (i.e., Burnett 2001, Church 2002). Domains of scale exist in ecology, and these describe the observation that patterns found at one spatial or temporal scale may be undetectable or look entirely different at another scale (Wiens 1989). For example, patterns detected at small spatial extents may reflect variation in the choices of individuals, while patterns over large extents may be associated with overall population level variation. The effect that spatial or temporal scale has on our comprehension of pattern associations in a stream network has rarely been explored by researchers. This may reflect the static or linear view of stream systems that results in analysis of disconnected sites in stream networks rather than continuous data collection throughout the network. Also, collecting comprehensive census information for a network is time consuming and costly, and few tools are available to analyze data that incorporate a stream network framework (see Analysis and Dynamic Network Topology section).

Ultimately, in many aquatic investigations, the nuances of scale and stream network relationships are lacking in the interpretation of patterns. This could result in misinterpretation of the meaning of spatial patterns of habitat, occupancy, or use within a stream network. For example, there is much debate about the effectiveness of instream habitat enhancement structures for juvenile salmonids. Studies have shown that such structures will result in greater numbers of juveniles at sites than were present before the structures were in place. Biologists assume that this means that juvenile survival has increased due to the structures. However, no research has attempted to identify where the juveniles came from that are now inhabiting the structure. They could simply have moved to the site from up or downstream. Or they could be emerged juveniles from the site itself. The pattern of juvenile occupancy has certainly changed within the stream system, but by only sampling at the site where the restoration was done, it is not possible to determine the overall effect of the habitat enhancement structures on the population of juveniles throughout the stream network.

A network perspective that includes dynamic network topology facilitates relevant ecological interpretations of patterns detected at multiple spatial scales by providing a framework within which to consider movement paths, habitat juxtaposition, and specific life history stage requirements. Flitcroft (2007) incorporated different network variables at several spatial scales to explore patterns in the distribution of juvenile coho salmon (*O. kisutch*). Juvenile coho salmon density, explored at the site scale, pointed to the importance of the close proximity of seasonal habitats among subbasins whose juvenile density changed between summers. Patch sizes were identified by variograms that used stream network, rather than Euclidean, distances between points. Patterns of juvenile clumping identified as patches appeared to reflect subbasin scale variation. Dynamic network topology provided a framework within which to consider local site conditions through measures of habitat juxtaposition and large scale subbasin conditions that may be associated with environmental changes over time.

Spatial scale and the consideration or interpretation of occupancy patterns and movement in the stream network may be further complicated by considering interactions among the life history stages of a species. Consider, for example, juvenile and adult anadromous coho salmon. As previously mentioned, these two life history stages of coho salmon share the same distribution in the stream network but have different habitat needs and mobility. Flitcroft (2007) found that network occupancy by juvenile coho salmon appeared to be related to adult spawning run sizes. In years of large adult run sizes, more of the stream network was occupied by juveniles. Therefore, the pattern of juvenile coho salmon network occupancy is mediated by the distribution pattern of spawning adults that were not necessarily seeking habitats necessary for juvenile survival. Analyses of local patterns of juvenile distribution that fail to include a consideration of larger scale patterns of adult run size may misrepresent the importance of local habitat conditions.

Isolation and Movement in Stream Networks

The ability to move among habitats is critical for survival of native aquatic organisms (Hanski and Gilpin 1991, Gresswell et al. 2006). The concept of isolation applies to habitats or individuals. Habitats may be isolated from one another due to the configuration of the stream network or environmental conditions (i.e., disturbance, discharge). Individuals may be isolated from one another or from the habitats that they need to survive. Isolation for individuals in either of these instances may be due to the physical configuration of the stream network, or to the level of mobility of the individual. For example, a species of salamander with limited mobility will need habitat patches that are close together to avoid isolation from necessary habitats. This compares to a highly mobile trout that may survive even when necessary habitats are separated by many kilometers of stream channel. Therefore, habitat topology necessary for the salamander to survive will be different than the topology for the trout, and not simply because they have different habitat needs. The implications of dynamic habitat changes due to disturbance or seasonal discharge will apply differently to species depending on mobility. This is ecologically important when assessments of stream habitat are part of population viability analyses. Analyses that do not consider species-specific habitat and the mobility of individuals may not accurately gauge the amount of habitat available for long-term persistence.

Isolation within and among stream networks may be a significant feature describing the distribution of a population of organisms. For example, in the arid mountain west of the United States, stream systems and their populations of species may become isolated seasonally, and some systems are permanently separated from one another, due to long-term climate change. In these arid environments, population viability assessments that span isolated stream systems should take into account the lack of connectivity between subpopulations. Consider redband trout (*Oncorhynchus mykiss*) that are distributed across the interior Great Basin of Oregon. Populations of trout are permanently isolated from one another in stream networks that were once connected as part of a large lake. Further, there is seasonal isolation of habitats in the Great Basin when low water summer months result in dry stream beds and high temperature stream reaches that may be impassable to redband trout. The lack of connectivity among streams means that there is no opportunity for a stream whose fish have been extirpated (due perhaps to a disturbance event or high stream temperatures) to be recolonized and recover to pre-extirpation levels. Current population assessments of redband trout (Jones et al. 2007) discuss the isolation of subpopulations in disconnected basins, but do not consider the lack of connectivity among or within stream systems in the anticipated long term survival of redband trout. By failing to consider system connectivity and the effects of disturbances in fragile desert streams, population assessments based simply on population estimates without considering the vulnerability to extinction of isolated subpopulations may exaggerate a species' anticipated long-term persistence.

Analysis and Dynamic Network Topology

How variables describing stream conditions are analyzed is an ongoing challenge to stream ecologists. The framework of dynamic network topology does not include new network based statistics for analysis. However, considering current statistical tools that include stream networks, and evaluating traditional statistical tools with regards to network relationships is an important element of any approach that is meant to contribute to a network-based ecological investigation.

Independence of observations is a fundamental assumption of many parametric statistical methods. Lack of independence, which includes correlation among observations, may mean that one observation contains some of the same information that is contained in other observations. Ignoring correlation can produce incorrect estimates and standard errors. Therefore, standard statistical methods for analyzing stream data may be compromised by the inherent connectivity of a stream network.

Often, researchers simply include models for correlated error terms in regression models, in an attempt to capture the lack of independence among sample sites in stream systems (i.e., Megalhaes et al. 2002, Joy and Death 2004, Grenouillet et al. 2004). Such work has indicated that stream network criteria can be critically important in understanding the patterns of aquatic biota. However, developing and using variables that reflect both network proximity and habitat types without reducing analysis to a comparison of network distances is challenging.

There have been some attempts at developing statistical sampling protocols that allow researchers to capture the variation in an entire population of streams (Larsen et al. 2001, Jacobs and Cooney 1995). Such techniques focus on sampling designs that allow for a spatially random selection of sample sites across a population of streams. This type of sampling design effectively describes the mean and variance of individual stream variables over a large region, but how clearly this reflects the subtle pulse and flow of contiguous stream use by populations of organisms continues to be an open question. Also, researchers must decide for themselves whether seeking to develop sampling strategies and analyses that negate the correlation inherent in most network based systems is the most ecologically intuitive approach. Statistical methods that take advantage of correlation, rather than viewing correlation as a nuisance, may more realistically reflect ecological systems and better inform our understanding of the interconnectedness of fluvial systems and the organisms that depend on them.

In terrestrial ecology, spatial statistical methods have been developed that take advantage of autocorrelation by considering the proximity between observations that is inherent in the landscape (Legendre and Fortin 1989). These statistical techniques allow researchers to explore and compare patterns across the landscape. Unfortunately for aquatic ecologists, such spatial statistics are generally inappropriate for work with stream systems, due to directionality of water and nutrient flow. Directionality is not a consideration of spatial statistics that seek shared variation among points in every direction, not just upstream or downstream, in order to detect patterns in a dataset.

Pioneering work has been done recently that attempts to modify spatial statistical tools (Ganio et al. 2005, Cressie et al. 2006, VerHoef et al. 2006) or analysis (Gresswell et al. 2006) to the strictures of stream environments. Because there is a direction of flow in stream systems, statistics may develop that are similar to the flow of time in time series data: a point in the past can influence a point in the future but not vice versa. Spatial statistical methods in streams would allow influence to flow directionally between two points. Aquatic species must be considered within the context of the stream network, and within the framework of their ability to move to areas upstream or downstream when patterns are described and interpreted using statistics. The current work with spatial statistics in streams that encompasses upstream or downstream directionality is promising and may well lead to analytical tools that more closely reflect the movement options of individual fish.

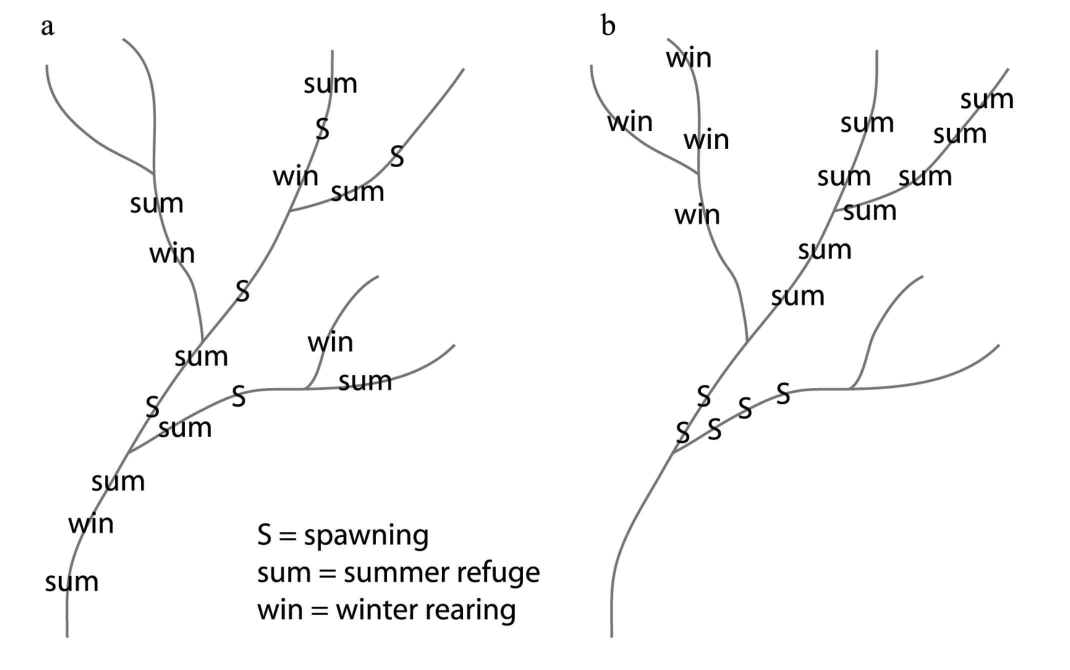
An Application of Dynamic Network Topology

The application of dynamic network topology may best be explained using an example. Consider coho salmon. As previously mentioned, these fish use freshwater streams in their adult and juvenile life history stages, and fish in these two life stages have different levels of mobility and habitat needs. In the Pacific Northwest, much time, energy, and expense has been spent on coho salmon habitat enhancement projects. However, these projects do not consider the juxtaposition of habitats for each life history stage. By including considerations of the proximity and quality of existing habitats, enhancement work may be more effective at accomplishing its goal of providing more habitat for coho salmon.

In many habitat assessments for coho salmon, the number of stream kilometers of certain types of stream habitat is summarized at a subbasin or basin scale or habitats for spawning adults, summer juvenile rearing pools, and winter off channel refuge habitats for juveniles are often calculated (i.e., Johnson 1999). For example, in subbasin “A” there might be 2 km of spawning beds associated with 5 spawning reaches, 4 km of summer rearing habitat corresponding with 8 pools, and 3 km of winter habitat corresponding with 4 off-channel habitats. This combination of habitats in a basin may be deemed adequate to sustain the population of coho salmon that live there. This may be the case if the habitats are intermixed and do not require great navigation in order for the fish at each life stage to find the necessary habitats. From a dynamic network topology perspective, summary information that might describe juxtaposition would include the proximity along the network between spawning habitat and summer pools, and then between summer pools and winter rearing habitats. This would be the progression between habitats that juvenile coho salmon would need.

Consider two different orientations of habitat in subbasin “A” that might depict extreme examples of habitat organization. In the first configuration, habitats are intermixed, and network distances between seasonal habitats are short (Figure 2.5a). In the second configuration, each set of habitats is isolated in individual tributaries, complicating navigation between seasonal habitats through the network, and also causing distances between habitats to be large (Figure 2.5b). Although both scenarios contain the same quantities of habitat, the implications of the configuration of habitats for juvenile survival are different. In the intermixed subbasin, juveniles may have little difficulty finding necessary habitats, but juveniles in subbasins with habitats isolated from one another may have difficulty finding particular habitats. Isolation of habitats may possibly result in lower juvenile survival or growth. If a watershed manager was faced with these two sets of subbasin configurations, targeting restoration projects that provide seasonal habitats in a pattern that reduces navigation difficulty or network distances might be the most successful course of action.

Figure 2.5. Two extreme examples of habitat arrangements may be conceptually useful when considering how an individual juvenile coho salmon must move within the network to find necessary seasonal. Figures (a) and (b) share the same stream network, and the same numbers of habitat sites classified for coho salmon as spawning (S), summer refuge (sum), or winter rearing (win). However, the arrangement of the habitats is quite different with figure (a) depicted interspersion of habitats while each seasonal habitat is restricted to specific tributaries in (b).



Another element of dynamic network topology is the landscape context, which affects how habitats will change over time. Consider the two subbasins described previously. If these two subbasins have the same underlying geology and land use, it might be efficient for a watershed manager to consider how the landscape may affect the stream in the future. For example, if a portion of the watershed was in an agricultural classification, it is possible that erosion in these areas would be detrimental to juvenile survival. Hence, restoration that encouraged juveniles to live in these areas would be counterproductive in the future. Rather, focusing work in areas where future disturbance events may deliver material necessary for habitat creation may be useful. For example, focusing on restoration in areas that have large trees in the riparian zone that may be expected to be delivered to the stream in future decades might be a more productive location to encourage fish to populate. Each watershed will have a unique configuration of habitats and potential for disturbances. However, dynamic network topology may provide a way of thinking about the current and future conditions of the stream network from the perspective of the aquatic species whose survival is being analyzed.

Dynamic network topology is not meant to describe a process of analysis as much as a framework from which to approach population level analysis of habitats in stream basins. Considering the topology of habitats and the effect that change will have in a watershed may be useful in developing management that seeks to restore populations of aquatic organisms.

Conclusions

With the accepted awareness by ecologists of the importance and fundamental place of disturbance in creating and maintaining ecosystems, new ways of thinking about organization are necessary. In aquatic ecology, a static or linear perspective is being replaced by a focus on dynamic processes. The need for a network perspective is becoming increasingly clear, as research shifts from a site-level focus to the consideration of watersheds and the movement patterns of populations of aquatic species. Dynamic network topology is a universal notion that can inform assessments of population viability, habitat quality and quantity, and the interrelationship between aquatic species and the environment. Dynamic network topology may help aquatic biologists understand patterns of occupancy, dispersal, and life history needs within the context of a stream network.

This paper is intended to raise the awareness of aquatic ecologists about the need for consideration of species within the framework of an interconnected stream environment. I propose the framework of dynamic network topology as a conceptual base from which to consider stream processes and the needs of aquatic species. Further research that incorporates movement paths, fragmentation, and isolation in a stream network would help deepen our understanding of the ecology and needs of aquatic species. Including spatial and temporal scale in the interpretation of patterns of occupancy and movement must also be considered. It is of critical importance for the conservation of aquatic obligate stream species that biologists develop an adequate working understanding of the mechanisms of dispersal and habitat use in the stream network.

The majority of examples and ideas that have informed the creation of a dynamic network topology come from Pacific salmon and trout. However, the concept that the configuration of stream network habitats changes over time, and that native species are adapted to cope with these changes may be applied to any species with an aquatic obligate life history stage. The complexity of habitat juxtaposition in stream networks, coupled with limited directions of movement due to network configuration and directionality of flow, are implicit in any population level analysis of an aquatic species. Further consideration and discussion of network connectivity, movement options, and habitat juxtaposition will enrich and define aquatic ecological theory and practice.

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Chapter 3

Exploring Network Patterns in the Habitat, Abundance and Distribution of Juvenile Coho Salmon (*Oncorhynchus kisutch*) in Oregon's Mid-Coast

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Abstract

Analyzing streams as networks may offer opportunities to understand the movement and distribution of aquatic species. Network analysis is challenging for aquatic ecologists due to limited research techniques and the need for census style field data collections. Further, a stream network may provide opportunities to explore multiple spatial scales within a stream system and identify ecological relationships that are scale specific. Studies that examine the implications of network patterns at different spatial scales may contribute new ideas about aquatic species persistence and habitat needs. In this study, the distribution of juvenile coho salmon in the stream network was investigated in eleven subbasins of Oregon’s Mid-Coast at three spatial scales (site, patch and subbasin). At the site scale, a comparison of traditional instream, site-specific habitat descriptors with network orientation and habitat juxtaposition variables was completed in order to explore the usefulness of both types of metrics in understanding juvenile stream use. Variograms using network distances were generated to describe patches of juvenile coho salmon. Patch size was compared to basin shape to explore whether underlying geomorphology effected how juvenile coho clumped around habitat. The subbasin scale allowed for the exploration of large-scale environmental conditions that may be important for of juvenile coho salmon distribution (adult spawning run size and precipitation). A variety of statistical tools including principle components analysis, discriminant analysis and a local-mean non-parametric multiplicative regression analysis were used to explore connections between juvenile density and explanatory variables at each spatial scale. At the site scale, modeling and principle components analyses were interpreted to mean that a

diversity of habitats in close network proximity is necessary for juvenile survival. Patches of juvenile coho were linked to the size of the watershed, and at a subbasin scale it appeared that juvenile network occupancy was tied to the size of the spawning adult run. Each spatial scale identified different relationships between juvenile coho and their environment and could be integrated to more fully describe how juvenile coho use the stream network. Using an analytical perspective that includes stream network relationships contributed to a meaningful interpretation of the pattern of juvenile occupancy, and conclusions about habitat needs at this life history stage.

Introduction

Stream systems in the Pacific Northwest are characterized by habitat and environmental conditions that may change dramatically over time. Dynamic stream processes, including disturbance (Nakamura et al. 2000), fire (Miller et al. 2003) and flooding (Benda and Dunne 1997, Swanson et al. 1998), work to connect or disconnect portions of the stream system. In the past century, additional disturbance from anthropogenic activities such as timber harvest, road building (Trombulak and Frissell 2000), farming and urbanization (Lichatowich 1999) have changed the extent and interval between disturbance events (Reeves et al. 1995).

A dynamic stream environment may lead to a variety of habitat types within the stream channel. Stream channels are organized as a network of interconnected tributaries. Ultimately, the stream network is the template upon which landscape processes act and the resulting stream mosaic will include a variety of habitat conditions (Naiman et al. 1992). Therefore, the consideration of stream habitat diversity and connectivity for aquatic species may benefit from including the topology or physical orientation of habitats within a stream network.

How aquatic obligate species respond to the configuration of habitats in a stream network may provide insight into behaviors or adaptations that have led to resilience in native organisms (Flitcroft 2007). Fagan (2002) showed that fragmentation in a stream system reduces connectivity among the different parts of the network making navigation among necessary habitats for aquatic species difficult. Fagan speculated that lack of connectivity and isolation of habitats and individuals could increase chances of biological extinction. Spatial location of stream features has been explored in assessments of fish assemblages (Megalhaes et al. 2002) and biotic diversity (Day et al. 1992, Wright and Li 2002) in attempts to link geomorphic patterns with biotic distributions. Montgomery et al. (1999) connected stream channel type with spawning distributions of salmonids and concluded that the size of spawning fish determined redd depth, thereby dictating the lowest range within the stream network that redds could be dug and not disturbed by annual river flow and the ability of rivers to move substrate.

An important research question facing modern ecologists is: "What are the implications of network patterns of habitat, occupancy and abundance for the long-term persistence of aquatic obligate species?" Network patterns lend themselves to analysis at multiple spatial scales. The network itself is one large scale, and the sites that compose the samples are another. Currently, ecologists recognize the need for analyses that explore broad spatial and temporal scales that may contribute to a better understanding of the needs of populations of species (Fausch et al. 2002, Frissell 1986, Schlosser 1991, Talley 2007). Burnett (2001) explored the use of different spatial extents in describing the distribution of juvenile salmonid assemblages in the Elk River Basin, Oregon. She found that spatial extent over time was important in describing the observed variability in assemblage distribution. However, much of our current understanding about the distribution and needs of stream fishes is derived from studies that consider relatively small spatial extents, generally habitat units or reaches, without the context of time, multiple spatial scales or network connectivity (Matthews and Marsh-Matthews 2003). Small scale studies are not able to detect patterns at larger scales (Wiens 1989) and may be unable to detect patterns of connectivity in an entire network. Studies that include network connectivity at multiple spatial scales may allow ecologists to learn about ecological processes that contribute to the persistence and resilience of native species.

Although many ecologists recognize the importance of spatial scale and stream connectivity, incorporating such a perspective continues to be challenging. In Chapter 2 (Flitcroft 2007), I explored why a network perspective has been elusive in the discipline of aquatic ecology. Two reasons I identified were the lack of research of domains of scale (patterns at different scales describe different processes, [Wiens 1989]) in aquatic ecology and the paucity of statistical methods developed for stream network applications. Analysis incorporating a network framework is difficult due to the lack of research on what patterns of stream fishes mean at multiple scales and network configurations and is compounded by a lack of independence in stream networks that violates assumptions of parametric statistics making any analysis challenging.

Aquatic obligate species such as Pacific salmon (*Oncorhynchus* spp.) face unique challenges living in and using multiple locations within a stream network. Individuals must be able to migrate into and out of a stream system and find appropriate habitats at each life history stage. The proximity and connectivity of habitats may be a significant consideration when trying to understand the distribution and abundance of salmonids (Benda et al. 2004). Coho salmon (*O. kisutch*) provide an opportunity to explore patterns of network use due to their broad distribution and the depth of research that has focused on their life history expression and needs. As an anadromous species, sexually mature adults home to their natal streams to spawn and then die (Groot and Margolis 1991). Some adult coho salmon stray rather than returning to their natal stream (Labelle 1992). Before migrating to the ocean, juveniles spend a year rearing in freshwater and may use different seasonal habitats that are located throughout a watershed (Nickelson et al. 1992a, Nickelson et al. 1992b, Sleeper 1993).

A network framework incorporated into an analysis of multiple spatial scales over time may provide insights into juvenile coho salmon occupancy, distribution and abundance. In this retrospective study, three objectives were identified that explore how a stream network framework may be incorporated into an analysis of juvenile coho over a five-year period across multiple stream systems and spatial scales. My first objective was to compare the explanatory power of instream and network habitat variables for each year of juvenile coho salmon density. The second objective was to characterize the size of habitat patches occupied by juvenile coho salmon and examine relationships with basin shape and area. The third objective was to describe juvenile coho salmon network occupancy in eleven subbasins and consider large-scale environmental conditions that might be important for explaining occupancy patterns. Due to the challenge of collecting multiple pre-existing datasets for this analysis, different objectives are explored with different combinations of subbasins.

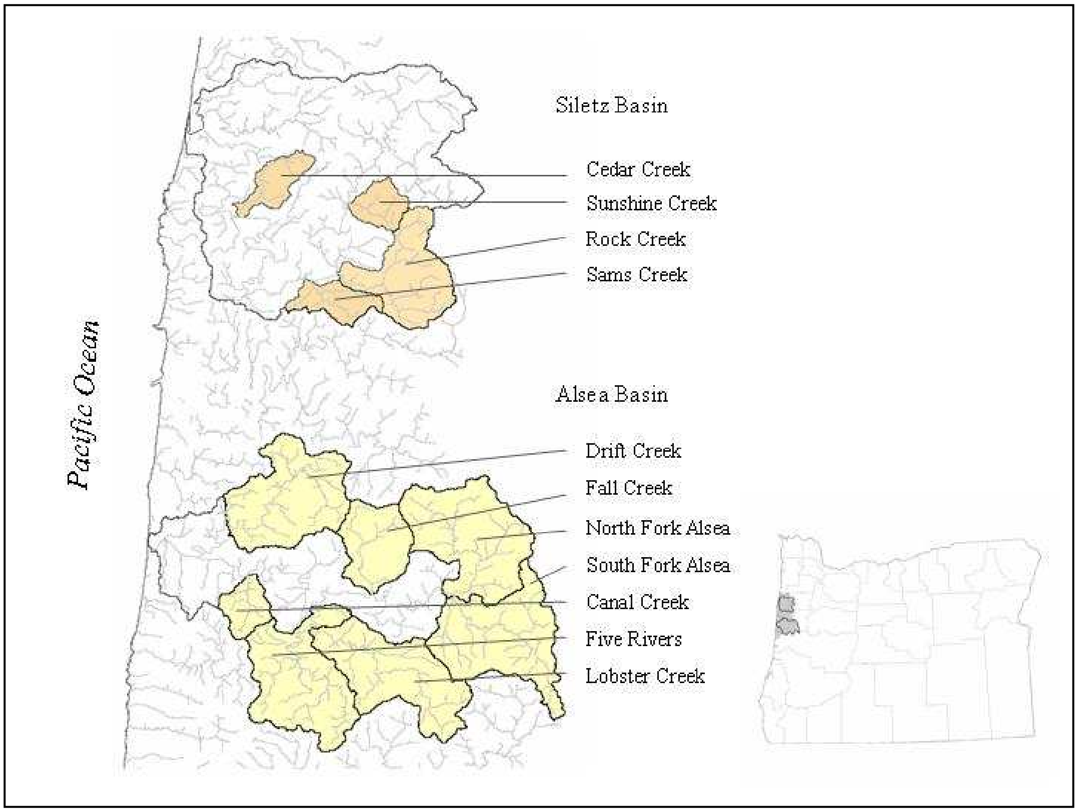
Materials and Methods

Study Area

Subbasins in the mid-coast of Oregon (Figure 3.1) were selected for analysis because several organizations (i.e., Oregon Department of Fish and Wildlife and the Mid-Coast Watershed Council) have studied adult and juvenile life history stages of coho salmon in this area. The mid-coast of Oregon is an area of similar geology, vegetation, land use and precipitation. The headwaters of the larger Siletz and Alsea River basins begin in the Oregon Coast Range and are covered predominantly by conifer forests. Timber harvest is an important economic activity in the higher elevation areas and agriculture is the dominant land use activity in the lowlands. The geology is a mixture of volcanic and sedimentary rocks, and volcanic terrain generally found to the north. The climate of this region is mild with precipitation occurring predominantly in the winter months (Redmond and Taylor 1997).

Some populations of coho salmon are listed as endangered by the state of Oregon (ODFW 2005). This species has significant commercial and recreational value for communities on the Oregon coast. However, the stream habitat of coho salmon has been heavily affected by anthropogenic disturbances that have increased sediment

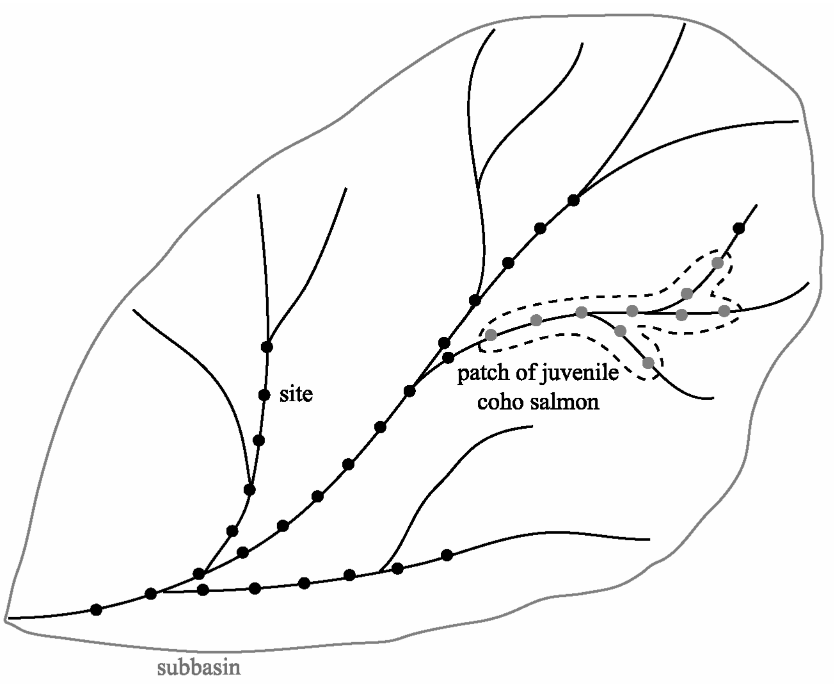
Figure 3.1. Highlighted subbasins in the Alsea and Siletz River Basins that were included in an analysis of multiple spatial scales that incorporated a stream network framework.



loads, decreased wood content of streams, and introduced barriers to migration such as culverts and water diversions (Lichatowich 1999). Juvenile coho salmon over-winter primarily in coastal streams of relatively small stream size (1st–3rd order on 1:100,000 scale maps, Strahler 1952) (Rosenfeld et al. 2000). Research and monitoring data are available that document juvenile coho salmon distribution, abundance, habitat, behavior and life history diversity.

Multiple spatial extents were incorporated into this analysis (Figure 3.2). The site scale corresponds with the size of pools where juvenile coho salmon were

Figure 3.2. The three spatial scales included in a multiple scale analysis of subbasins in the Alsea and Siletz River basins are the site, patch and subbasin.



snorkeled and was used to explore instream and network habitat variables in close proximity to the pools. The patch scale varied between 100 and 5000 meters and described the size of clumps of juvenile coho salmon. Patch size was compared to subbasin scale conditions. The subbasin scale ranged in size from 32 to 300 km^2 and allowed for the characterization of subbasins with regard to juvenile occupancy changes over the five years of this study.

Datasets

Juvenile coho salmon counts for the years 1998, 1999, 2001 and 2002 came from snorkel surveys conducted by the Mid-Coast Watershed Council. Survey data from 2000 were not used because accurate field maps necessary for georeferencing were unavailable. During a summer field season (June through September), every fifth pool was snorkeled, and all fish were counted from the stream mouth to the headwaters, including all tributaries. Surveys ended for a particular stream when five consecutive pools surveyed contained no juvenile coho salmon. Although juvenile coho salmon may move during any season of the year (Kahler et al. 2001), summer surveys are important because this is the time of year when juveniles are assumed to move the least (Nickelson et al. 1992b). Therefore, summer snorkel surveys permitted collection of comparable snorkel information over several months across years.

Adult coho salmon spawning run sizes for the mid-coast of Oregon were taken from reports prepared by the Oregon Department of Fish and Wildlife's spawning survey program (Jacobs et al. 2002). The spawning run size estimates were calculated using randomly selected sample locations that were revisited regularly by field crews during the spawning season to count both spawning fish and redds (Jacobs and Nickelson 1989). The randomly collected data was then used to estimate the size of the adult coho salmon spawning run.

Fine scale instream site specific habitat survey information came from the Oregon Department of Fish and Wildlife Aquatic Inventories Program (AIP). Field habitat survey crews walked from the stream mouth to the headwaters during the summer, gathering measurements of the physical stream environment and identifying discrete habitat units such as pools, riffles and glides (Moore et al. 1997). Field surveys from 1997 through 2002 were pieced together to encompass the subbasins of interest for this study. A total of seventeen instream habitat metrics were considered in this analysis and were transformed, as necessary, for normality (Table 3.1).

Table 3.1. Variables in network and habitat datasets with source information and transformations.

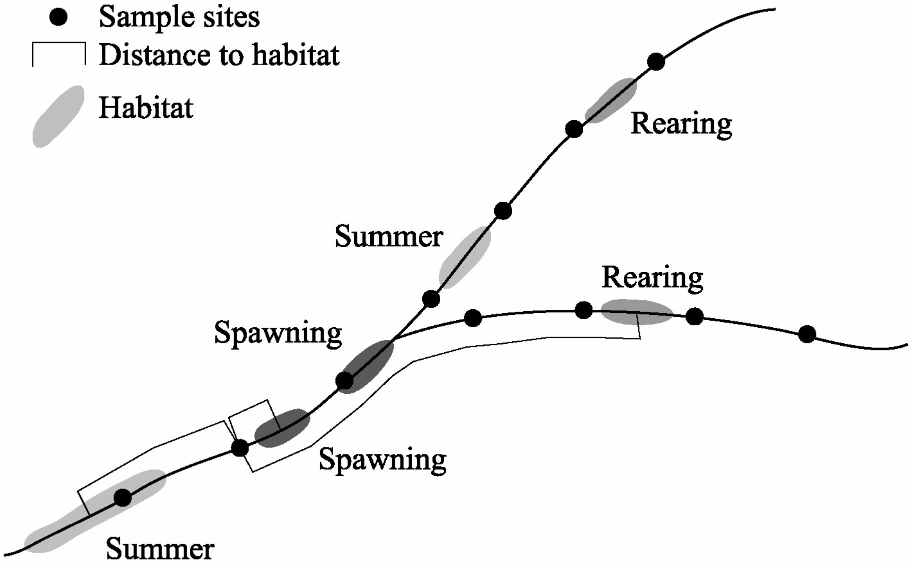
Variable	Transformations	Source Dataset	Measurement Type
Network Dataset			
Stream Order	None	CLAMS	Modeled
Mean Annual Precipitation	None	CLAMS	Modeled
Intrinsic Potential Coho	None	CLAMS	Modeled
Intrinsic Potential Coho – Gradient	None	CLAMS	Modeled
Stream Width	Logarithmic	CLAMS	Modeled
Valley Width Index	Logarithmic	CLAMS	Modeled
Elevation	Square Root	CLAMS	Modeled
Mean Gradient Downstream	Logarithmic	CLAMS	Modeled
Dist. to Spawning Habitat	None	CLAMS	Modeled
Dist. to Winter Rearing Habitat	None	CLAMS	Modeled
Dist. to Summer Habitat	None	CLAMS	Modeled
Habitat Dataset			
Shade	None	ODFW AQI	Field Estimated
Valley Form	None	ODFW AQI	Field Estimated
Slope	None	ODFW AQI	Field Estimated
Depth	None	ODFW AQI	Field Estimated
Percent Silt and Organic Substrate	None	ODFW AQI	Field Estimated
Percent Sand in Substrate	None	ODFW AQI	Field Estimated
Percent Gravel in Substrate	None	ODFW AQI	Field Estimated
Percent Cobble in Substrate	None	ODFW AQI	Field Estimated
Percent Boulder in Substrate	None	ODFW AQI	Field Estimated
Percent Bedrock in Substrate	None	ODFW AQI	Field Estimated
Boulder Count	None	ODFW AQI	Field Estimated
Active Channel Erosion	None	ODFW AQI	Field Estimated
Percent Undercut Bank	None	ODFW AQI	Field Estimated
Number of Pieces of Wood	None	ODFW AQI	Field Estimated
Wood Volume	None	ODFW AQI	Field Estimated
Key Pieces of Wood	None	ODFW AQI	Field Estimated
Percent Canopy Closure	None	ODFW AQI	Field Estimated
Other Variables			
Subbasin	None	Descriptive	Locator
Basin	None	Descriptive	Locator

Information about geology was acquired from a dataset created by the United States Geological Survey (USGS) that contained digitized geology information at a 1:500,000 scale. Mean annual precipitation for Oregon was compiled by the PRISM (Parameter-elevation Regressions on Independent Slopes Model) group at Oregon State University, part of the Oregon Climate Service. Rainfall records between 1971 and 2000 were used in an assessment process that incorporated spatial effects of rain shadows and coastal effects (Daly et al. 1999).

Generating Stream Network Variables

Stream network variables need to represent the complexity, connection, and hierarchical organization of a stream. These variables and the stream network itself were derived by the Coastal Landscape Analysis and Modeling Study (CLAMS). Stream lines were generated from 10-m digital elevation models (Miller 2003, Clarke et al. in review). A geographic information system (GIS) (ArcInfo version 9.1) was used to overlay the modeled stream data from the CLAMS dataset, site-specific survey information from the AIP project, and the juvenile snorkel survey points. Stream network variables that represented habitat interconnectedness and network spatial organization included stream order, mean annual precipitation (mm), mean gradient downstream (from the stream segment under consideration), coho salmon intrinsic potential (Burnett et al. 2007), gradient of intrinsic potential for coho salmon, elevation, stream width and valley width index. Because variables were on many different scales, some variables were modified for normality using logarithmic or square root transformations as necessary to ease modeling and analysis (Table 3.1).

Figure 3.3. Generalized pictorial of network distance calculation: network distances were calculated from juvenile snorkel sites to the closest available seasonal habitat.



The network juxtaposition of critical seasonal habitats (spawning, summer refuge and winter rearing) required the identification of adequate seasonal habitats. Seasonal habitats were queried from the ODFW AIP habitat surveys. The criteria used to define “adequate” habitat were based on the ODFW Benchmarks (Appendix 3.1) for site-specific habitat features (Foster et al. 2001). Adequate spawning habitat was defined as riffle units with ≥ 50 percent gravel and ≤ 8 percent silt. Summer habitat was defined as pools ≥ 0.5 m in depth. Winter rearing habitat included all off-channel habitats defined as backwater pools, alcoves or isolated pools. While the importance of beaver pools as rearing habitat is well known (Collen and Gibson 2001, Pollock et al. 2004), these habitats were not included because they occurred in only one subbasin. I did not want to misrepresent the importance of beaver pools throughout the region. Also, in the subbasin that had beavers present, there were alcoves and other off channel habitat that represented available winter habitat. Each habitat unit that met the criteria for adequate habitat was selected from the main coverage and placed into a new coverage for that type of habitat. The ArcView 3.2 (ESRI) extension, Shortest Network Paths Version 1.1 (Remington 1999) was used to calculate network distances between the juvenile snorkel sites and seasonal habitats (Figure 3.3).

Network occupancy metrics were meant to represent the amount of stream network in which juvenile coho salmon were present at a subbasin scale. After the juvenile snorkel survey data was plotted in a GIS, the number of stream kilometers that encompassed the range of juvenile coho for each year, and in each subbasin, could be calculated.

Variable Selection

A large number of instream and network variables were available for analysis (Table 3.1). Three steps were used to reduce this list for modeling and statistical analysis. Each year was assessed individually because the snorkel surveys were not designed to survey the same pools every year. First, a correlation analysis of the original suite of variables available in the network and habitat datasets was completed for each year of data. Three of the network variables were excluded from the correlation analysis (CA) because of interest in their inclusion in later analysis and modeling (the variables described the nearest distance to habitats important in summer, for winter rearing and adult spawning), while one categorical variable (valley form) was excluded from the CA of instream metrics. Next, variables were dropped based on similarity and a preliminary principle components analysis (PCA) (PC Ord software, McCune and Mefford 1999). A PCA of the reduced network and instream habitat metrics guided the final selection of variables for models of juvenile density with instream and network metrics. Only variables that were important in the eigenvalues of the first three PCA axes were selected. This PCA was also used to describe the habitat structure in each year of data.

Objective One: Juvenile Density at the Site Scale

Juvenile coho salmon use different habitats in different seasons during their year of freshwater residency. The juxtaposition of these habitats in the stream network may be important when considering patterns of juvenile occupancy and site-specific density. In order to explore the efficacy of network metrics in describing juvenile density, I compared the effectiveness of instream site-specific habitat variables with stream network variables. Data were analyzed from three subbasins in the Alsea River basin (note: Upper Drift Creek, Five Rivers, and the South Fork Alsea) and four subbasins in the Siletz River basin (note: Rock, Cedar, Sams and Sunshine Creeks) that contained overlapping juvenile snorkel survey locations and ODFW aquatic inventory survey sites. Sites (n=1990) included data from 1998, 1999, 2001 and 2002 juvenile surveys. Throughout the site-scale analysis, juvenile density was log transformed to meet assumptions of normality.

Before modeling instream and network metrics, I explored the variability within the dataset. First, an Analysis of Variance (ANOVA) (using SAS 9.1 software) was used to test for differences in juvenile density among and within subbasins over the four years of data (1998, 1999, 2001 and 2002). The distance from the site to the stream mouth was included in the ANOVA to control for autocorrelation (tested for with Durbin-Watson test). Second, I explored whether the habitat used by juvenile fish changed among years. The identification of predominant metrics describing habitat were explored using a PCA of both the instream and network datasets.

In preliminary data analysis I noticed that some subbasins had increasing juvenile density between 2001 and 2002 and others had decreasing densities. I used a discriminant analysis (DA) (grouping on increasing and decreasing subbasins) and PCA to explore whether the network or habitat datasets could help explain subbasin differences.

I next modeled juvenile density using the instream and network datasets independently and together. I sought a modeling technique that uses non-parametric relationships between dependent and independent variables because preliminary analysis using parametric relationships was unsatisfactory due to low R^2 values. I chose a local-mean non-parametric multiplicative regression (LM-NPMR) for modeling (Hyperniche software, McCune and Mefford 2004). The form of non-parametric multiplicative regression used in the Hyperniche software is characterized by a leave-one-out cross-validation model selection technique meant to guard against model overfitting. Model quality was evaluated using a cross-validated R^2 value and examination of model fit in graphs of residuals and estimated values. The LM-NPMR used in my analysis incorporates a Gaussian local mean as the local model. The local model describes the shape of the function used to fit each point with the variables for that model (McCune 2004).

The dependent variable for all site level analysis was the log density of juvenile coho salmon (number of fish per meter of stream length). This analysis was not an attempt to define the best habitat for juveniles or adults. I recognize that density is a misleading indicator of habitat quality because density depends, in part, on the length of the pool in which the fish are counted. For juveniles, large and long pools in the lower portion of a watershed will have less unusable space for juveniles than small and short pools in the headwaters. So even though the larger downstream pool has a lower density, it may contain higher quality habitat than the pool upstream. In addition, juvenile coho salmon exhibit territorial behavior so territory size may be a more accurate tool for measuring habitat quality (Grant et al. 1998). However, in the interests of inventorying entire watersheds in a timely manner, only counts of fish in pools were taken by field survey crews. Describing habitat quality based on density alone may be misleading, but density provides a means of standardizing the data relative to the size of the pool and is useful for models that are attempts to understand abundance.

Objective Two: Juvenile Coho Patches

The second objective is meant to explore the physical context and meaning of patches of juvenile coho. The spatial autocorrelation structure of juvenile coho salmon density was generated for each subbasin and each year using variograms. Eleven subbasins were used in this analysis (Siletz: Cedar, Sunshine, Rock and Sams Creeks; Alsea: Drift, Fall, Canal, Lobster Creeks and North Fork Alsea, South Fork Alsea and Five Rivers). In this application, the area of autocorrelation, or variogram range, was interpreted to represent the size of patches occupied by juvenile coho. Variograms were used that included stream network distances between pools, rather than Euclidean distance between pools that is the typical method. The code and technique for using network distances were developed by Ganio et al. (2005). Also, juvenile density was detrended for this analysis by using the residuals of a regression that incorporated the distance to the mouth from every site. Distance downstream was the variable selected for detrending because the correlation between distance downstream and juvenile density was comparable to other network metrics and has been used by other researchers doing similar variogram detrending (personal communication L. Ganio, Oregon State University).

The manner in which a stream network branches might be important when describing patch sizes of juvenile coho salmon. For example, a stream that is more linear with few tributaries might reflect a different pattern of occupancy, described by patch size, than a stream system with multiple large branches that contained branched tributaries. Therefore, subbasins were clustered into groups based on the average gradient in first through third order streams. Higher-gradient low-order streams imply a steeper geomorphology than lower-gradient low-order streams. This difference in gradient could result in different shaped basins with low gradient streams tending toward a round and more dendritic shape and high gradient corresponding with a linear topology. A discriminant analysis tested whether linear and dendritic subbasins had different patch sizes of juvenile coho salmon.

Objective Three: Patterns of Juvenile Occupancy in Subbasins

Analyzing juvenile coho salmon occupancy at the subbasin scale was meant to provide a large-scale context within which patterns at smaller scales might better be interpreted. Summarizing occupancy at the subbasin scale also provided an opportunity to test whether occupancy changed between years. Further, subbasins were compared to spawning adult coho salmon run sizes and precipitation summarized at the mid-coast regional scale.

Juvenile coho salmon occupancy at the subbasin scale was summarized in a detailed count of stream kilometers in subbasins that were surveyed in at least three of the four survey years available. This included seven subbasins in the Alsea River basin (note: Drift, Canal, Five Rivers, Fall and Lobster Creeks, the North Fork Alsea and South Fork Alsea) and four in the Siletz River basin (note: Rock Creek, Cedar Creek, Sams Creek and Sunshine Creek). Visual inspection has been identified as a useful preliminary assessment tool (Torgersen et al. 2004). Subbasin maps of juvenile distribution were examined visually to explore how juvenile occupancy expands or contracts within the network. An unbalanced repeated measures analysis of variance (ANOVA - using SAS 9.1 software) tested whether there was a difference in subbasin occupancy over time. In this test, subbasins are assumed to be independent, but subbasins themselves are correlated through time. Therefore, subbasin forms the unit of replication.

Juvenile occupancy at the subbasin scale was explored with respect to two-large scale environmental conditions that might be important when exploring juvenile coho salmon distribution: adult spawning run size, and precipitation during spawning.

In this retrospective analysis, no causal relationships were sought. Rather, this part of the study attempts to incorporate large-scale relationships in an interpretation of network patterns. Adult spawning run size was chosen for interpretation because I assumed that more parents would lead to more juveniles. This might result in wider network use or different patterns of juvenile density. Precipitation was chosen for interpretation because it has been used as a surrogate measure of streamflow (Swift et al. 1988). It is possible that in years of higher precipitation, adults might mover further into the network following higher water levels and more habitats. Precipitation records for Oregon's mid-coast were averaged through the months of the spawning run (November through February).

Results

Variable Selection

The results of the correlation analysis was the same for each year. This could reflect the similar spatial location of sites between years. Based on an assessment of the correlation matrix in each year, the dataset of network variables was reduced from eight to four (Table 3.2). The four selected variables were stream order, elevation, mean gradient downstream, and valley width index. Stream order was selected because it was not highly correlated with any other network metrics. Mean annual precipitation was removed because it was correlated with elevation. Intrinsic potential for coho salmon, gradient of intrinsic potential for coho salmon and total stream width were removed because all were correlated with mean gradient downstream. Although

Table 3.2. Summary of correlation matrix showing significant correlation relationships (> 0.60) used in variable reduction from Oregon's Mid-Coast region in 1999 (n = 987), 2001 (n = 1288), and 2002 (n = 1416): Habitat and network datasets.

		Correlation Values by year:		
Selected Variable	Correlated Variable	1999	2001	2002
Network Dataset				
Elevation	Mean annual precipitation	0.81	0.72	0.69
Mean gradient downstream	intrinsic potential for coho salmon	-0.77	-0.76	-0.76
	gradient of potential for coho salmon	-0.74	-0.74	-0.74
	total stream width	-0.77	-0.69	-0.71
Valley width index	intrinsic potential for coho salmon	0.74	0.69	0.68
	gradient of potential for coho salmon	0.69	0.64	0.64
	total stream width	0.72	0.65	0.66
In-Stream Habitat				
Wood Count	Wood Volume	0.83	0.79	0.71

valley width index was also correlated with the intrinsic potential for coho salmon, gradient of intrinsic potential for coho salmon, and total stream width, it was kept because it was not highly correlated with mean gradient downstream. The correlation analysis of the site-specific habitat variables only resulted in the exclusion of wood volume, because of its high correlation with the wood count (Table 3.2).

Although the correlation analysis was useful in reducing variables in the network dataset, it did not make a significant reduction in the number of variables in the site-specific habitat dataset. However, I opted to use five of the seventeen site-specific habitat variables to represent the entire dataset. This selection was guided by a PCA and also by the biological importance of certain physical features. This variable reduction was an attempt to avoid duplication of metrics. The five representative habitat variables are valley form (a categorical variable), water depth, percent sand, percent gravel, percent undercut bank, and number of pieces of wood. Valley form was meant to encapsulate slope, shade and canopy closure. Percent sand and gravel represented substrate, while silt/organics, cobble, boulder, bedrock and boulder count were omitted. Also, percent sand measured fine-grained material, which can be detrimental to juvenile survival to emergence, and gravel measured the coarse-grained substrate necessary for spawning adults (Groot and Margolis 1991). Undercut bank was chosen as an indicator of active channel erosion. Number of pieces of wood was chosen to represent all wood variables, including wood volume and key pieces of wood.

To further reduce the number of instream habitat variables for modeling purposes, an additional level of variable selection incorporated a principle components analysis for each year of data. The results were different for every year (Table 3.3 for network dataset and Table 3.4 for instream habitat), so any variable that was identified throughout the four years was included in the final list of network and instream variables to be used for modeling. These variables were chosen for modeling because they were important in describing the variation in habitat for these two datasets over the four years of study data (network variables: distance to summer pools, distance to spawning habitat, distance to rearing habitat, order, subbasin, valley width index and mean gradient downstream; in stream variables: valley form, percent gravel, percent sand, undercut and number of pieces of wood).

Table 3.3. Principle components analysis results for sites in Oregon’s Mid-Coast in 1998, 1999, 2001 and 2002 using a dataset of variables describing network relationships.

Year	Axis	Eigenvalue	Percent of Variance	Cumulative Percent of Variance	Broken-stick Eigenvalue	Dominant Variables in Eigenvector
1998	1	2.342	33.451	33.451	2.593	Distance to summer pools; Distance to spawning
	2	1.51	21.575	55.026	1.593	Order
	3	1.078	15.407	70.433	1.093	Subbasin
1999	1	1.61	26.88	26.88	2.45	Order; Valley width index
	2	1.36	22.62	49.50	1.45	Mean grad downstream
	3	1.31	21.81	71.31	0.95	Distance to rearing
2001	1	2.06	34.26	34.26	2.45	Distance to spawning; Distance to rearing
	2	1.46	24.39	58.65	1.45	Mean grad downstream
	3	1.09	18.22	76.78	0.95	Valley width index
2002	1	2.11	35.20	35.20	2.45	Distance to spawning; Distance to rearing
	2	1.48	24.73	59.93	1.45	Mean grad downstream
	3	1.11	18.41	78.34	0.95	Valley width index

Table 3.4. Principle components analysis results for sites in Oregon's Mid-Coast in 1998, 1999, 2001 and 2002 using a dataset of variables describing instream habitat conditions.

Year	Axis	Eigenvalue	Percent of Variance	Cumulative Percent of Variance	Broken-stick Eigenvalue	Dominant Variables in Eigenvector
1998	1	1.854	26.491	26.491	2.593	Valley form
	2	1.292	18.463	44.954	1.593	Percent gravel
	3	1.121	16.019	60.973	1.093	Undercut
1999	1	2.07	29.50	29.50	2.59	Percent sand; Percent gravel
	2	1.23	17.62	47.12	1.59	Undercut
	3	1.01	14.44	61.55	1.09	Number wood pieces
2001	1	1.99	28.40	28.40	2.59	Percent sand
	2	1.24	17.74	46.14	1.59	Valley form
	3	1.06	15.10	61.24	1.09	Number wood pieces
2002	1	2.14	30.60	30.60	2.59	Percent sand
	2	1.26	17.93	48.53	1.59	Valley form
	3	1.12	15.96	64.50	1.09	Number wood pieces

Objective One: Site Scale Patterns

Objective one incorporated stream network metrics into an analysis at the site scale. This process explored the usefulness of stream network metrics and how they contribute to an understanding of habitat use by juvenile fish in the context of their diverse life history (Groot and Margolis 1991) and behaviors (Chapman 1962, Nielsen 1992). Before exploring network metrics directly, I tested the subbasins to see if juvenile density or habitat configurations changed across years.

Table 3.5. ANOVA results examining juvenile coho density and subbasins in Oregon's Mid-Coast region over time.

Log Juvenile Coho Density ~
Year + subbasin + year*subbasin + downdist

Effect	df	F Value	Pr > F
Year	3	35.82	< 0.0001
Subbasin	6	13.2	< 0.0001
Year*subbasin	13	18.8	< 0.0001
Downdist	1	15.15	0.0001

Test of whether there were significant differences in juvenile coho density within individual subbasins over available years

Subbasin	df	F value	Pr > F
Cedar	2	18.05	< 0.0001
Upper Drift	2	35.99	< 0.0001
Five Rivers	2	6.85	0.0011
Rock	3	54.08	< 0.0001
Sams	2	6.46	0.0016
S.F. Alsea	2	26.39	< 0.0001
Sunshine	3	21.96	< 0.0001

Analysis of Variance (ANOVA) results indicated that there was a subbasin-by-year effect in the densities (p-value < 0.001) (Table 3.5). This means that juvenile density changes within subbasins in different ways across years. The ratio of change between these years varied by subbasin with some subbasins showing lower densities between years (ratio > 1.0) and some subbasins with higher densities (ratio < 1.0) (Table 3.6). Sunshine Creek was the only subbasin in which 1998 had a higher density relative to later survey years (1998 to 1999 ratio = 24.6132, 1998 to 2001 ratio =

Table 3.6. Pairwise comparisons of the difference in juvenile coho density between years for each subbasin.

Start Year	Start Subbasin	To Year	To Subbasin	bt lower	Ratio	br upper
1998	Five Rivers	2001	Five Rivers	0.0738	0.1829	0.4523
1998	Five Rivers	2002	Five Rivers	0.1320	0.3233	0.7913
1998	Rock	1999	Rock	0.2759	0.6882	1.7169
1998	Rock	2001	Rock	0.0020	0.0129	0.0334
1998	Rock	2002	Rock	0.0036	0.0094	0.0243
1998	S.F. Alsea	2001	S.F. Alsea	0.0283	0.0608	0.1308
1998	S.F. Alsea	2002	S.F. Alsea	0.1203	0.2345	0.4574
1998	Sunshine	1999	Sunshine	11.0252	24.6132	54.9477
1998	Sunshine	2001	Sunshine	3.5005	7.3161	15.2905
1998	Sunshine	2002	Sunshine	1.8910	3.8349	7.7646
1999	Cedar	2001	Cedar	2.9093	13.8146	65.5982
1999	Cedar	2002	Cedar	0.1764	0.8007	3.6336
1999	Upper Drift	2001	Upper Drift	0.0213	0.0448	0.0870
1999	Upper Drift	2002	Upper Drift	0.0629	0.1281	0.2609
1999	Rock	2001	Rock	0.0074	0.0188	0.0480
1999	Rock	2002	Rock	0.0054	0.0137	0.0349
1999	Sams	2001	Sams	0.1220	0.2587	0.5486
1999	Sams	2002	Sams	0.1874	0.3944	0.8398
1999	Sunshine	2001	Sunshine	0.1310	0.2972	0.6744
1999	Sunshine	2002	Sunshine	0.0706	0.1558	0.3436
2001	Cedar	2002	Cedar	0.0223	0.0580	0.1503
2001	Upper Drift	2002	Upper Drift	1.3429	2.8559	6.0864
2001	Five Rivers	2002	Five Rivers	0.7740	1.7698	4.0467
2001	Rock	2002	Rock	0.2757	0.7265	1.9161
2001	Sams	2002	Sams	0.7384	1.5245	3.1474
2001	S.F. Alsea	2002	S.F. Alsea	1.8075	3.8551	8.2221
2001	Sunshine	2002	Sunshine	0.2542	0.5242	1.0808

7.3161, and 1998 to 2002 ratio = 3.8349). Cedar Creek was the only subbasin with a higher density of juvenile coho in 1999 than in 2001 (ratio of 13.8146). With the afore mentioned exceptions of Sunshine and Cedar Creeks, all subbasins had higher density between years from 1998 through 2001. However, between 2001 and 2002 several subbasins had increasing densities of juvenile coho salmon while others had decreasing densities. Drift Creek, Five Rivers, Sam Creek and the South Fork Alsea all had higher densities in 2001 than in 2002. Cedar, Rock and Sunshine Creeks had higher densities in 2002 than 2001 (Table 3.6).

The principle components analysis indicated that the variation in the habitat characteristics was portioned similarly each year. In 1998 and 1999 the set of habitat variables that dominate axes 1, 2 and 3 are slightly different in both the network and instream datasets, with 2001 and 2002 appearing nearly identical (Tables 3.3 and 3.4). The network variables of distance to summer pools, distance to spawning habitat, distance to rearing habitat, order, subbasin, valley width index and mean gradient downstream dominated one of the first three pca axes in at least one year of data. From the instream dataset, valley form, percent sand, percent gravel, undercut and the number of pieces of wood dominated one of the first three pca axes in at least one year of data.

The explanatory ability of the network and instream datasets, independently and together, in describing the abundance of juvenile coho salmon was explored using a local-mean, non-parametric multiplicative regression (LM-NPMR) process. The best model for each dataset was selected by a comparison of R^2 values and model fit in graphs of residuals and estimated values. In every year the best network models (1998,

Table 3.7. Local-mean non-parametric multiplicative regression model results for 1998, 1999, 2001 and 2002 for sites in Oregon's Mid-Coast region. The dependent variable is log juvenile coho density.

Year	Variable set	R^2	Variable 1	Variable 2	Variable 3	Variable 4
1998	Network Variables	0.3624	Subbasin	Distance to rearing habitat	Order	Mean gradient downstream
	Instream Variables	0.0594	Valley Code	Percent sand	Percent gravel	Wood pieces
	Instream and Network Variables	0.3896	Subbasin	Wood pieces	Order	Mean gradient downstream
1999	Network Variables	0.1716	Order	Valley width index	Subbasin	
	Instream Variables	0.1178	Percent Sand	Percent gravel	Undercut	Wood pieces
	Instream and Network Variables	0.2345	Distance to rearing habitat	Mean gradient downstream	Valley code	Subbasin
2001	Network Variables	0.2571	Distance to spawning habitat	Mean gradient downstream	Distance to summer pools	
	Instream Variables	0.151	Valley Code	Percent sand	Undercut	Wood Pieces
	Instream and Network Variables	0.2873	Percent Sand	Distance to spawning habitat	Mean gradient downstream	Distance to summer pools
2002	Network Variables	0.2433	Distance to rearing habitat	Mean gradient downstream	Distance to summer pools	Subbasin
	Instream Variables	0.105	Valley Code	Percent sand	Percent gravel	Undercut
	Instream and Network Variables	0.2861	Valley Code	Undercut	Distance to rearing habitat	Subbasin

$R^2 = 0.3624$; 1999, $R^2 = 0.1716$; 2001, $R^2 = 0.2571$; 2002, $R^2 = 0.2433$) had higher explanatory power than the best instream models (1998, $R^2 = 0.0594$; 1999, $R^2 = 0.1178$; 2001, $R^2 = 0.1510$; 2002, $R^2 = 0.1050$) for the log of juvenile density. Models from the combined dataset in each year had a slightly higher explanatory power than the network models (1998, $R^2 = 0.3896$; 1999, $R^2 = 0.2345$; 2001, $R^2 = 0.2873$; 2002, $R^2 = 0.2861$). Because the network and combined models have such similar R^2 values neither sets of models may be deemed better than the other.

Variables selected in LM-NPMR varied for each year and dataset (Table 3.7). In the network dataset, the variables subbasin, distance to rearing habitat, distance to spawning habitat, distance to summer pools, mean gradient downstream and stream order were present at least once. In the instream habitat dataset, the variables percent sand, percent gravel, wood pieces, valley code, and undercut were present at least once.

A discriminant analysis (DA) was conducted to test whether the observation of increasing or decreasing density ratios within subbasins between 2001 and 2002 could be tied to stream network or instream characteristics. The DA found a statistically significant division between these two clusters in both datasets (Hotelling’s T-Squared value of < 0.001 for both datasets) (Table 3.8). The log of juvenile density, coded for increasing or decreasing subbasins, was graphically overlaid on the network and instream PCA ordinations for 2002 (a PCA for 2002 was used because the PCAs for 2001 and 2002 were nearly identical). There appeared to be little differentiation between subbasins with increasing or decreasing juvenile density in the instream dataset (Figure 3.4). However, there appeared to be a demarcation between these two clusters of subbasins in the network dataset along the first axis, which predominately represents the juxtaposition variables of distance to spawning and distance to rearing (Figure 3.5). This is visible in the graph as the clumping of grey and black triangles (sites) into two groups along the gradient of the first axis.

Objective Two: Patches and Basin Shape

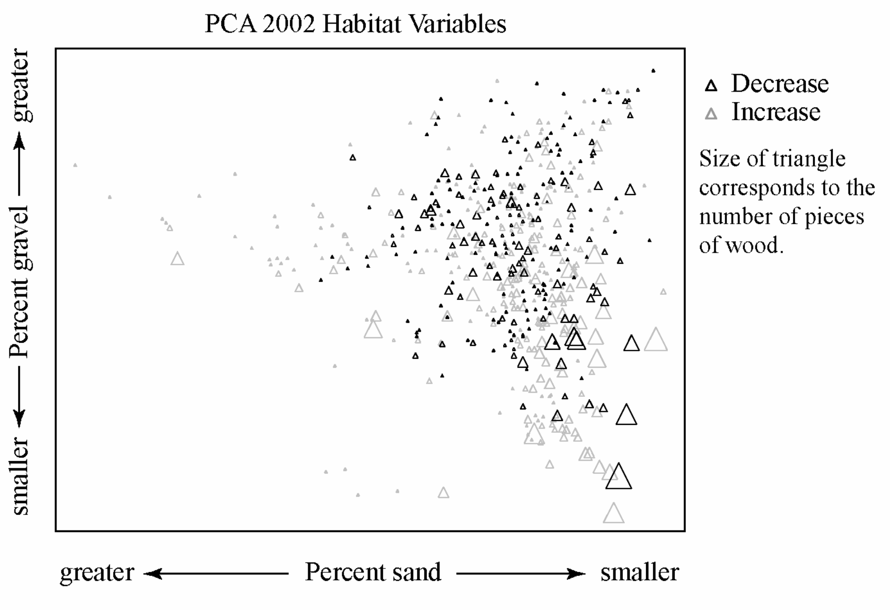
Variograms were generated in order to compare the spatial clumping pattern exhibited by the log of juvenile coho salmon density (detrended with the variable distance downstream) in the stream network among subbasins over time (Appendix 3.2). The robust variograms allow for the estimation of the interval (estimated variogram range) in which survey points exhibit spatial autocorrelation. Because the range was estimated, it included an unquantifiable amount of error. Therefore, no rigorous statistical tests were completed using this metric as a dependent variable. However, this metric may be summarized graphically. Examining the graph of variogram range size per year in each subbasin indicated that range tends to change within subbasins among years (Figure 3.6). In addition, the estimated variogram range size appears to be smaller in small subbasins compared to larger subbasins. Variogram shape also appeared to change as watershed area increased with a small “hump” appearing low in the variogram of larger watersheds (Figure 3.7). This “hump” pattern is present in at least one year for six of the eleven subbasins in this analysis (North Fork Alsea, Upper Drift, Rock and Lobster Creeks, South Fork Alsea and Five (Figure 3.8). The shapes of the subbasins in the cluster with lower average gradients

Table 3.8. Discriminant Analysis results for two sets of analysis of groups in subbasins of Oregon's Mid-Coast: groups of subbasins identified as increasing or decreasing juvenile coho density (between 2001 and 2002); groups of subbasins classified as linear or branched in shape.

Hotelling's T- Squared	Group	Variable Category	Variable List
<0.001	Increase or Decrease	Habitat	Percent sand; Percent gravel; Undercut; Wood pieces; Valley code
<0.001	Increase or Decrease	Network	Distance to spawning; Distance to rearing; Distance to summer pools; Order; Mean gradient downstream; Valley width index
0.53	Linear or Branched	1998	Area; Stream km occupied by juvenile coho; Number of streams occupied by juvenile coho; Juvenile coho count; Range size
sample size too small	Linear or Branched	1999	Area; Stream km occupied by juvenile coho; Number of streams occupied by juvenile coho; Juvenile coho count; Range size
0.82	Linear or Branched	2001	Area; Stream km occupied by juvenile coho; Number of streams occupied by juvenile coho; Juvenile coho count; Range size
0.7	Linear or Branched	2002	Area; Stream km occupied by juvenile coho; Number of streams occupied by juvenile coho; Juvenile coho count; Range size

appeared more rounded and branched than the subbasins with higher average gradients. Therefore, two cluster groups of branched and linear subbasins were identified. Discriminant analysis of the two basin shape clusters for 1998, 1999, 2001 and 2002 incorporated network summary information such as area, stream kilometers occupied by juvenile coho, number of streams occupied by juvenile coho, total

Figure 3.4. Principle Components Analysis graph of 2002 habitat dataset displaying the number of pieces of wood with subbasins of increasing or decreasing juvenile density (between 2001 and 2002) as an overlay. Each triangle corresponds with a specific pool and the size of the triangle represents the relative number of pieces of wood associated with each pool. The x-axis is associated a gradient of greater to smaller percentages of fine substrate material and the y-axis is associated with smaller to greater percentages of coarse substrate material.

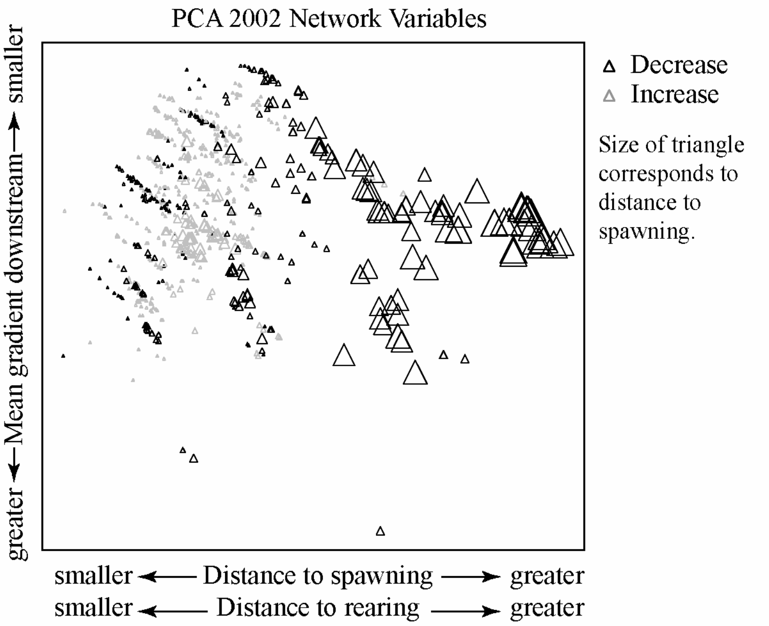


juvenile coho counted and estimated variogram range size. None of the DA resulted in statistically significant differentiation between basin shape clusters (Table 3.8).

Objective Three: Subbasins and Juvenile Network Occupancy

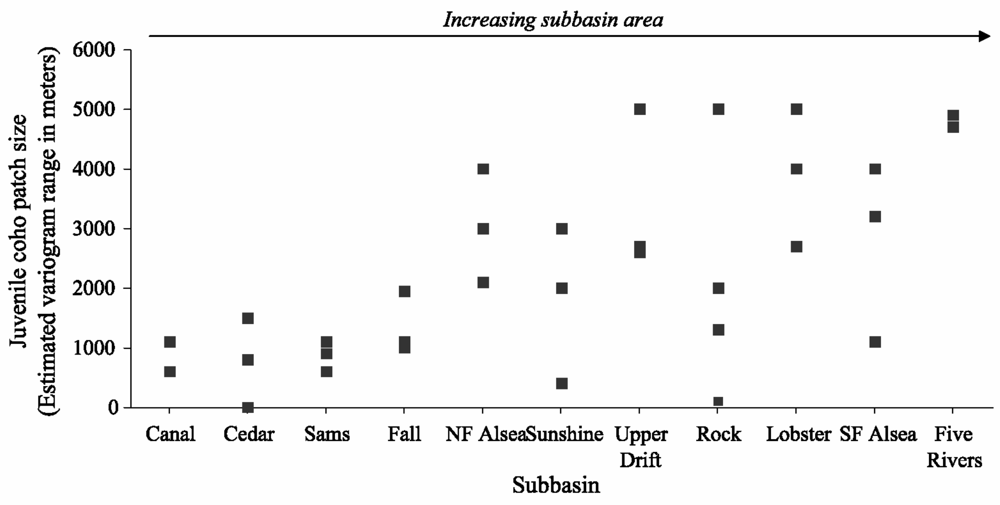
Stream occupancy descriptors such as stream kilometers occupied and number of streams occupied per year were summarized for each subbasin (Table 3.9). An unbalanced repeated measures ANOVA was used to test whether subbasin occupancy changed similarly over time within and among subbasins. There were statistically

Figure 3.5. Principle Components Analysis graph of 2002 network dataset displaying distance to spawning habitat with basins of increasing or decreasing juvenile density (between 2001 and 2002) as an overlay. Each triangle corresponds with a specific pool and the size of the triangle represents the measured distance to spawning habitat associated with each pool. The x-axis is associated with a gradient of smaller to larger distances between seasonal habitats while the y-axis represents a continuum of mean gradient downstream.



significant differences in juvenile coho salmon occupancy among years ($p < 0.001$, df = 3, F value = 9.19) and also among subbasins within years ($p < 0.001$ with Bonferroni correction of alpha level to 0.0125) (Table 3.10). With a Tukey-Kramer adjustment, differences in subbasin occupancy between years were statistically significant (p-value < 0.05) for three pairs of years (1998 to 2002 adjusted p = 0.0169; 1999 to 2001 adjusted p = 0.0081; 1999 to 2002 adjusted p = 0.0021) (Table 3.11). After Torgersen et al. (2004), a visual inspection of subbasin maps (Appendix 3.3)

Figure 3.6. Juvenile coho salmon patch size (estimated variogram range) for 1998, 1999, 2001 and 2002 in subbasins of the Alsea and Siletz River basins. The subbasins are listed from smallest to largest.



was completed to suggest further analysis or interpretation. The patterns of juvenile coho salmon distribution in the maps of network occupancy imply that when higher numbers of stream kilometers are occupied, the distribution of juvenile coho salmon moves into the headwaters, while lower numbers of stream kilometers occupied has the reverse effect (Figure 3.9).

Figure 3.7. Variograms for subbasins in Oregon’s Mid-Coast (in each year available between 1998 and 2002) with arrows pointing to “hump” shape that is common in larger basins and may be associated with a nested spatial autocorrelation structure. Lines show the upper and lower bounds of a 95% confidence interval.

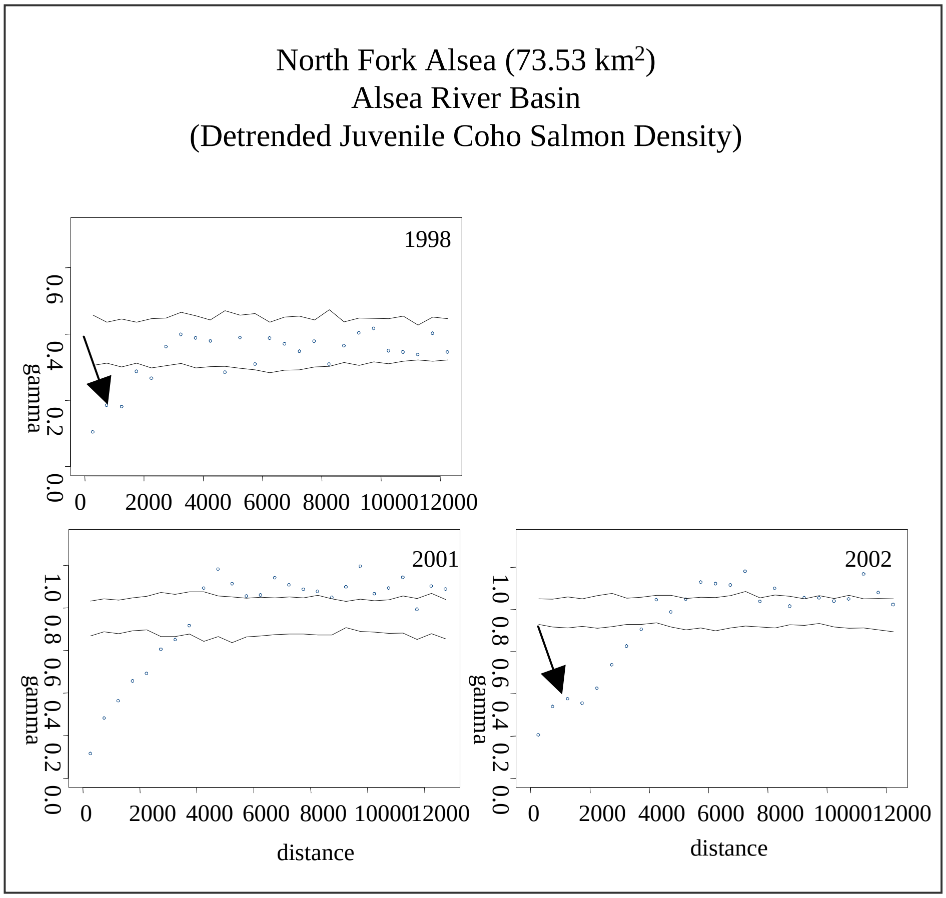


Figure 3.7. Continued.

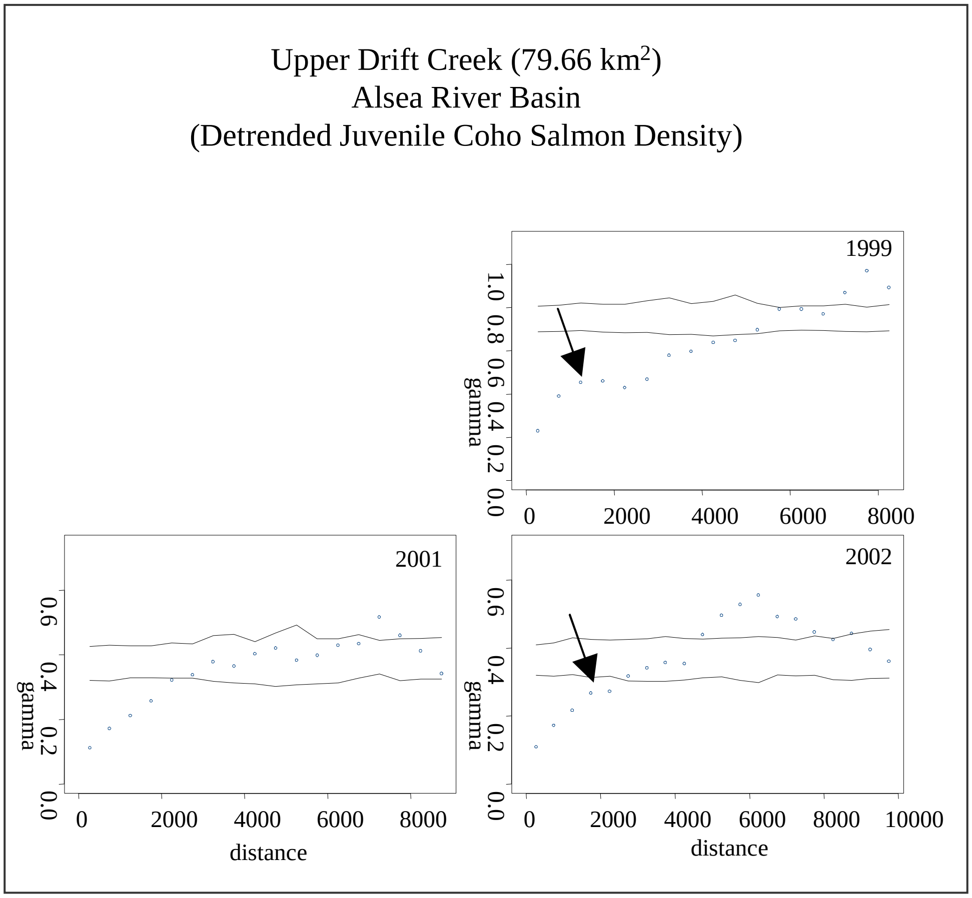
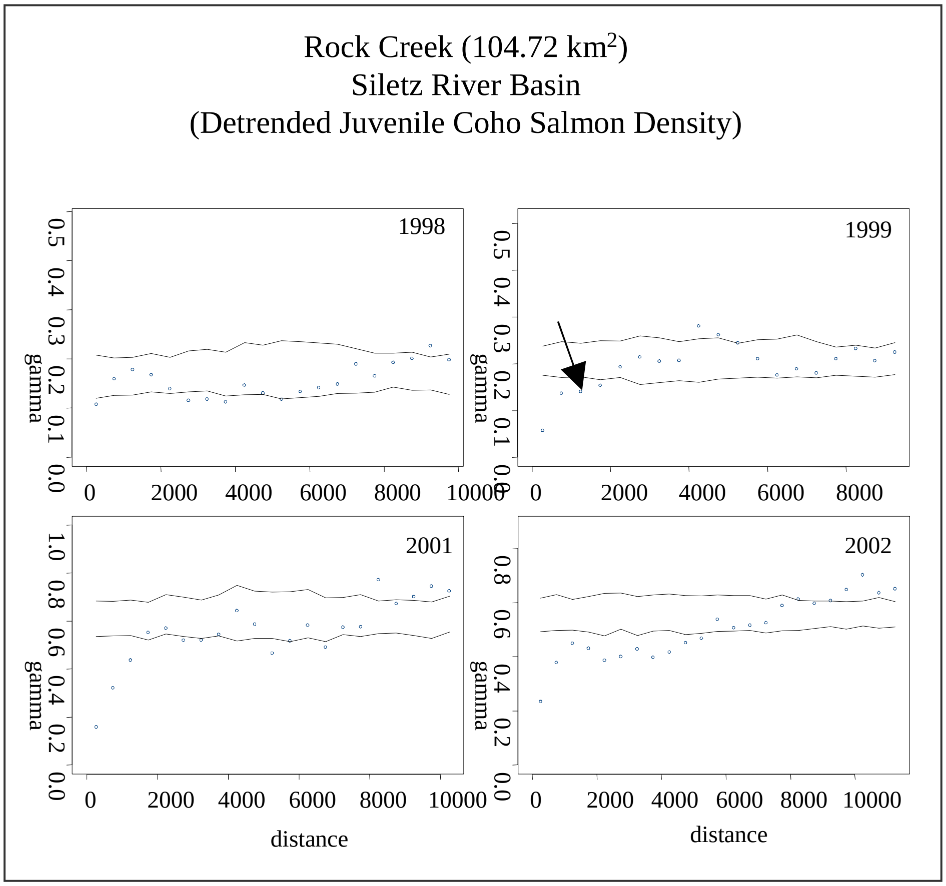


Figure 3.7. Continued.



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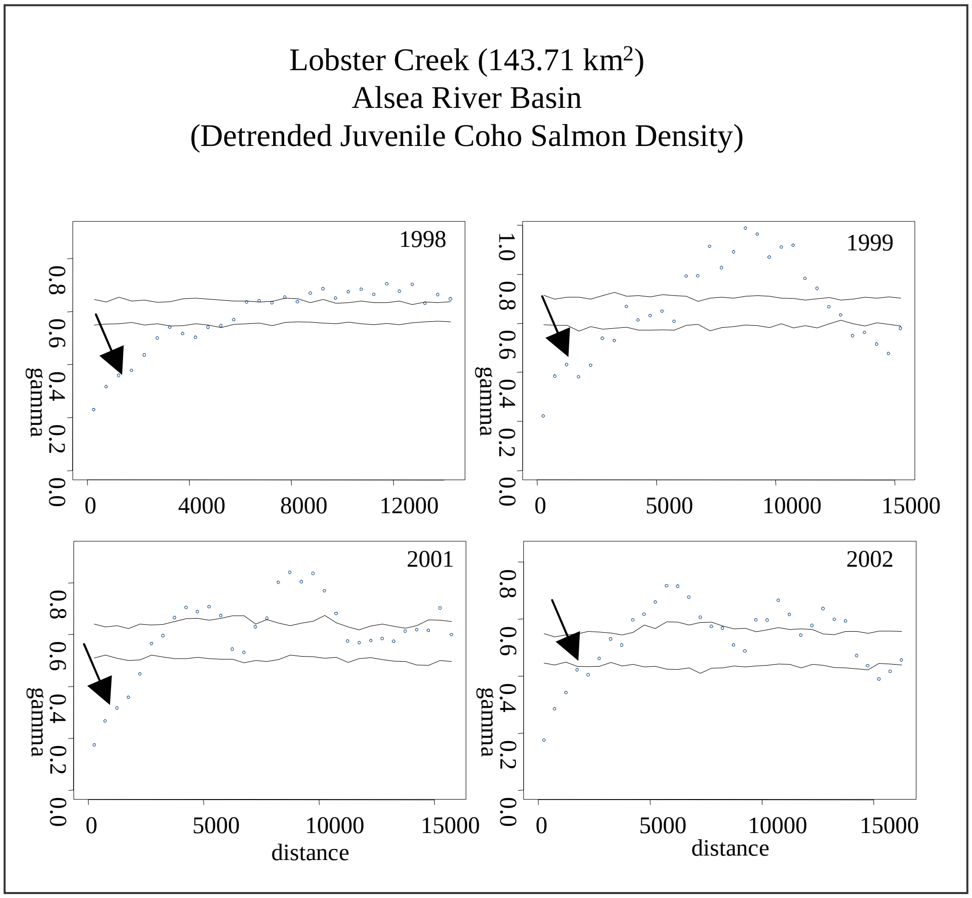
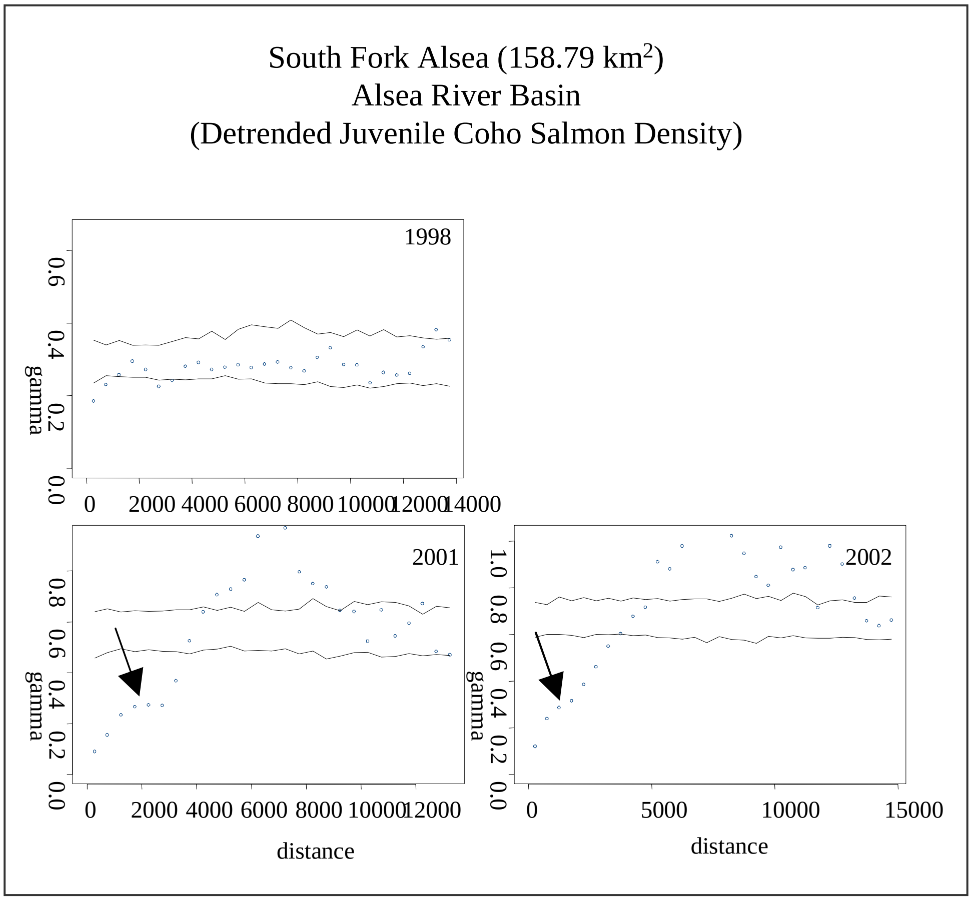


Figure 3.7. Continued.



South Fork Alsea (158.79 km^2)
Alsea River Basin
(Detrended Juvenile Coho Salmon Density)

Figure 3.7. Continued.

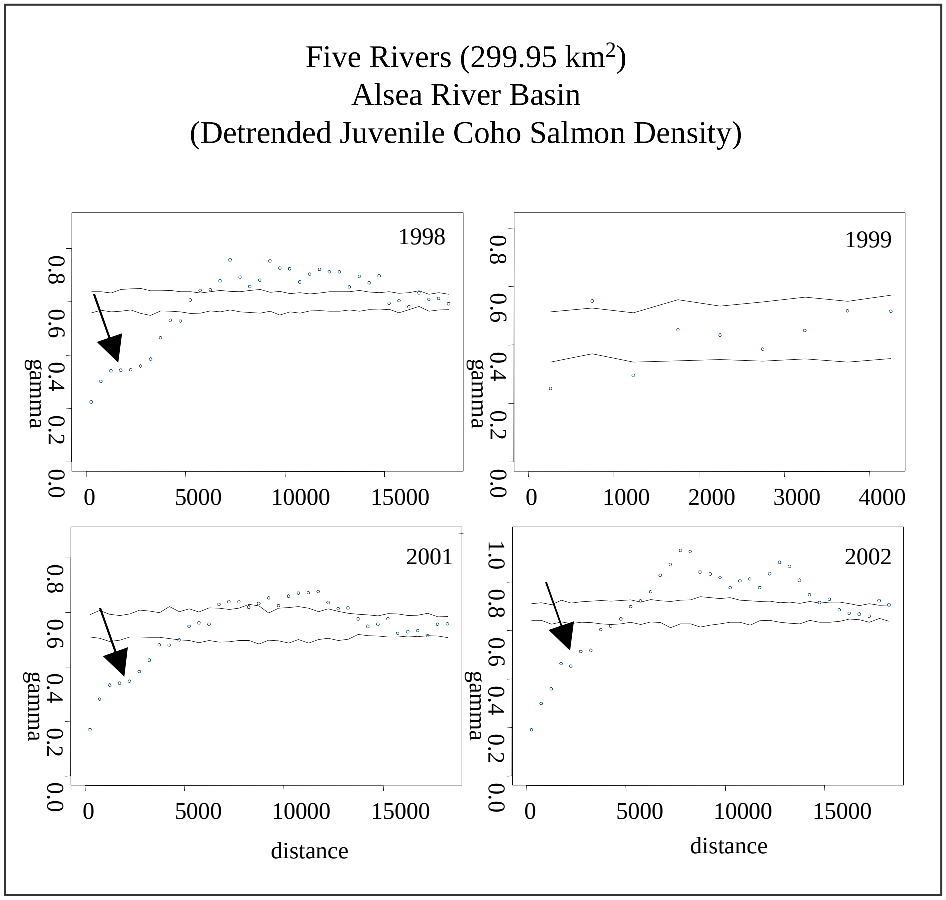
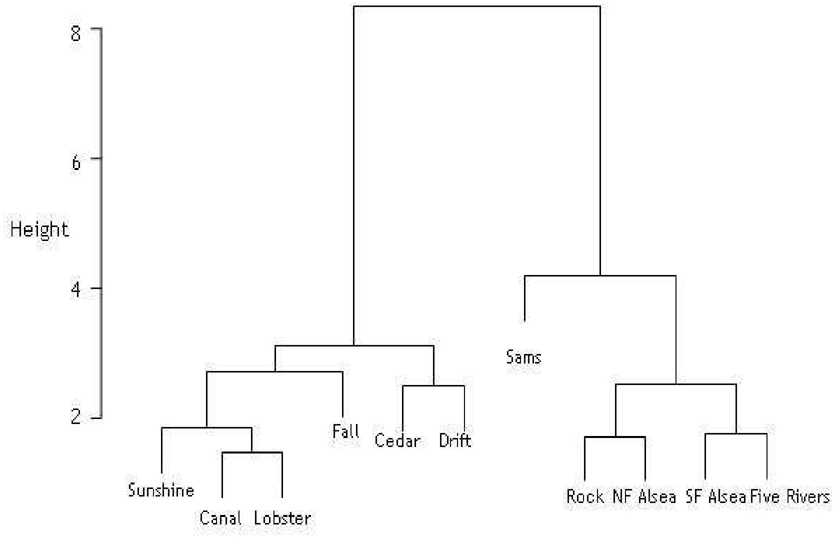


Figure 3.8. Dendrogram showing two clusters of subbasins described as branched or linear in shape due to their geomorphology.



The patterns of juvenile coho salmon stream occupancy in the subbasins of the Alsea and Siletz appear similar to pattern of the adult spawning run size for the entire Mid-Coast region. Adult spawning run sizes increase between 1997 (parents of 1998 juveniles) and 2001 (parents of the 2002 juveniles) (Figure 3.10). Subbasin occupancy summary information shows an increase in the number of stream kilometers occupied during this time period in most basins. Fall, Lobster, Sams, and Sunshine Creeks showed increases and decreases in occupancy among years rather than a consistent increase (Table 3.9). Also, in all basins except Sunshine Creek, the number of kilometers occupied by juveniles increased between 2001 and 2002. Precipitation during the spawning run time for the entire mid-coast was the highest in 1998 and lowest in 2000 (Figure 3.10).

Table 3.9. Summary table showing number of sites occupied, total number of sites surveyed, juvenile coho count, number of streams occupied and stream miles occupied for the 11 subbasins of interest in Oregon's Mid-Coast region.

Alsea Basin	Year	# Sites Surveyed	# Sites Occupied	# Juvenile Coho	# Streams Occupied	Stream (km) Occupied
Canal Creek Basin	1998	90	88	1082	4	11.806
(32.964 km^2)	2001	135	85	2753	8	14.244
	2002	156	130	2588	9	18.121
Fall Creek	1998	127	86	1134	7	17.620
(71.80 km^2)	2001	108	63	2113	5	16.234
Hatchery in mid-basin	2002	107	58	1057	6	17.185
NF Alsea	1998	186	112	1461	6	19.125
(73.532 km^2)	2001	195	135	3483	11	24.793
Below hatchery	2002	277	198	4607	15	29.027
Upper Drift Creek	1999	328	231	2990	16	28.351
(79.66 km^2)	2001	267	234	19162	13	30.728
	2002	308	308	10919	15	40.446
Lobster Creek	1998	476	313	4010	17	41.488
(143.71 km^2)	1999	389	257	2499	18	29.788
	2001	411	351	12033	23	60.934
	2002	487	431	13279	22	65.795
SF Alsea	1998	230	107	350	7	94.555
(158.79 km^2)	2001	189	138	1825	7	107.317
	2002	268	216	3086	10	115.741
Five Rivers						
(299.95 km^2)	1998	648	474	5332	25	62.596
1999 data excluded uneven coverage with	2001	632	501	18808	33	81.465
other years	2002	922	756	18782	48	97.460
Siletz Basin						
Cedar	1999	16	10	84	1	4.328
(33.44 km^2)	2001	83	67	4074	4	14.245
	2002	121	81	2029	5	17.551
Sams	1999	283	202	2194	10	15.708
(37.71 km^2)	2001	233	200	8826	10	14.678
	2002	303	269	8841	10	18.956
Sunshine	1998	138	102	2352	6	13.673
(77.0 km^2)	1999	85	54	470	4	7.896
	2001	173	133	5515	9	16.423
	2002	175	134	6360	7	13.13
Rock Creek	1998	239	103	601	8	21.448
(104.72 km^2)	1999	239	93	789	8	28.442
	2001	267	184	6378	13	34.852
	2002	295	224	3902	10	38.999

Table 3.10. Unbalanced repeated measures ANOVA for subbasins in the Alsea and Siletz Basins that tested for differences in least squares means of the number of stream kilometers occupied by juvenile coho between 1998 and 2002.

Year	Juvenile Coho Salmon Mean Occupancy (km)	Standard Error	Confidence Interval
1998	30.76	9.43	11.20 - 50.32
1999	27.83	9.53	8.06 - 47.60
2001	37.86	9.35	18.48 - 57.24
2002	43.00	9.35	23.62 - 62.38

Table 3.11. Unbalanced repeated measures ANOVA for subbasins in the Alsea and Siletz Basins that tested for differences in least squares means in the number of stream kilometers occupied by juvenile coho salmon between years from 1998 and 2002.

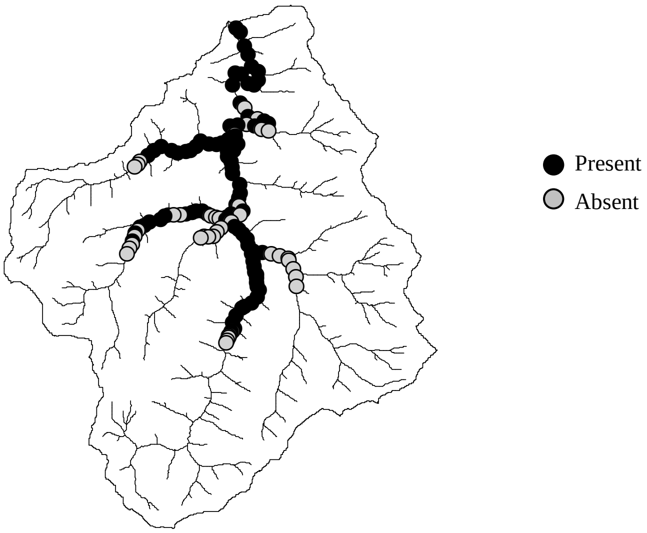
From Year	To Year	Juvenile Coho Salmon Mean Occupancy (km)	Standard Error	df	t-value	Tukey-Kramer Adjusted P
1998	1999	2.9314	3.2622	22	0.9	0.8056
1998	2001	-7.0982	2.941	22	-2.41	0.1038
1998	2002	-12.233	3.7361	22	-3.27	0.0169
1999	2001	-10.03	2.7881	22	-3.6	0.0081
1999	2002	-15.164	3.6282	22	-4.18	0.0021
2001	2002	-5.1346	2.3522	22	-2.18	0.1592

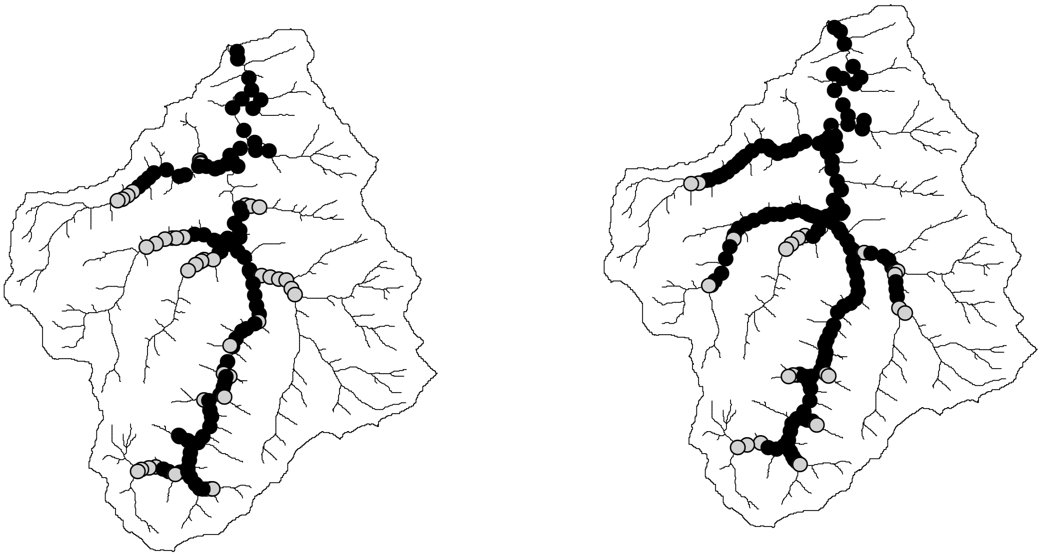
Discussion

Patterns of juvenile coho abundance, distribution and occupancy were analyzed at three spatial scales that incorporated elements of stream network structure in variables or statistical analyses. The analysis and synthesis of these scales provides an opportunity to consider the complex population ecology of coho salmon.

Figure 3.9. The series of Canal Creek maps (1a, 1c, 1d) show an increase in juvenile network occupancy upstream from 1998 to 2002 while Sunshine Creek (2a-2d) shows variation in network occupancy including a decrease in occupancy between 1998 and 1999 and 2001 and 2002.

1a. Canal Creek 1998



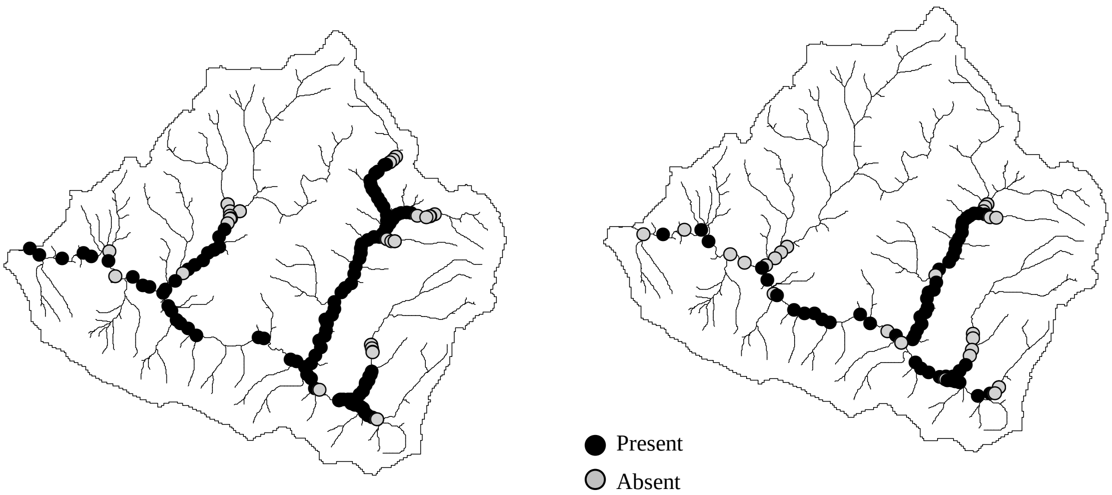

1c. Canal Creek 2001

1d. Canal Creek 2002

Figure 3.9. Continued.

2a. Sunshine Creek 1998

2b. Sunshine Creek 1999



2c. Sunshine Creek 2001

2d. Sunshine Creek 2002

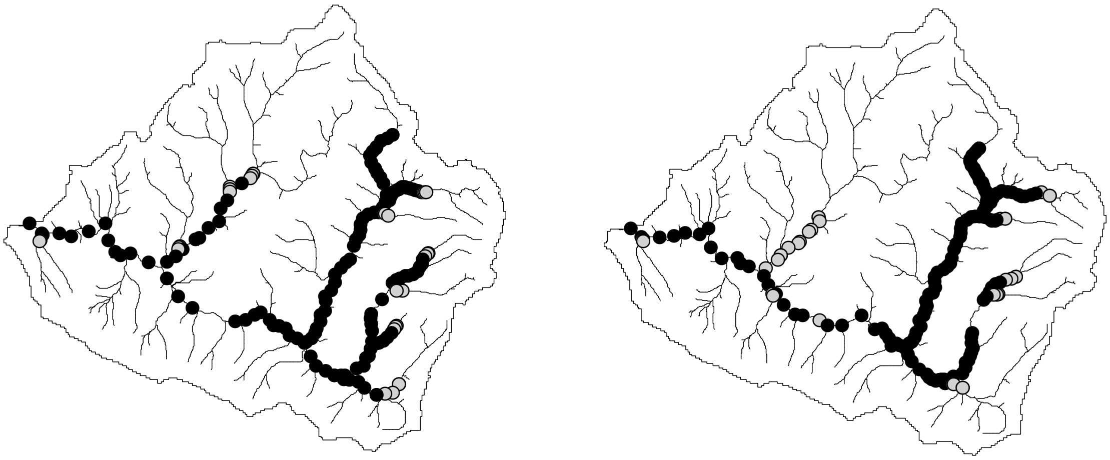
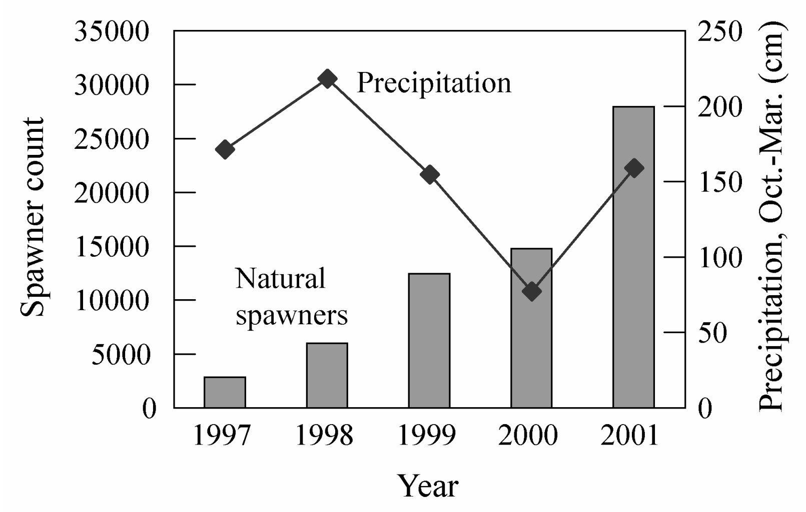


Figure 3.10. Number of coho salmon spawners in Oregon’s Mid-Coast and precipitation during the spawning run (October through March).



Objective One: Site Scale

Site-scale analysis allows for the exploration of local habitat conditions that may be important for individual fish. Results show that juvenile density changes among years within subbasins, but the core complement of stream habitats occupied by juvenile coho salmon remains similar over time. This means that while juvenile density may change over time, the fish tend to occupy the same types of habitat presumably in the same portions of the stream network. Juveniles appear to have high site fidelity (Bell et al. 2001) and occupancy in similar habitats in the network is consistent with the tendency of the majority of adults to home to their natal habitats to spawn (Labelle 1992). Site scale analysis highlighted the relevance of a stream network framework in exploring juvenile coho salmon density. Although the overall explanatory power of models using the instream or network datasets individually or together was low, even for ecological datasets, network variables were consistently useful in each year. Clearly, other variables that were not captured in this analysis explain most of the variation in the juvenile coho salmon dataset. These might include micro habitat variables, intra and inter-species interactions, food availability and predation. The low explanatory power of the models could also be due to the ability of juveniles to exploit a wide variety of pool habitats, as is consistent with the diversity of their behaviors (Nielsen 1992). However, it is important to note that the spatial arrangement or topology of stream habitats has been shown to be helpful in assessments of habitat quality in other species (Jones et al. 2003) and explains the density patterns of juvenile coho salmon at least as well as instream habitat metrics.

Juvenile coho salmon density might have been expected to increase or decrease in synchrony across subbasins as each subbasin responded to the same set of environmental conditions such as rainfall. Indeed, juvenile density appeared to increase or decrease relatively consistently across years within subbasins except between 2001 and 2002. The lack of consistency in changes of juvenile coho salmon density among subbasins between 2001 and 2002 is intriguing and led to an investigation that pointed to network variables, in particular habitat juxtaposition variables, as a possible difference between subbasins having opposite variation in juvenile density between 2001 and 2002. This study’s results imply that in some years, juvenile density is higher in watersheds with close proximity among important seasonal habitats. This interpretation is supported by Kocik and Ferreri (1998) who found that the productivity for Atlantic salmon (*Salmo salar*) depends on the proximity of the array of habitats necessary for freshwater spawning and rearing.

Dynamic stream conditions include disturbance, climate and physical habitat, and mean that different sets of habitats or entirely different subbasins may be most hospitable for juvenile coho salmon over time (Reeves et al. 1995, Quinn and Peterson 1996). I suspect a difference in a large scale environmental condition that may have made subbasins with a large distance between seasonal habitats a greater impediment to juvenile survival in 2002 compared to 2001. One possible difference could be related to streamflow during emergence. Stream flow levels have been shown to effect juvenile abundance in other stream fishes (Schlosser 1985). For salmonids, higher flow could possibly scour redds (Montgomery et al. 1999) reducing survival to emergence. Also, high streamflow could impair movement of juvenile coho that are less adapted to high velocity environments than other salmonids (Bisson et al. 1988). Therefore, moving from spawning beds to summer rearing pools could be more difficult under high flow conditions in subbasins in which the proximity between seasonal habitats is great. Unfortunately, precipitation and streamflow measures which would be necessary to test this hypothesis were not available for individual subbasins. Another, simpler reason for the differences in juvenile numbers between 2001 and 2002 could be that lower numbers of spawning adults returned to some of the subbasins thereby creating fewer progeny to be counted in the following summer. Unfortunately, detailed spawner estimates at the subbasin scale that track spawner occupancy patterns are not available. Further research that tracks adult spawner counts, streamflow, and precipitation at a subbasin scale is necessary to fully understand the implications of habitat topology and stream conditions on juvenile coho salmon density and survival.

Objective Two: Patch Scale

Salmonids, like other species, are not randomly distributed across the landscape (Dunham et al. 2002). Coho salmon are no exception and individuals are found in patches that may correspond with behavior, intra and interspecies interactions, predation or habitat. Habitat is often associated with environmental gradients such as elevation or a hierarchy of nested organization such as stream order. Understanding how and why individuals are distributed on the landscape may contribute to ecological knowledge about habitat preferences and survival thresholds across spatial scales (Peters et al. 2006). The size of the area within which measures of juvenile coho salmon are correlated might help explain the spatial structure of the stream network as it is interpreted by juvenile fish. This structure in turn may inform interpretations of population dynamics at multiple spatial scales.

The spatial extent of autocorrelation within the stream network was measured using variograms of juvenile coho salmon density, controlling for spatial network position. Results indicate that there are differences in estimated variogram range, or patch size, among years both within and across subbasins. It also appears that subbasin area may be related to patch size. While it is intuitive that smaller subbasins might have smaller clusters of juvenile coho salmon, such an observation has not been quantified before. Small subbasins tended to have smaller patch sizes than larger subbasins, and larger subbasins exhibited symptoms of nesting. Patch size could represent the neighborhood of habitats accessible to a group of interacting juvenile coho salmon. Therefore, patches may correspond to the predominant range of movement for juvenile coho salmon between available habitats in a particular stream system. The similarity and variation in patch sizes identified in this study may support the definition of a patch as a grouping of juvenile coho salmon around available habitats within the stream network.

In site-scale analysis, the topology or orientation of habitats appeared to be an important distinction among subbasins when exploring changes in juvenile density. It would be reasonable to assume that more habitats are available in a larger stream network and that juveniles may move further among habitats in larger systems. This could correspond to larger range sizes in bigger subbasins, as was found in this study. However, other research indicates that juvenile coho salmon tend to access locally available habitats within their natal stream systems. Bell et al. (2001) showed that juvenile coho salmon exhibit high site fidelity in off-channel habitat during winter floods. Also, Lonzarich et al. (2000) found that in pool- riffle habitat sequences, fish will move out of pools adjacent to short riffles more than from pools adjacent to long riffles. Therefore, the hierarchical organization and larger patch sizes in larger subbasins could correspond to overlapping patches of juvenile coho salmon rather than a cohesive group of fish and habitats. Further exploration of patch size and area is necessary to more fully describe and identify the ecological significance of variogram range sizes.

I speculated that basin shape could influence the pattern of juvenile coho occupancy reflected by patch size. Basin shape was explored by clustering watersheds based on the average gradient of low-order streams to identify two distinct groups. The shape of the watersheds with low gradient headwaters appeared to be rounder (branched) than the shape of watersheds with higher-gradient headwaters (linear).

However, the patch sizes of juvenile coho that were identified using variograms were not different between the two shape groupings. It is possible that this dataset did not contain enough variation in geology or geomorphology to detect differences in juvenile coho salmon patch size between basin shape clusters. Unpublished research conducted by Christian Torgersen (2006 personal communication, USGS, Seattle, Washington) links patch sizes of coastal cutthroat trout (*O. clarki clarki*) with underlying geology across a large region. Further research across a larger regional frame incorporating different underlying geologic structure is necessary to more fully explore the question of watershed shape and patch sizes of juvenile coho salmon.

What can be deduced from the results of the patch analysis is that juvenile coho salmon patch sizes change across years, and variogram shapes suggest that larger watersheds include multiple scales of patchiness in juvenile coho salmon abundance. Such differences in spatial arrangement between small and large watersheds imply the need for different management expectations based on watershed size. While larger watersheds may indeed produce more fish, the nested structure of spatial autocorrelation could mean that the relationship between watershed size and fish numbers is not linear. This implies that comparisons of patch and fish population sizes should be done among basins of similar size.

Objective Three: Subbasin Scale

The convergence of life history stages in patterns of juvenile occupancy informs an interpretation of population processes at the subbasin scale. The number of stream kilometers occupied by juvenile coho salmon at the subbasin scale increased in

7 of 11 subbasins between 1998 (or 1999) to 2002. This parallels the trend of increasing mid-coast spawning adult runs during these years. However, some subbasins did not show steadily increasing numbers of stream kilometers occupied as the spawning run size increased. Because accurate counts of spawning run sizes and distributions at the subbasin scale are unavailable, I cannot discern whether some subbasins simply had spawning run sizes that did not match the overall mid-coast trend. Therefore, greater variability in run sizes that the subbasin scale could correspond with the lower numbers of kilometers occupied by juveniles that were observed in other basins. What is discernable at the subbasin scale is that there is greater variation within and among subbasins over time in the amount of stream kilometers occupied by juvenile coho salmon than is found in the overall size of the adult spawning run. Increasing variation coupled with smaller spatial extents has been established in other studies (i.e., Wimberly et al. 2000). Further research that includes the collection of accurate estimates of precipitation, adult spawning run size, and streamflow at the subbasin scale would allow for greater discernment of the interrelationship between life stages that may be interpreted from patterns of stream network occupancy by juveniles.

Maps of individual subbasins showed that when stream network occupancy was high, juvenile coho were found upstream in the headwaters, while in years of low stream network occupancy juvenile coho salmon were only lower in the subbasin. In seven of the eleven subbasins assessed, occupancy by juvenile coho salmon seemed to increase and decrease in relation with adult spawner run sizes in the entire mid-coast over the 5 years of this study. It appears then, that in these subbasins, it is possible that more spawning adults resulted in a greater portion of the stream network occupied by juvenile coho salmon. This connection may be useful for assessments of juvenile occupancy patterns.

How juvenile coho salmon come to occupy locations low or high in the stream network is an important question. If the pattern of juvenile occupancy reflects the spawning location of their parents, then I can interpret the coupling of adult spawner abundance and juvenile coho stream network occupancy to suggest that more spawners use more stream kilometers for spawning, hence, more stream kilometers are occupied by juvenile coho salmon. If this is the case, then when adult runs are low, spawning occurs successfully in lower stream reaches, as reflected by lower juvenile network occupancy. It is also interesting to note that higher numbers of stream kilometers occupied by juveniles does not appear to be connected to higher precipitation during the parental spawning run. If the location of spawning adults helps define the upper distribution of juvenile coho salmon, then this observation could mean that adults are not necessarily moving high in the stream network with high water during the spawning run, but are responding to something else. Isaak and Thurow (2006) found that in years of low abundance, Chinook salmon (*O. tshawytscha*) spawned in specific core locations, expanding into other areas as their abundance increased. I speculate that in years of low abundance, adults did not return to their natal stream beds further up the network in order to spawn. Perhaps access to available spawning partners that could be found lower in the stream network was a more important consideration for spawning adults than migration further upstream.

Synthesis Among Scales

Salmonid population ecology identifies a wide variety of behavioral mechanisms of both adults and juveniles that help the fish cope with dynamic environmental conditions (Reeves et al. 1995). Some needs for survival of coho salmon, such as spawning gravels, summer pools and winter habitat have few substitutes. However, individuals may modify their behavior to take advantage of current stream and environmental conditions. Isaak and Thurow (2006) used continuous replicate surveys of stream networks over 9 years to describe patterns in Chinook salmon redd distributions in Idaho. They determined that core spawning areas were important in years of low and high adult abundance, but maintaining additional spawning areas in the network was important in years of varying environmental conditions. Location in the stream network becomes a critical contextual consideration for the successful fulfillment of specific life history needs.

In this study, physical evidence of coho salmon behavioral diversity and responsiveness to current population and environmental conditions was found in the form of network habitat topology and juvenile occupancy patterns across multiple subbasins. Schlosser (1995) identified the importance of large scale landscape conditions and the presence of refugia as potentially important considerations of fish population dynamics. These two considerations appeared relevant in this study when all three spatial scales are considered. Site scale differences in juvenile density among subbasins were connected with the juxtaposition of necessary seasonal habitats and network variables were found to be important in modeling juvenile density. Patch sizes of juveniles varied with subbasin and year, with potential nesting of juvenile clusters in larger subbasins. This makes network connectivity and subbasin size important contextual considerations for juvenile subpopulations as individuals seek necessary seasonal habitats. Further, subbasin occupancy patterns of juvenile coho salmon support the idea that the location of habitats is not an obligate consideration for spawning adults. Rather, adults may take advantage of habitats with reference to the annual conditions in which they find themselves.

An analysis of many subbasins with several spatial scales highlights complexities in juvenile coho salmon density and occupancy. The observed diversity of site scale instream habitat topology and occupancy at the subbasin scale may be important in considering the survival and adaptability of coho salmon populations. Large scale variability has been shown to influence the capacity of streams to produce brook trout (Kocovsky and Carline 2006). The site scale observation that several subbasins had either decreasing or increasing juvenile density between 2001 and 2002 is made more interesting when the observation at the subbasin scale of an almost universal increase in stream kilometers occupied between these two years is noted. If stream occupancy is associated with spawning run size, then it may be possible that the site scale observation of decreased density may indeed be related to differential survival of juveniles. In this case, the identification of juxtaposition variables as important in differentiating between subbasins with increasing or decreasing coho density shows the influence of habitat topology on survival even in a region of similar topography.

Conclusions

There is more to an assessment of habitat than simple calculations of habitat area and amount. The spatial arrangement of habitats throughout the year and the accessibility of habitats appear to be important in describing distribution and abundance of juvenile coho salmon. In particular, considering the spatial arrangement of habitats and patches of juvenile coho salmon provided a spatial context for the interpretation of multiple spatial scales that represent different population and environmental processes. Juvenile patterns of network occupancy appear to depend on site-specific habitat, the proximity of necessary seasonal habitats, adult dispersal through the spawning grounds and spawning run size. All of these factors work together to create the patterns of occupancy that are observed in the stream network. Ecological analysis that incorporates multiple spatial scales and processes may inform management actions that are intended to preserve or restore populations of coho salmon. Management actions that consider the interrelationships between life history stages, habitats, and movement within the stream network may be more effective at maintaining the complex habitat configurations necessary for the persistence of populations of coho salmon.

The varied response of juvenile coho salmon to the complexity and diversity of stream habitats was mirrored in patterns of occupancy and density across spatial scales. The stream network became an important lens through which to view juvenile density and provided connectivity of interpretation across scales. Site-scale analysis that identified the importance of juxtaposition variables informed the interpretation of possible definitions of patch sizes at the subbasin scale. Complex subbasin patterns of juvenile coho salmon occupancy were shown to vary within and among subbasins over time and suggested the importance of the size of the adult spawning run.

Integrating the context of the stream network into analysis at multiple spatial scales included an important dimension of the environment in which coho salmon evolved, and juvenile fish must survive. The riverscape in which coho salmon must endure includes a diversity of habitats with varied productivity and connectivity among years and environmental conditions. Ultimately, the persistence of coho salmon depends on access to multiple, diverse and connected habitat. Salmon evolved the ability to embrace the diversity of habitats and environmental conditions that naturally occur in the Pacific Northwest. This adaptability is how they have coped with the frequent disturbances and the inconsistent spawning and rearing conditions that are present around the Pacific Rim.

Management strategies that fail to consider the environmental context of the stream network ignore a critical element of the riverscape for coho salmon. Depending on small areas with historically high runs and juvenile survival is not an adequate management strategy. Rather, management strategies that consider the spatial distribution of habitats and the variety of habitat topologies in different subbasins will be better suited to the complex environmental conditions in which coho salmon evolved and continue to persist.

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Appendices

Appendix 3.1: ODFW Aquatic Inventory and Analysis Project: Habitat Benchmarks.

POOLS	UNDESIRABLE	DESIRABLE
POOL AREA (% Total Stream Area)	<10	>35
POOL FREQUENCY (Channel Widths Between Pools)	>20	5-8
RESIDUAL POOL DEPTH (m)		
SMALL STREAMS (<7m width)	<0.2	>0.5
MEDIUM STREAMS (≥ 7m and < 15m width)		
LOW GRADIENT (slope <3%)	<0.3	>0.6
HIGH GRADIENT (slope >3%)	<0.5	>1.0
LARGE STREAMS (≥15m width)	<0.8	>1.5
COMPLEX POOLS (Pools w/ LWD pieces ≥3) / km	<1.0	>2.5
RIFFLES		
WIDTH / DEPTH RATIO (Active Channel Based)		
EAST SIDE	>30	<10
WEST SIDE	>30	<15
GRAVEL (% AREA)	<15	≥35
SILT-SAND-ORGANICS (% AREA)		
VOLCANIC PARENT MATERIAL	>15	<8
SEDIMENTARY PARENT MATERIAL	>20	<10
CHANNEL GRADIENT <1.5%	>25	<12
SHADE (Reach Average, Percent)		
STREAM WIDTH <12 meters		
WEST SIDE	<60	>70
NORTHEAST	<50	>60
CENTRAL - SOUTHEAST	<40	>50
STREAM WIDTH >12 meters		
WEST SIDE	<50	>60
NORTHEAST	<40	>50
CENTRAL - SOUTHEAST	<30	>40
LARGE WOODY DEBRIS* (15cm x 3m minimum piece size)		
PIECES / 100 m STREAM LENGTH	<10	>20
VOLUME / 100 m STREAM LENGTH	<20	>30
"KEY" PIECES (>60cm dia. & ≥10m long)/100m	<1	>3
RIPARIAN CONIFERS (30m FROM BOTH SIDES CHANNEL)		
NUMBER >20in dbh/ 1000ft STREAM LENGTH	<150	>300
NUMBER >35in dbh/ 1000ft STREAM LENGTH	<75	>200

*Values for Streams in Forested Basins

Citation:

Foster, S.C., C.H. Stein and K.K. Jones. 2001. *A guide to interpreting stream survey reports*. Edited by P.A. Bowers. Oregon Department of Fish and Wildlife, Information Reports 2001-06, Portland.

Appendix 3.2. Variograms for Small Basins in Oregon’s Mid-Coast Region in Each Year Available Between 1998 and 2002 (Figure Series 3.2.1-3.2.5.)

Figure 3.2.1. Canal Creek Variograms from 1998, 2001 and 2002.

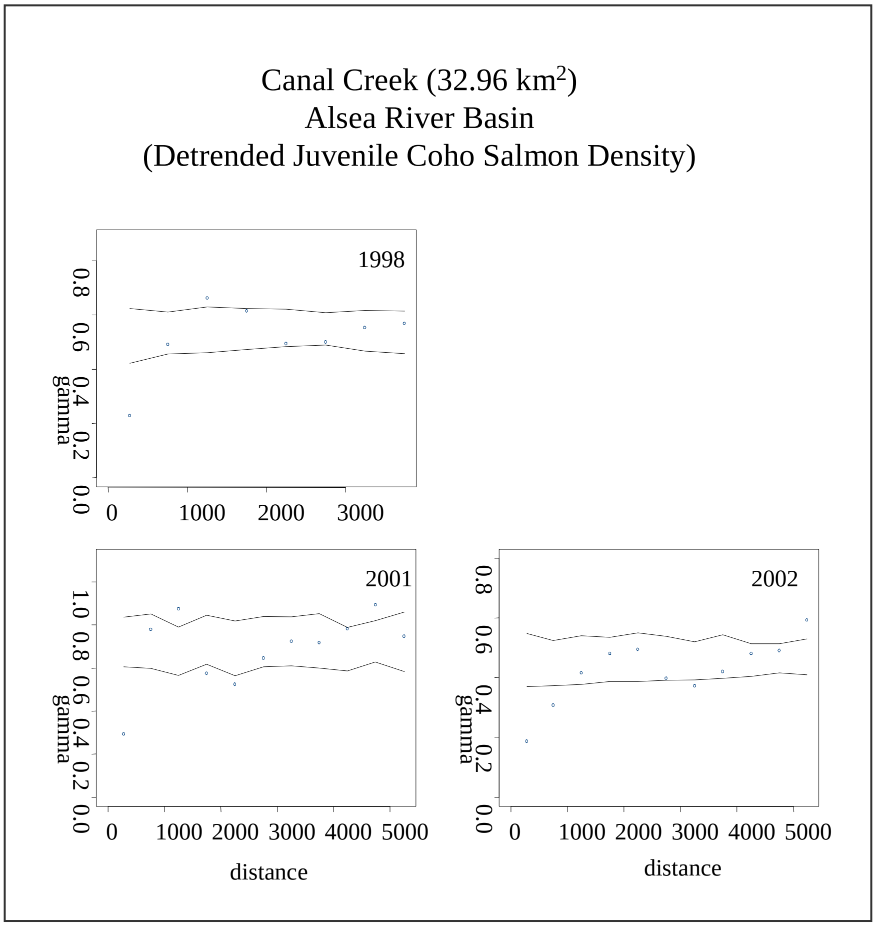


Figure 3.2.2. Cedar Creek Variograms from 1999, 2001 and 2002.

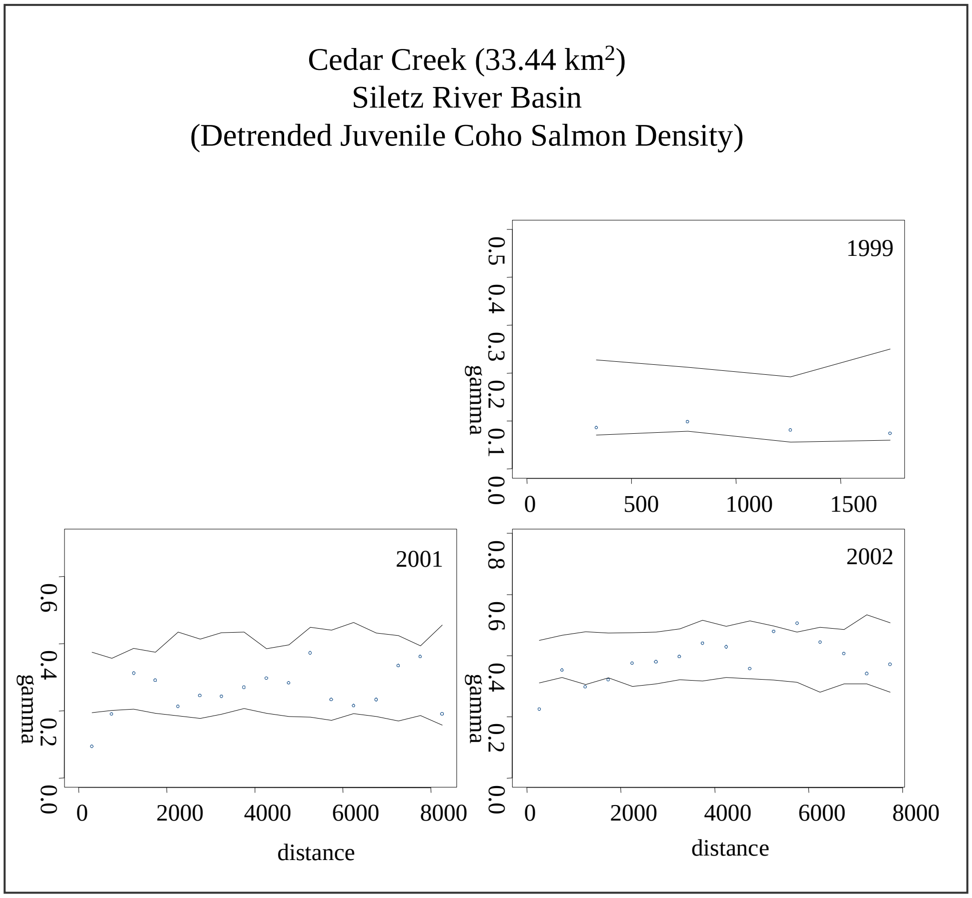
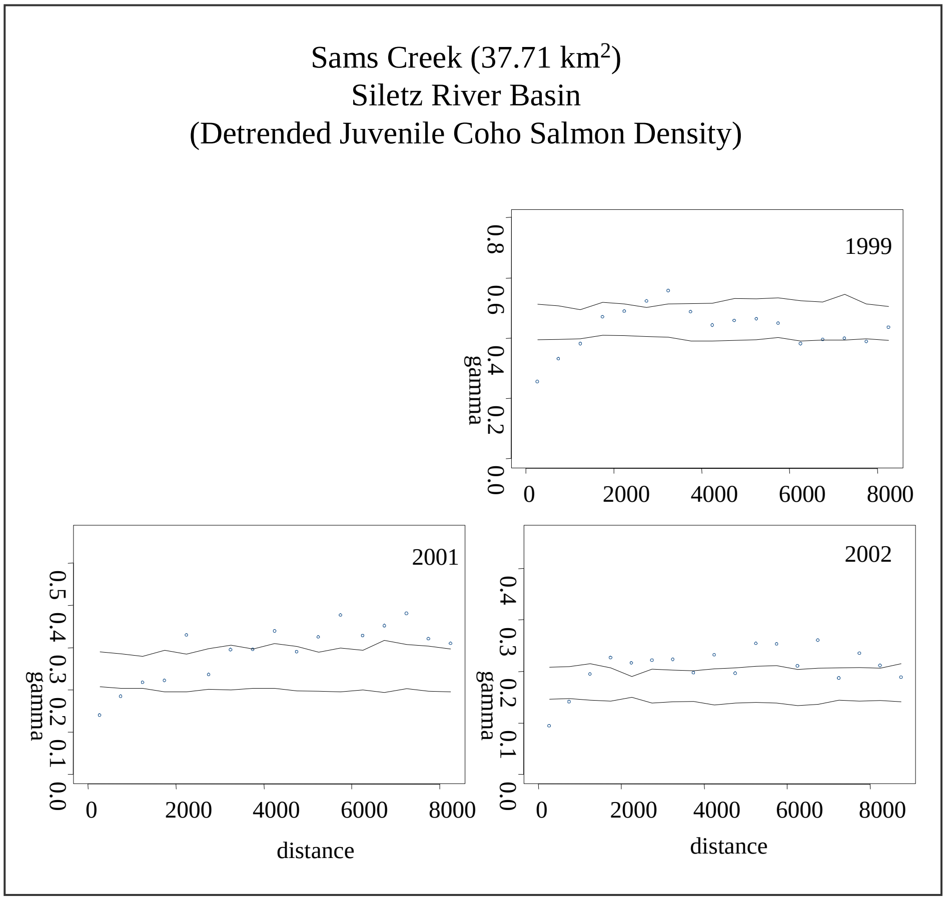


Figure 3.2.3. Sams Creek Variograms from 1999, 2001 and 2002.



Sams Creek (37.71 km^2)
Siletz River Basin
(Detrended Juvenile Coho Salmon Density)

Figure 3.2.4. Fall Creek Variograms from 1998, 2001 and 2002.

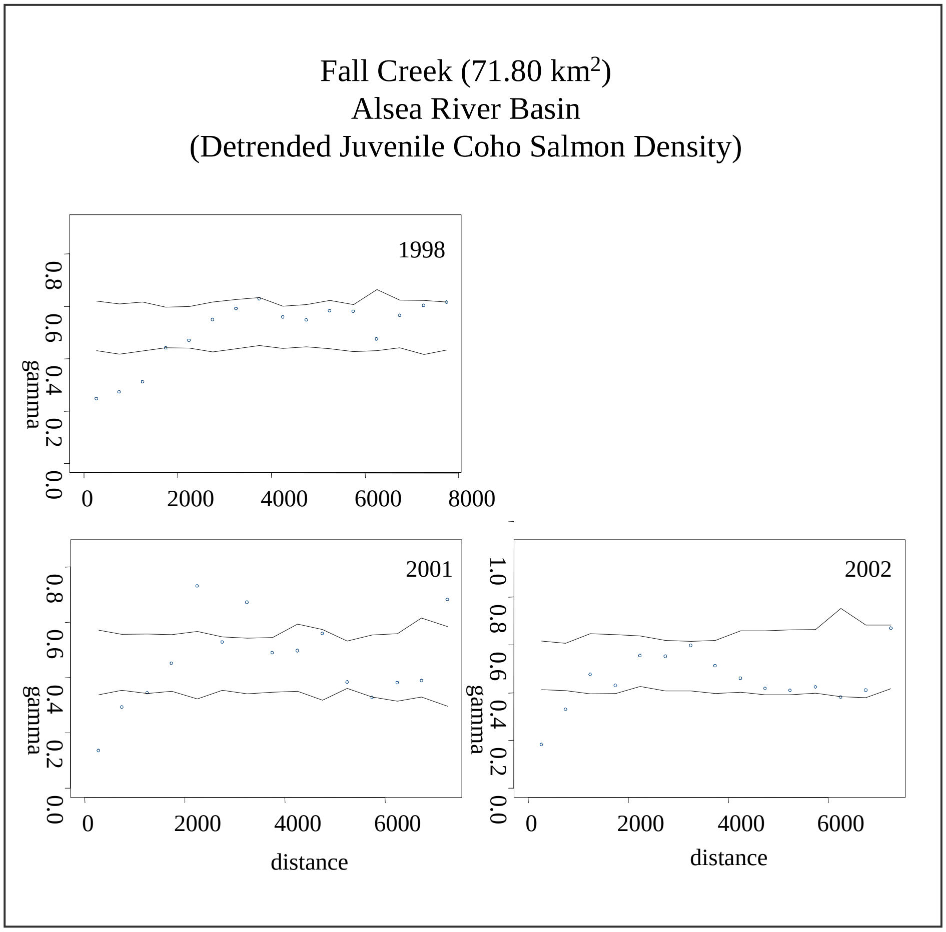
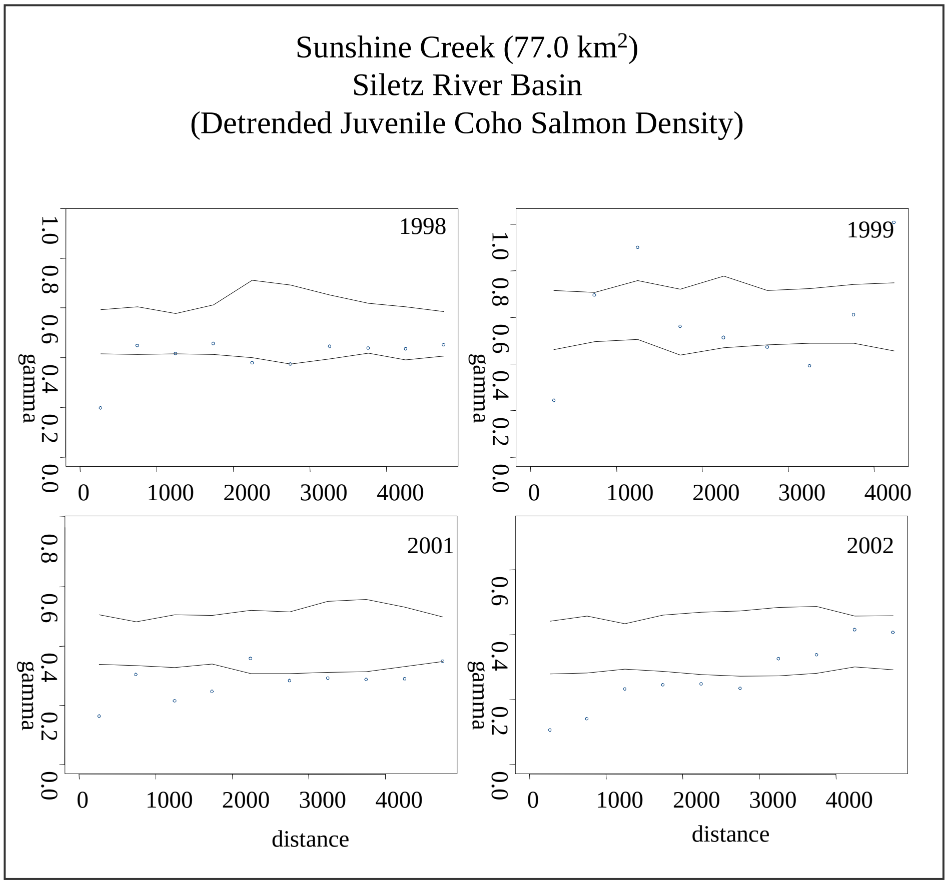
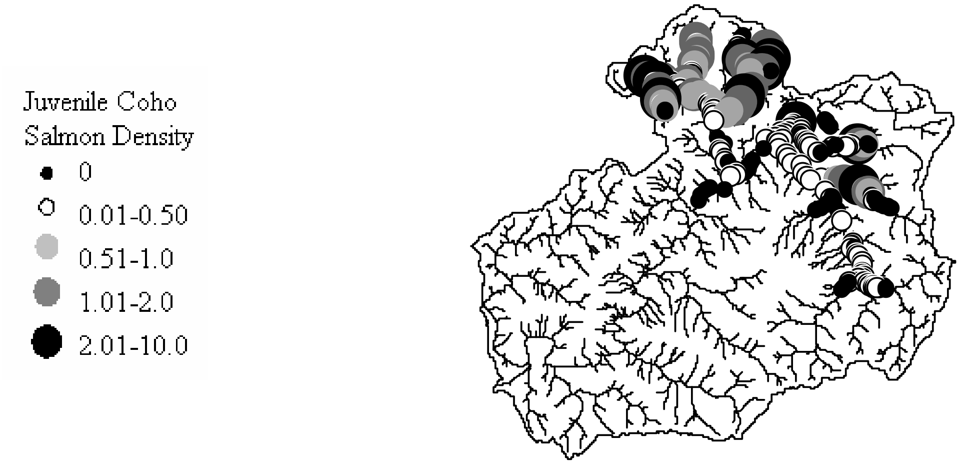


Figure 3.2.5. Sunshine Creek Variograms from 1998, 1999, 2001 and 2002.



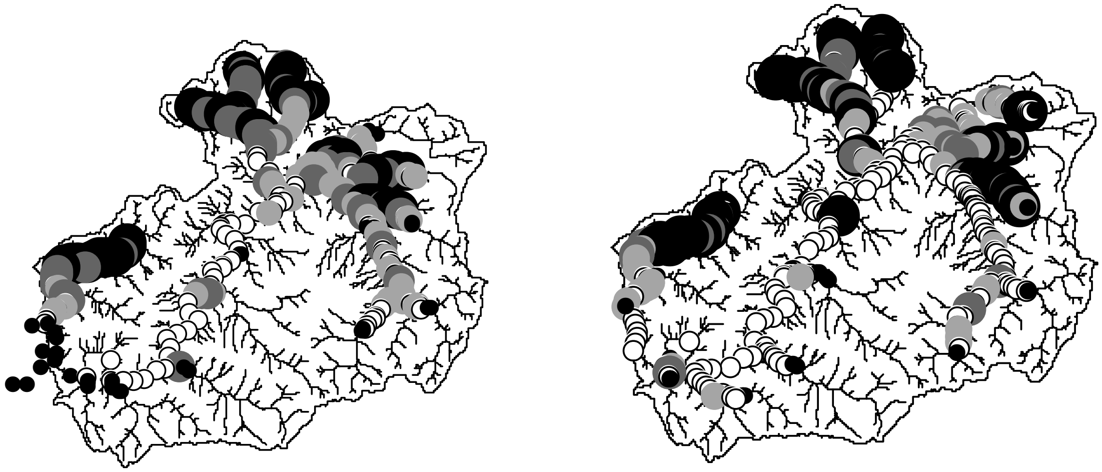
Appendix 3.3. Maps (1b-10d) of juvenile coho salmon density in eleven basins of Oregon's Mid-Coast in selected years from 1998 through 2002.

1b. Drift Creek 1999

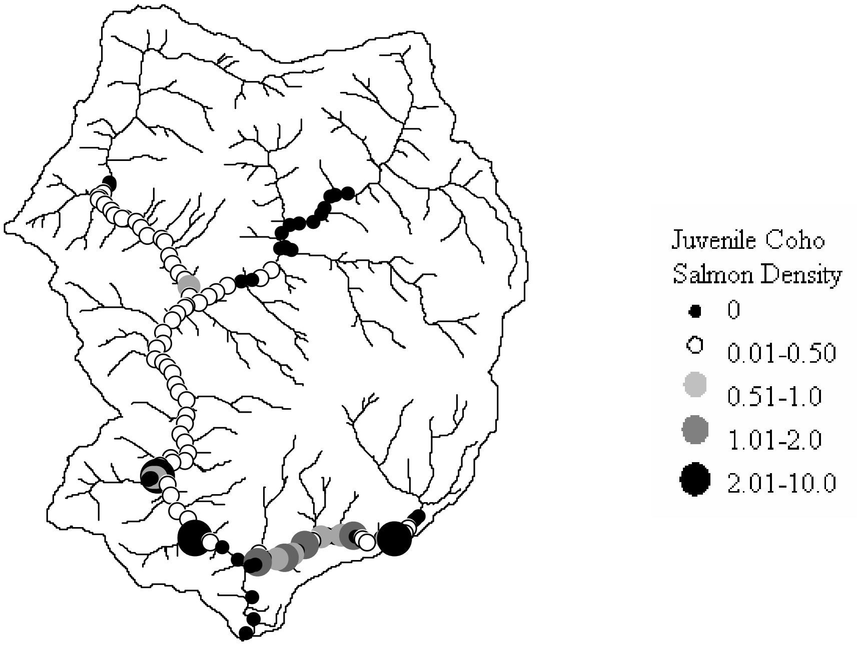


1c. Drift Creek 2001

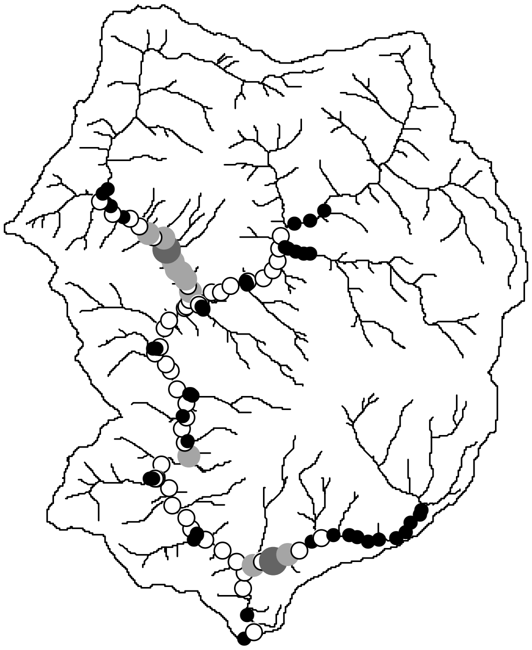
1d. Drift Creek 2002



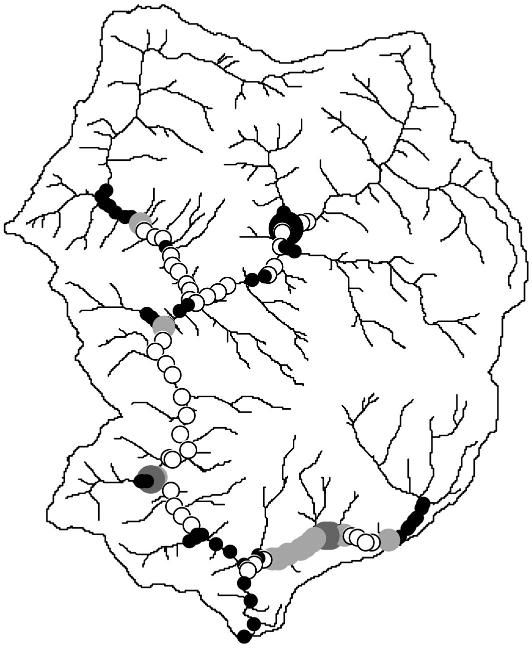
2a. Fall Creek 1998



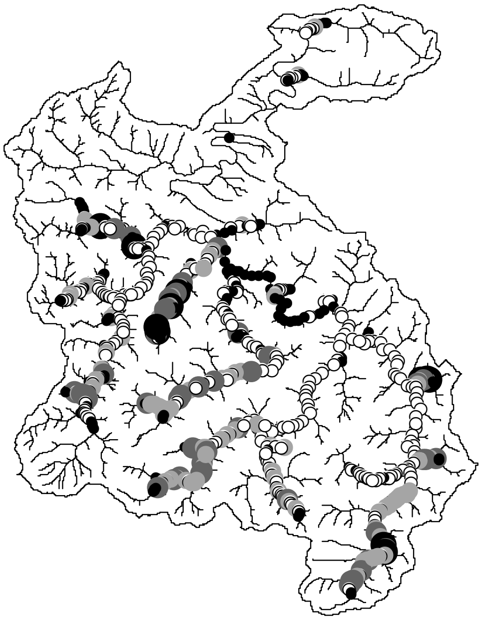
2c. Fall Creek 2001



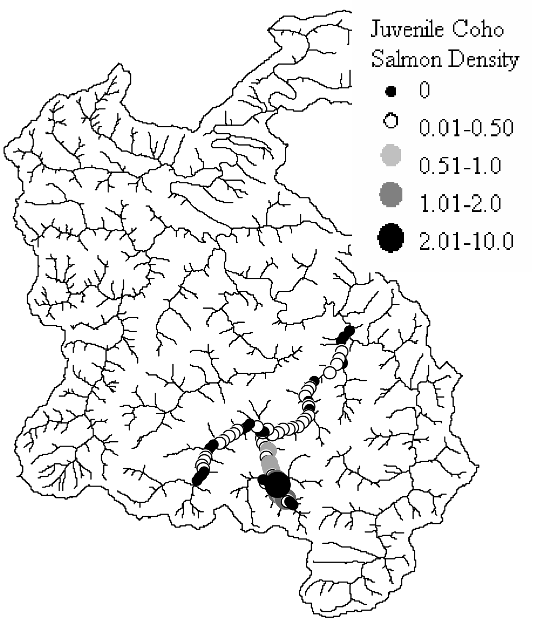
2d. Fall Creek 2002



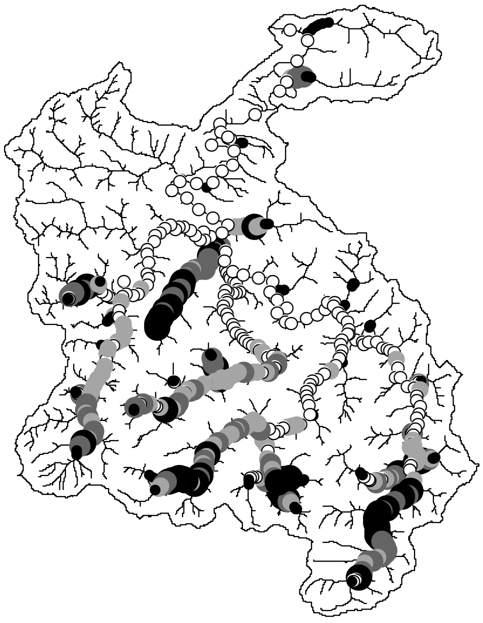
3a. Five Rivers 1998



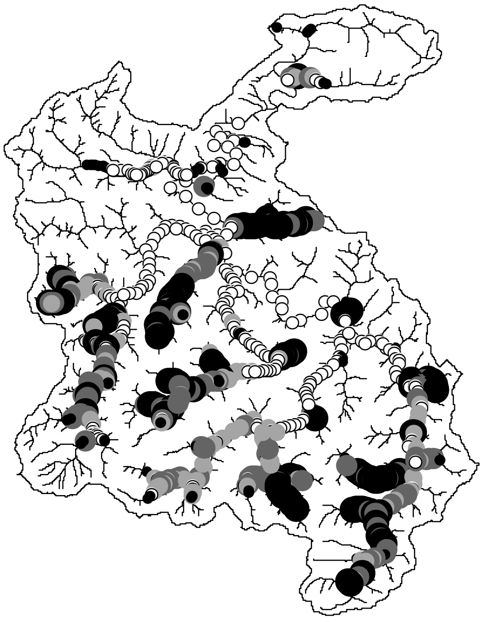
3b. Five Rivers 1999



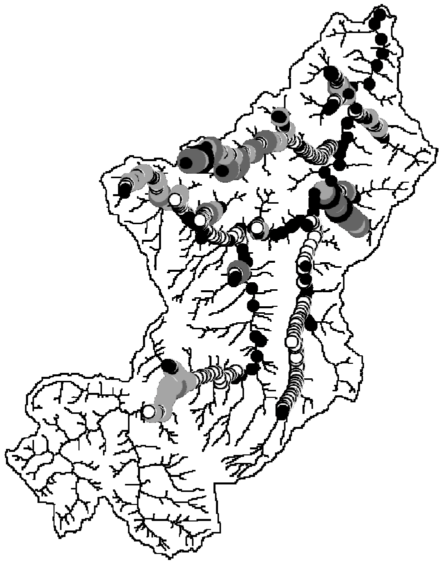
3c. Five Rivers 2001



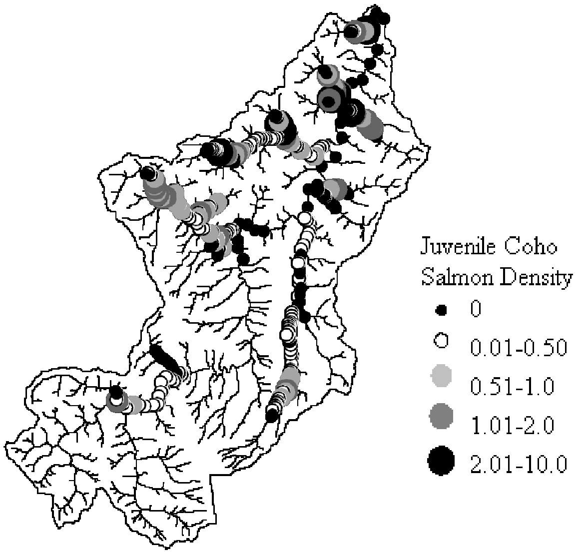
3d. Five Rivers 2002



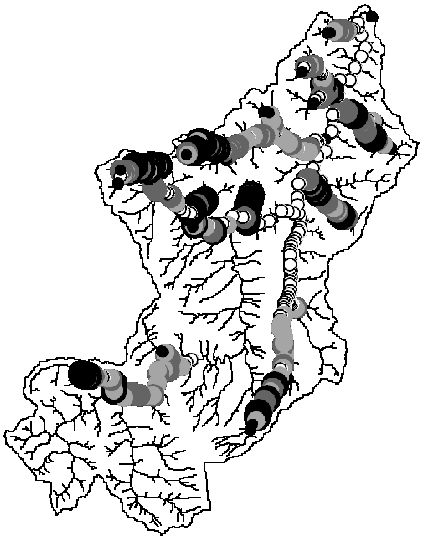
4a. Lobster Creek 1998



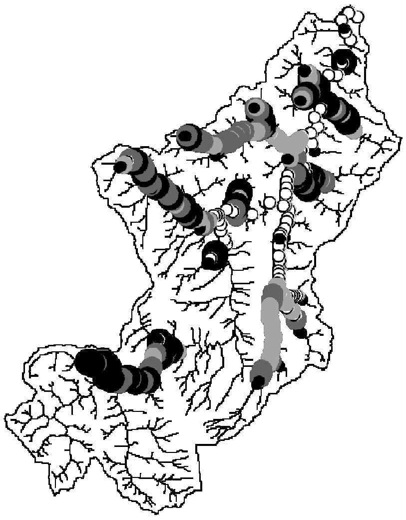
4b. Lobster Creek 1999



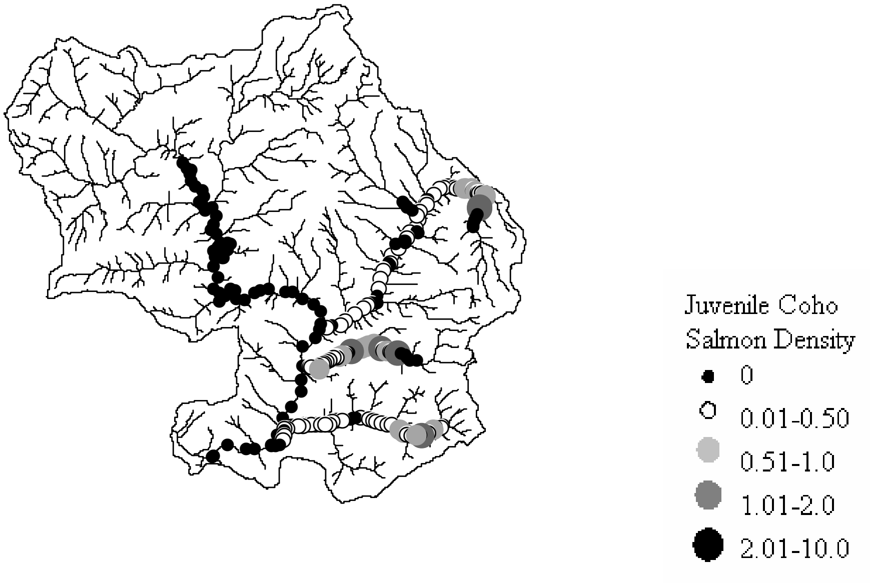
4c. Lobster Creek 2001



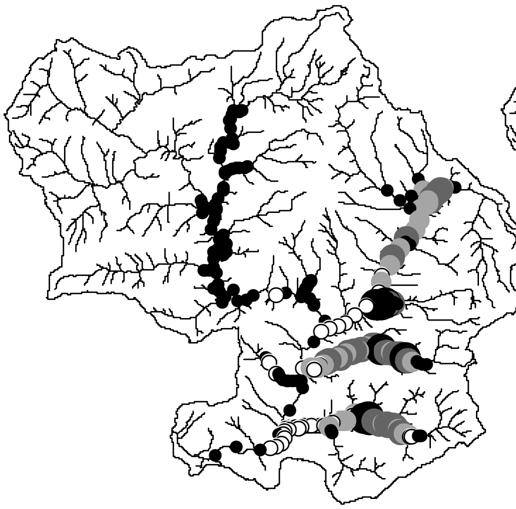
4d. Lobster Creek 2002



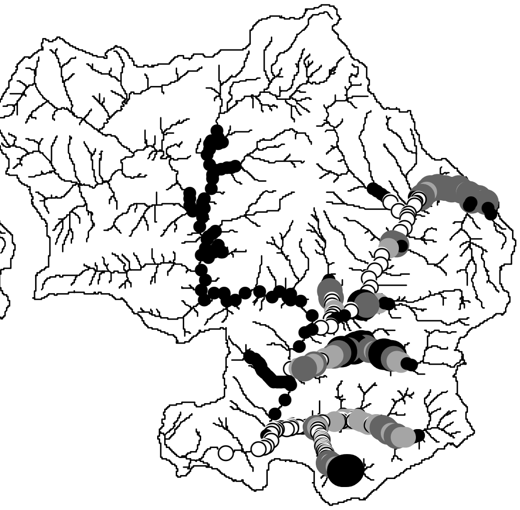
5a. North Fork Alsea 1998



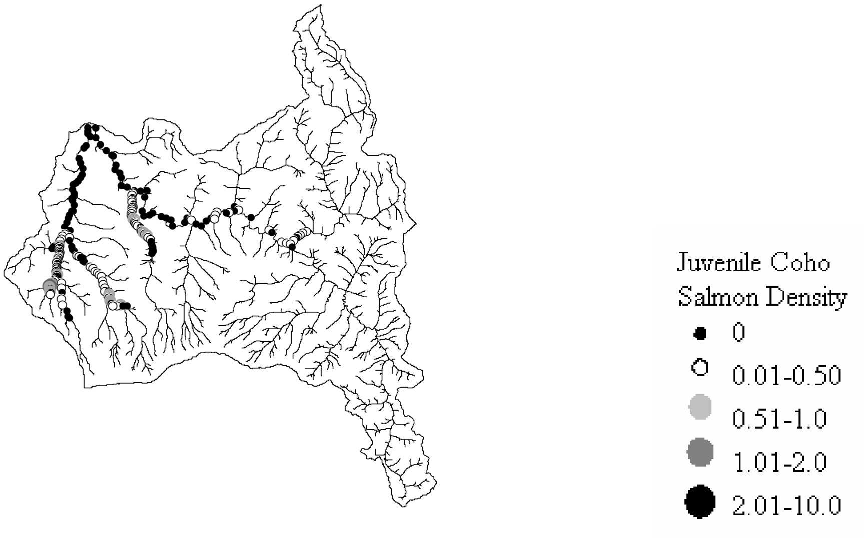
5c. North Fork Alsea 2001



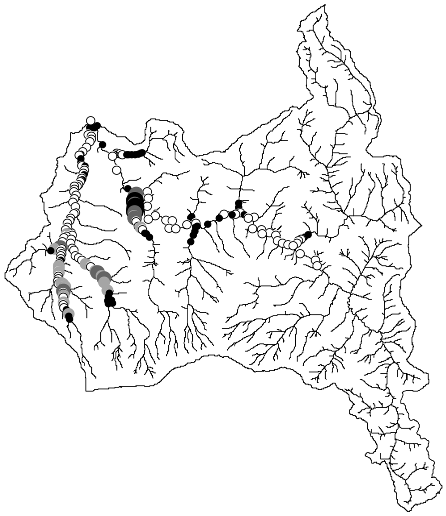
5d. North Fork Alsea 2002



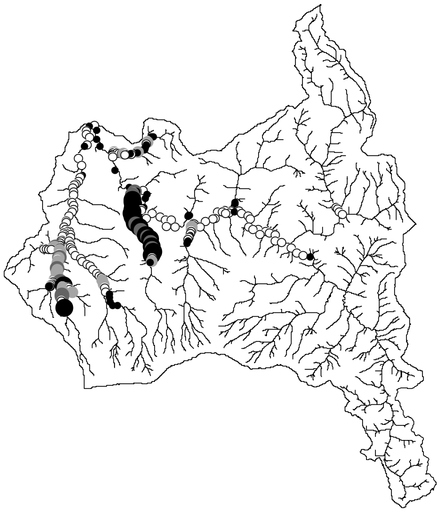
6a. South Fork Alsea 1998

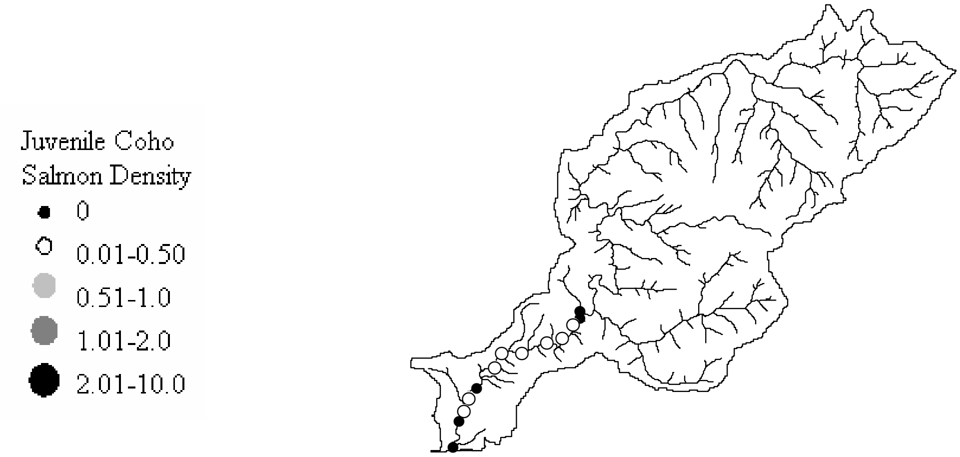


6c. South Fork Alsea 2001

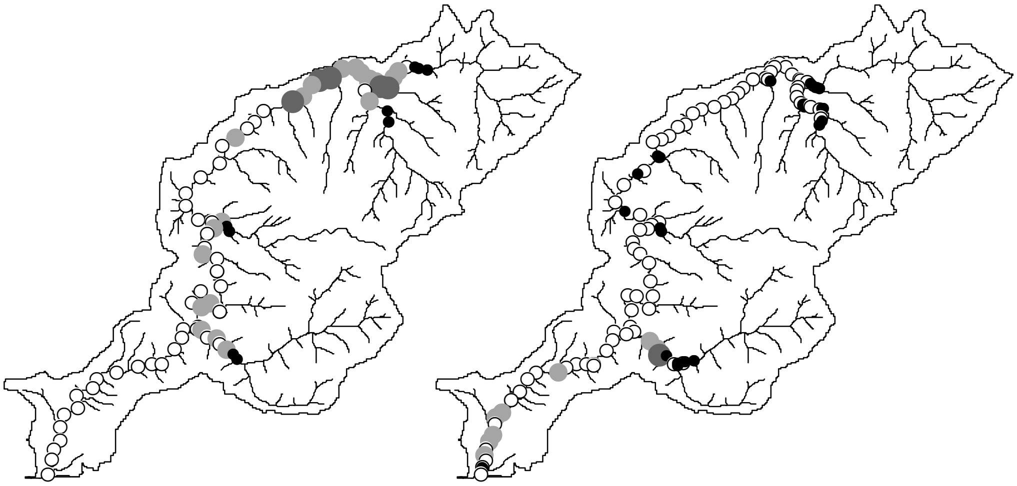


6d. South Fork Alsea 2002





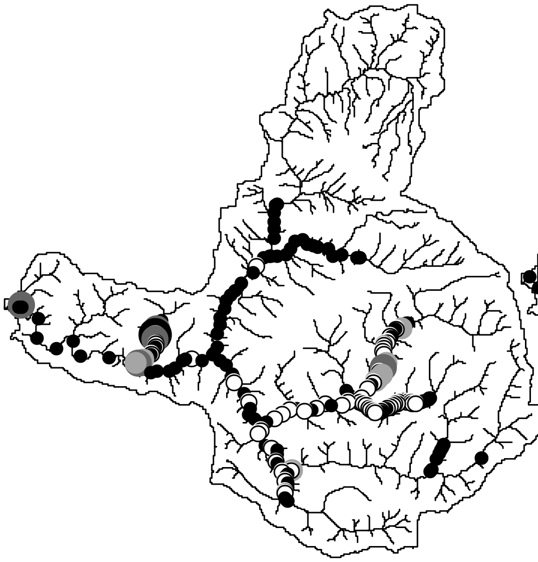
7b. Cedar Creek 1999



7c. Cedar Creek 2001

7d. Cedar Creek 2002

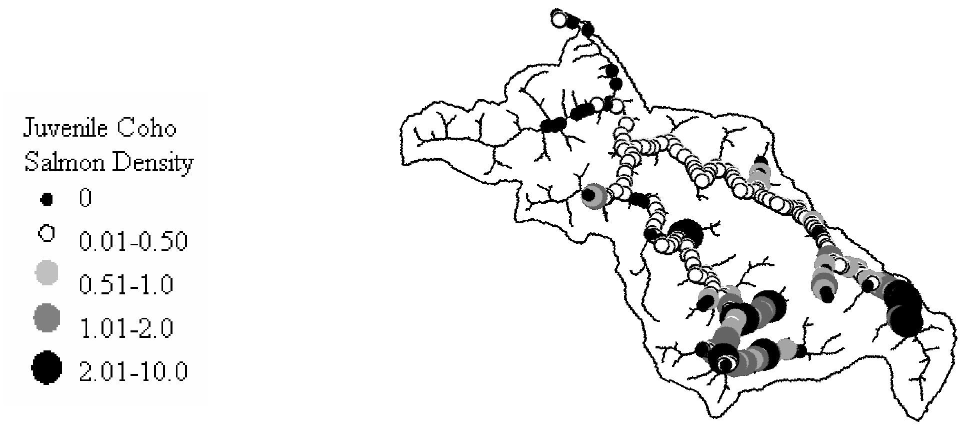
8b. Rock Creek 1998

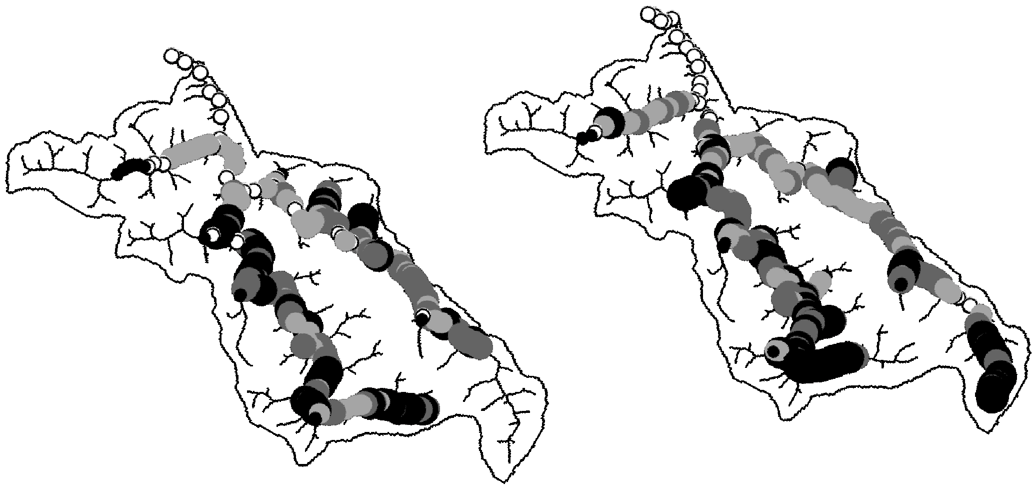


8b. Rock Creek 1999

8c. Rock Creek 2001

9b. Sams Creek 1999





9c. Sams Creek 2001

9d. Sams Creek 2002

Chapter 4

Multiple Spatial Scales in an Analysis of Two Life History Stages of Coho Salmon (*Oncorhynchus kisutch*): A Hierarchical Bayesian Approach

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Corvallis, Oregon, USA 97331-3803

Abstract

Life history diversity over broad spatial extents characterizes populations of anadromous salmonids in the Pacific Northwest. The life history of coho salmon, *Oncorhynchus kisutch*, is a complex example of adaptation in response to diverse habitats in a dynamic environment. It is possible that ecological processes acting at different spatial scales influence the abundance and distribution of coho salmon. Adult distribution reflects dispersal patterns adapted to maintain salmonid populations as large scale disturbances render entire basins suitable or unsuitable over time. Meanwhile, juvenile distribution reflects adaptation to local conditions as individuals seek habitats for a year of freshwater occupancy. The usefulness of incorporating multiple spatial scales in models of abundance for each life history stage was explored in this study. Hierarchical modeling of two spatial scales for each life history stage was completed using Bayesian methods. Results indicated that adult coho salmon abundance could be explained using two-level hierarchical models that incorporated the subbasin variable, percent large trees in a 100-m riparian buffer, modeled with the basin scale variable, mean annual precipitation. This contrasts with juvenile distributions that were adequately represented by a two-level hierarchical model that included three site scale variables, percent sand, stream order, and network distance to spawning habitat, hierarchically linked to non-specific subbasin scale variation. This suggests that effective recovery strategies for endangered salmonids may require targeting habitat features at different spatial scales that are relevant to individual life history stages.

Introduction

The spatial scale at which scientists analyze the ecological world greatly influences a studys' result (Wiens 1989) which means that choosing the proper spatial scale for analysis is important and may be challenging. Small spatial scales are readily accessible to researchers (Matthews and Marsh-Matthews 2003) even when the species under investigation may also be described at large spatial scales. Unfortunately, small spatial scales may not capture the diversity of environmental conditions under which individual species evolved (Pacific Fisheries Resource Conservation Council 1999). Also, the same ecological process may manifest differently across spatial scales (Wiens 1989). Therefore, studies that examine small scales may not accurately address questions of species needs or ecological processes that are important for larger scale management or restoration efforts.

It may also be important to incorporate multiple spatial scales in order to explore potential synergisms between scales when addressing ecological phenomena (Lowe et al. 2006). Because ecological processes do not work in isolation, there may be interaction among processes, thereby introducing interactions across scales. Multiple scales included in an analysis may better represent interactions between geomorphic and ecological processes. Poff and Huryn (1998) found that multiple scales of processes interact in the determination of freshwater production of Atlantic salmon (*Salmo salar*). They concluded that a multi-scale perspective was informative in determining conservation, restoration and management actions. Such a multi-scale perspective could be useful in approaching analysis of other wide ranging anadromous fish.

Some aquatic ecologists are beginning to recognize the importance of analysis that encompasses entire stream systems (Fausch et al. 2002). For example, Torgersen et al. (2004) used continuous surveys of coastal cutthroat trout (*O. clarki clarki*) to describe differences in patterns of juvenile occupancy with underlying geomorphic conditions. They found that analysis of continuous survey data could be used to precisely correlate patterns of juvenile occupancy at three spatial scales that corresponded with local stream conditions and the network structure of tributaries in the stream system. It is possible that analysis encompassing spatial scales ranging from individual sites to regions may contribute important information regarding abundance, distribution, and life history needs that is necessary to understand the adaptation and survival of anadromous fish species.

Anadromous fish species exemplify a life strategy that encompasses multiple spatial scales and extents at different life stages (Armstrong 2005, Bradford et al. 1997, Myers et al. 1997). For example, Pacific salmon (*Oncorhynchus spp.*) may migrate thousands of miles in the ocean. The majority of mature individuals in a population return to their natal freshwater streams to spawn, while some may stray into neighboring streams or entirely different basins or regions (Cooper and Mangel 1999, Labelle 1992). Therefore, the spatial extent for adult anadromous salmon movement includes potentially extensive tracts of ocean as well as freshwater areas. The diversity of adult behavior that involves homing or straying allows for the distribution of genetic material and opportunities to explore and recolonize habitat over large areas and ultimately contributes to population persistence (Cooper and Mangel 1999).

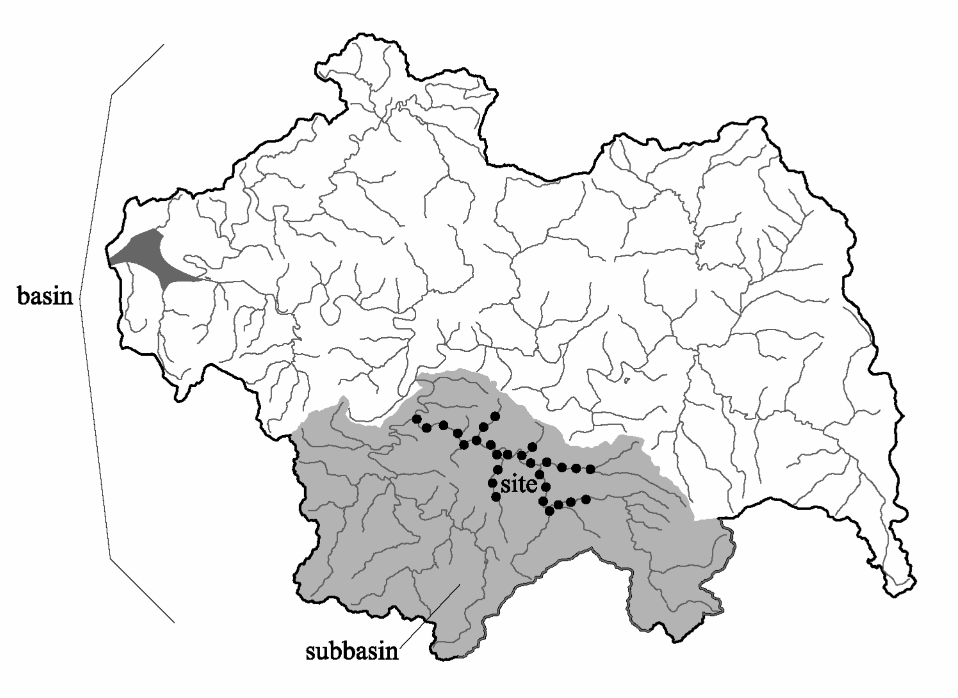
Depending on the species, juvenile anadromous salmonids may use the stream system for up to two years before migrating to the ocean to mature. For juveniles that overwinter in streams, the spatial extent occupied in the stream network by the juvenile life stage is comparable to that of adults. However, unlike adults, juveniles do not migrate between basins through the ocean as spawning adults may do when they home or stray. Therefore, the spatial extent of movement of juveniles is smaller than that of adults, with juveniles restricted by mobility and life history needs to the basin of their birth. Within their natal stream system, juveniles display a variety of movement behaviors with some moving only small distances while others move among tributaries (Murray and Rosenau 1989, Quinn 2005). Variety of movement behaviors allows different individuals to take advantage of the habitats of the stream environment (Nielsen 1992).

In this study I explore spatial scale, stream network variables, instream habitat conditions and regional habitat variation in assessing the abundance of adult and juvenile coho salmon (*O. kisutch*) in western Oregon. Coho salmon are a natural choice for an investigation of the relationship between spatial scales and life history stage because of the extensive research on freshwater habitat preferences for adult and juvenile fishes. In addition, monitoring efforts have made available data documenting entire populations of coho salmon at juvenile and adult life stages. In the course of their lives, coho salmon may migrate thousands of miles from their birth streams to the ocean and back again. The spatial scale of movement and dispersal of adult coho salmon encompasses large regions of freshwater through ocean migration and subsequent homing or straying to spawn (Labelle 1992, Li et al. 1995). The spatial extent of freshwater movement by juvenile coho salmon contrasts with adults. Juveniles occupy multiple habitat types in fresh water and may move among tributaries in their birth streams (Kahler et al. 2001, Bolton et al. 2002) but do not tend to move between large basins as adults may when they return to freshwater to spawn.

An assumption of this work is that adults define the distribution of populations of coho salmon both within stream systems and among stream basins. I will refer to adult coho salmon freshwater distribution as the *topology of dispersal*. The term dispersal implies movement and change while topology (Flitcroft 2007b) refers to the overall distribution of adults in the stream network. Another assumption is that juveniles do not move beyond their natal basin and the pattern of their distribution reflects local survivorship and the spawning location of their parents (Flitcroft 2007b). I will refer to the pattern of juvenile coho salmon freshwater stream use as the *topology of juvenile occupancy*. The term occupancy reflects the year of juvenile freshwater residence in the stream network.

Three spatial scales (site, subbasin, and basin) (Figure 4.1) were chosen for analysis and are meant to represent different resolutions of habitat and fish movement. The site scale is the smallest, and includes local habitat and the proximity among habitats in the stream network. The subbasin (5th-field Hydrologic Unit ranging in size between 11,179 and 33,225 hectares) represents a drainage network small enough to allow adults and juveniles to move within and among networks. The basin (4th-field Hydrologic Unit ranging in size between 33,787 and 291,746 hectares) represents a drainage network large enough to contain all

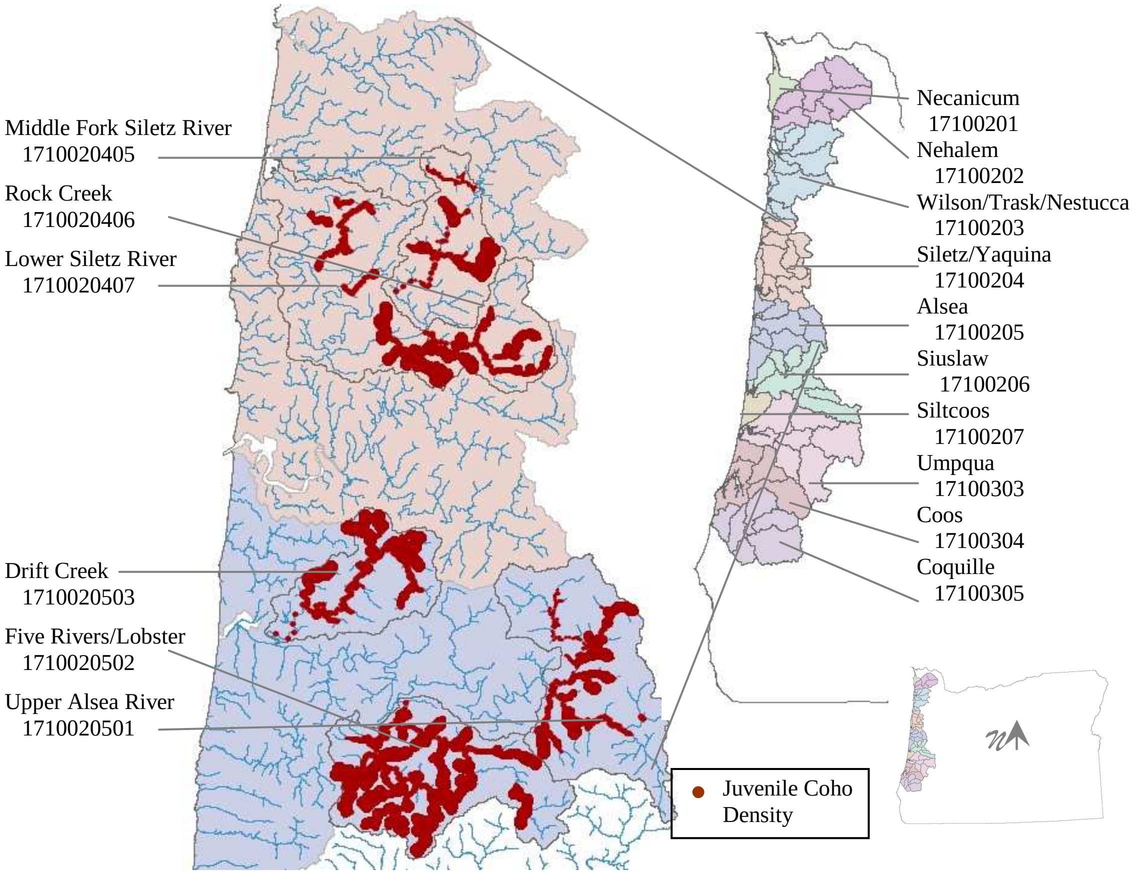
Figure 4.1. Three spatial scales used in hierarchical Bayesian analysis of adult and juvenile coho salmon. Basin and subbasin scales were used to hierarchically model adult coho salmon and subbasin and site scales were used to hierarchically model juveniles.



potential juvenile movement, while allowing adults to choose between basins when returning to spawn.

In this research, the usefulness of including multiple spatial scales in assessments of the abundance of the juvenile and adult life history stages of coho salmon was explored. First, I hypothesize that the spatial scales appropriate for understanding adult density are subbasins and basins. When the metapopulation organization of the fish (Cooper and Mangel 1999), the large scale of movement, and the fact that adult salmon are the colonizers and recolonizers of basins are considered (Labelle 1992), I speculate that the scale of the ecological process of adult coho salmon dispersal will be basins coupled with the moderate scale of the subbasin. I

Figure 4.2. Oregon’s coastal region encompassed the 5th field and 4th field hydrologic units used in a multi-scale hierarchical Bayesian analysis.



explored this hypothesis using datasets that encompass the ocean draining streams in coastal Oregon (Figure 4.2).

Secondly, I hypothesize that the spatial scales of sites and subbasins will be important in understanding juvenile density. This reflects the limited movement of individual juveniles in their year of freshwater occupancy (Bell 2001, Bramblett et al. 2002, Quinn and Peterson 1996). I explore this hypothesis in six subbasins of the Alsea (Upper Drift Creek, Five Rivers including Lobster Creek, and Upper Alsea River) and Siletz (Middle Fork Siletz and Lower Siletz River and Rock Creek) river systems in Oregon’s mid-coast region in which comprehensive survey information for juveniles was available (Figure 4.2).

Hierarchical Bayesian models that incorporated spatial variables at scales appropriate for local sites, subbasins and basins were used for analysis. A hierarchical Bayesian approach provided flexibility in the hierarchical structure of the models (Browne and Draper 2006, Carlin et al. 2006, Gelman et al. 2004). Hierarchical Bayesian methods have been used to explore a variety of ecological questions including monitoring of harbor seals over time (VerHoef and Frost 2003), the incorporation of spatial variation in population modeling (Gelfand et al. 2006), and modeling multi-scale relationships (Monlean et al. 2002). Use of hierarchical Bayesian models is rare in fish ecology literature possibly reflecting the novelty of incorporating multiple spatial scales in analysis. Two examples include Wyatt (2002) who used Bayesian hierarchical models to map fish populations in a river network and Harley and Myers (2001) who modeled trawl survey effectiveness. However, applications of other Bayesian methods such as the Kalman Filter are not uncommon in fish ecology (Lee 2000, Lee and Rieman 1997, Marcot et al. 2001).

Methods

Study Area

Coastal basins in Oregon were used in this study (Figure 4.2). Oregon’s coastal region is demarcated to the west by the Pacific Ocean and to the east by the Coast Range Mountains. The coastal region is characterized by a mild climate with precipitation heaviest in the winter months (Redmond and Taylor 1997). The geology of Oregon’s coast ranges from sedimentary to volcanic, with volcanic rock types found towards the north. Lowland areas are fertile for agriculture and coniferous forests are found throughout the region. Timber harvest and fishing are strong economic enterprises in coastal Oregon and are also culturally important (Lichatowich 1999).

Datasets and Variables

The exploration of multiple spatial scales requires the acquisition of data describing adult and juvenile run sizes, stream characteristics such as instream habitat and riparian vegetation, geology and rainfall. After a preliminary literature review, I identified six categories of stream characteristics as important: habitat structure, shape/sinuosity, network relationships, landscape conditions, lithology and rainfall. Within each category, variables were identified that represent each scale (Table 4.1). Datasets were compiled that contained the variables of interest (Table 4.2). Averaging variables over space is a distortion of information (Gotway and Young 2002). This consideration guided the selection of variables that were meant to accurately represent each scale. For example, a variable associated with the large spatial extent of a basin would need to characterize the entire area, compared to a variable at the small spatial extent of study site which would reflect local conditions such as the amount and type of substrates available at the site. This is particularly important when using remotely sensed data that is collected based on pixel sizes that may range from 1 meter to 100

Table 4.1. Variables that represent different spatial scale were used in multi-scale hierarchical Bayesian models of the adult and juvenile life history stages of coho salmon. *Variable was standardized ((X-(mean))/standard deviation).

Scale	Habitat Structure	Shape Sinuosity	Network Relationships	Landscape Condition	Lithology	Rainfall
Site	*No. pieces of wood	Slope	*Distance to spawning	---	Percent gravel	---
	*Boulder count		*Distance to rearing		Percent sand	
			*Distance to summer		Percent bedrock	
			*Stream order			
Subbasin (5th-Field HUC)	Percent lrg trees in 100-m riparian buffer	*Number of tribs	Percent subbasin km in high intrinsic potential class	Percent subbasin in conifer veg class	Percent sedimentary geology	*Mean annual precipitation
	Percent subbasin in valley class	*Area			Percent volcanic geology	
Basin (4th-Field HUC)	Percent lrg trees in 100-m riparian buffer	*Number of tribs	Percent basin km in high intrinsic potential class	Percent basin in conifer veg class	Percent sedimentary geology	*Mean annual precipitation
	Percent basin in valley class	*Area			Percent volcanic geology	

Table 4.2. Datasets that were assembled to derive variables that could be used to represent multiple spatial scales.

Dataset	Source	Available Area	Variables	How Data Were Collected
Spawning Salmon	Oregon Dept. of Fish and Wildlife Salmon Spawning Survey Program	Coastal Draining streams of Western Oregon.	adult spawning coho density	The sample sites were identified using a stratified random sample design (Jacobs and Nickelson 1998) and were used in the long term monitoring of trends in spawning populations in Western Oregon (Jacobs et al. 2000, Jacobs et al. 2001, Jacobs et al. 2002). Data collected at these sites included the number of coho redds and adults on the spawning grounds. Sample sites were revisited multiple times throughout the spawning season. The salmon counted are called naturally spawning adults (Jacobs et al. 2002).
Juvenile Snorkel Counts	Mid Coast Basin Council	Alsea River and Siletz River Basins	juvenile coho density	This dataset was a systematic sample of every fifth pool from the mouth of the river to the upper extent of juvenile coho distribution. The upper extent was determined as the point at which 5 consecutively sampled pools held no fish (Mills 2003). The entire stream network including tributaries bearing coho were surveyed and the data recorded.
Stream Lines	USDA Forest Service Coastal Landscape Analysis and Modeling Study	Coastal draining streams of Western Oregon from Astoria in the north to Cape Blanco in the south	active channel width, gradient, stream order, percent basin in valley classification, percent basin km in high intrinsic potential classification	Stream networks and geomorphic characteristics were modeled from 10 meter digital elevation models (DEM's) (Miller 2003). Supplemental information such as precipitation records were used to characterize water flow.
Vegetation	USDA Forest Service Coastal Landscape Analysis and Modeling Study	Coastal draining basins of Western Oregon from Astoria in the north to Cape Blanco in the south	percent basin in conifer vegetation class, percent large trees in 100m riparian buffer	This layer was created using a Gradient Nearest Neighbor method that integrated vegetation measurements from regional grids of field plots, mapped environmental data, and Landsat TM imagery (Ohmann and Gregory 1996).
Instream Habitat	Oregon Dept. of Fish and Wildlife Aquatic Inventories Project	Scattered streams throughout Oregon	percent gravel substrate in unit, percent sand substrate in unit, percent bedrock substrate in unit	Continuous instream habitat survey information was gathered by field crews that walked the entire stream from mouth to headwaters. The stream is broken down into habitat units such as pools, riffles and glides. Measurements such as water depth, substrate composition, boulder counts and wood were taken for each habitat unit (Moore et al. 1997).
Precipitation	PRISM group at Oregon State University - provided through the Oregon Climate Service	All of Oregon	mean annual precipitation for the basin	Rainfall records were compiled by the PRISM group at Oregon State University through the Oregon Climate Service. Rainfall records between 1971 and 2000 were used in an assessment process that incorporated spatial effects of rain shadows and coastal effects (Daly and Johnson 1998).
Geology	United States Geologic Service	All of Oregon	percent basin with sedimentary geology, percent basin with volcanic geology	Geology was digitized from the 1:500000 Oregon Geologic Map, which was created by the USGS.

meters in size. A large pixel size such as 100 meters will contain coarser information than the 1 meter pixel. Therefore, a 100 meter pixel may not be appropriate for site specific habitat characterization, but may be adequate for basin scale descriptions.

Juvenile coho salmon survey counts were conducted by the Mid-Coast Watershed Council. Every fifth pool was snorkeled and all fish were counted from the stream mouth to the headwaters, including all tributaries, during the summer of 2002 (June through September). A summer juvenile survey is meant to capture a snapshot of coho salmon distribution during the time of year when the fish are assumed to move the least (Nickelson et al. 1992). Density was calculated by dividing fish counts by the length of the pool unit, and was the measure used for modeling.

Information about spawning coho salmon came from the Oregon Department of Fish and Wildlife's (ODFW) Spawning Survey program for spawners in 2001 (spawning season of October 2001 through February 2002) and 2002 (spawning season of October 2002 through February 2003). Field survey crews repeatedly visited survey sites (selected using a spatially random design) in the study basins through the spawning season as part of the effort to monitor spawning coho salmon across the entire coast (Jacobs and Nickelson 1989, Jacobs et al. 2002). The salmon spawning survey sites were modified using a GIS with a protocol developed by researchers associated with the Environmental Protection Agency's STAR Grant program (R. Smith 2007 personal communication). This allowed for the interpolation of the spawning survey sites across the landscape using a grid of points (R. Smith 2007 personal communication). The final product was a landscape interpolation that displayed the estimated number of spawners across the entire coast for each year of spawning data. The mean number of spawners at the subbasin scale was used for modeling.

Instream fish habitat survey information came from the Oregon Department of Fish and Wildlife's Aquatic Inventories Program (ODFW-AIP). Field habitat survey crews walk from the stream mouth to the headwaters during the summer, taking measurements of the physical stream environment and identifying discrete habitat units such as pools, riffles and glides (Moore et al. 1997). Field surveys from 1997 through 2002 were pieced together to encompass the subbasins of interest for this study.

Geology classifications were acquired from a dataset created by the United States Geological Survey (USGS) that contained digitized geology information at a 1:500000 scale. Mean annual precipitation that incorporated the spatial effects of rain shadows and coastal influences was compiled by the PRISM (Parameter-elevation Regressions on Independent Slopes Model) group at Oregon State University through the Oregon Climate Service (Daly et al. 1999).

Stream linework and stream network characteristics were modeled by the Coastal Landscape Analysis and Modeling Study (CLAMS) based on 1:10 m digital elevation models (DEMs) (Miller 2003). Vegetation was also mapped by CLAMS based on aerial photographs and remotely sensed imagery (Ohmann and Gregory 2002).

As with any project that seeks to use datasets collected by different groups for different purposes, a significant challenge was identifying consistent and compatible data from different sources that could then be compiled for this study. I chose to develop a geographic information system (GIS) to produce spatially accurate map layers. First, I georeferenced ODFW habitat data and the juvenile snorkel survey counts to the stream linework generated by CLAMS. The dynamic segmentation protocol in ESRI's ArcInfo software was used to attach information to the linework (Tables 4.1 and 4.2).

At the scale of a site, the location of juvenile coho salmon snorkel surveys was used as the spatial base. Information was extracted from the ODFW habitat surveys and CLAMS stream layers using a 100-m buffer around each site. At the scales of subbasin and basin, variables of interest (i.e., geology, vegetation, precipitation) were calculated as the mean value over the area of interest. Riparian information was derived from the vegetation layer by buffering (100 m) fish bearing streams and calculating the percent of the buffer covered by large trees.

The number of observations varies at each spatial scale. At the site scale there were a total of 742 observations. At the subbasin scale there were 59 observations, and at the basin scale there were 10 observations. The number of observations for juvenile models exploring site and subbasin variation include 742 sites and 6 subbasins. The number of observations for adult models using subbasin and basin scales includes 59 subbasins and 10 basins (Table 4.3). All explanatory variables that were not a percentage were standardized in order to facilitate convergence of simulation models ((X-(mean))/standard deviation).

Table 4.3. The number of 5th field HUCs within 4th field HUCs and the number of sites sampled in each 5th field HUC.

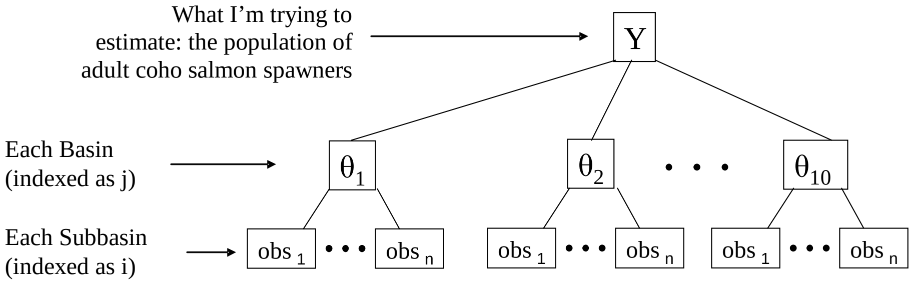
Adult Spawner Dataset			Juvenile Dataset		
4th Field HUC	HUC Area (hectares)	# of 5th Field HUC's	5th Field HUC	HUC Area (hectares)	Number of Sites
17100201	35426	1	1710020405	16763	123
17100202	221214	6	1710020406	11179	55
17100203	249861	9	1710020407	32415	178
17100204	196371	10	1710020501	33225	131
17100205	178566	7	1710020502	30903	85
17100206	200744	8	1710020503	17925	182
17100207	33787	1			
17100303	391746	7			
17100304	190672	4			
17100305	273714	6			

Bayesian Methods and Models

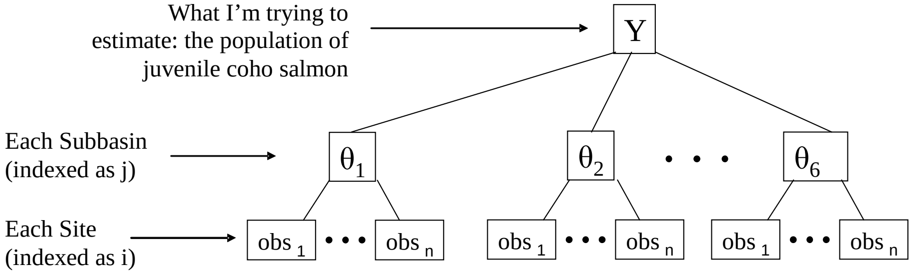
In my first hypothesis I propose that spatial scales appropriate for understanding adult coho salmon abundance are subbasin and basin. In my second hypothesis, I propose that the spatial scales appropriate for understanding juvenile coho salmon density are site and subbasin. The hypotheses for both juvenile and adult coho salmon explored the use of multiple spatial scales for analysis and description. In order to explore these hypothesis, I used Bayesian hierarchical modeling, which allows the use of information from each basin for adults, and each subbasin for juvenile coho salmon, without the restriction that effects or variation within basins or subbasins must remain constant. While frequentist models allow this as well, Bayesian methods are more intuitive and easier to interpret (Carlin et al. 2006).

Figure 4.3. Hierarchical Bayesian model structure for adult (a) and juvenile (b) coho salmon.

a. Structure of Hierarchical Model Describing Adult Spawner Abundance



b. Structure of Hierarchical Model Describing Juvenile Coho Density



In this application, the different levels of the Bayesian hierarchical models correspond with spatial scales of interest. Models for adult coho salmon include two hierarchical levels that correspond to subbasin and basin scales (Figure 4.3a). Models for juvenile coho salmon also include two hierarchical levels that correspond to site and subbasin scales (Figure 4.3b). Models were evaluated using the Bayesian Information Criterion (BIC), which captures the residual variance and a penalty term. The penalty term combines the number of parameters and the natural log of the number of samples, in an attempt to compensate for the ability of large sample sizes to identify statistically significant but unimportant coefficients (Ramsey and Schaefer 2002). By nesting the hierarchical structure of the models using spatial scale I hoped

Table 4.4. Bayesian hierarchical models for adult coho salmon on the Oregon coast. For each model, subbasin-scale variables that are hierarchically connected to basin-scale variables are listed next to one another in the table columns. The Bayesian Information Criterion or BIC value allows for a comparison of model effectiveness by capturing the residual variance and a penalty term. The model with the lowest BIC value is considered to be the best fitting model.

Model Number	Subbasin-scale Variables	Basin-scale Variables	BIC, 2001	BIC, 2002
1	Percent large trees in 100-m riparian buffer;	Percent basin in conifer vegetation class;	801.8	853.469
	Area;	Area;		
	Percent subbasin in high intrinsic potential;	---		
	Percent subbasin in sedimentary geology;	---		
	Percent subbasin in volcanic geology;	---		
	Mean annual precipitation	Percent basin in sedimentary geology		
2	Percent large trees in 100-m riparian buffer;	Percent basin in conifer vegetation class;	914.467	971.093
	Percent subbasin in valley classification;	Percent basin in conifer vegetation class;		
	Number of tributaries;	Area;		
	Area;	Area;		
	Percent subbasin in high intrinsic potential;	Percent basin in high intrinsic potential;		
	Percent subbasin in sedimentary geology;	---		
	Percent subbasin in volcanic geology;	---		
	Mean annual precipitation	Percent basin in sedimentary geology		
3	Percent subbasin in valley classification;	Area;	811.938	877.450
	Percent subbasin in high intrinsic potential;	Mean annual precipitation;		
	Percent subbasin in conifer vegetation class;	Percent basin in conifer vegetation class;		
	Percent subbasin in sedimentary geology;	Mean annual precipitation;		
	Mean annual precipitation;	---		
	Percent subbasin in volcanic geology	Mean annual precipitation		
4	Percent large trees in 100-m riparian buffer;	Mean annual precipitation;	716.114	771.228
	Percent subbasin in high intrinsic potential;	Mean annual precipitation;		
	Percent subbasin in sedimentary geology;	Percent basin in conifer vegetation class;		
	Percent subbasin in volcanic geology	---		

Table 4.4. Continued.

Model Number	Subbasin-scale Variables	Basin-scale Variables	BIC, 2001	BIC, 2002
5	Percent large trees in 100-m riparian buffer; Percent subbasin in high intrinsic potential	Mean annual precipitation; Percent basin in sedimentary geology	616.312	686.807
5b	Percent large trees in 100-m riparian buffer	Mean annual precipitation	603.107	637.881
6	Percent large trees in 100-m riparian buffer; Percent subbasin in sedimentary geology; Percent subbasin in volcanic geology	--- Mean annual precipitation; Mean annual precipitation	694.491	720.085
7	Percent large trees in 100-m riparian buffer; Percent subbasin in high intrinsic potential; Percent subbasin in sedimentary geology; Percent subbasin in volcanic geology	Percent basin in conifer vegetation class; Mean annual precipitation; Mean annual precipitation; Mean annual precipitation	726.729	785.104
8	Percent large trees in 100-m riparian buffer; Percent subbasin in high intrinsic potential; Percent subbasin in sedimentary geology	Percent basin in conifer vegetation class; --- Mean annual precipitation	649.651	719.133
9	Area; Percent large trees in 100-m riparian buffer; Percent subbasin in high intrinsic potential; Percent subbasin in conifer vegetation class	--- Percent basin in volcanic geology; Percent basin in conifer vegetation class; ---	703.840	757.154
10	Percent subbasin in high intrinsic potential; Mean annual precipitation	Percent basin in sedimentary geology; Area	677.200	700.701
11	Percent subbasin in high intrinsic potential; Percent subbasin in conifer vegetation class; Percent subbasin in sedimentary geology; Number of tributaries	Mean annual precipitation; Percent basin in high intrinsic potential; Mean annual precipitation; ---	734.423	764.998

Table 4.4. Continued.

Model Number	Subbasin-scale Variables	Basin-scale Variables	BIC, 2001	BIC, 2002
12	Area;	---	746.984	793.538
	Percent large trees in 100-m riparian buffer;	Percent basin in valley classification;		
	Percent subbasin in conifer vegetation class;	Percent basin in high intrinsic potential;		
	Percent subbasin in sedimentary geology;	---		
	Percent subbasin in volcanic geology	---		
13	Percent large trees in 100-m riparian buffer;	Mean annual precipitation;	611.470	694.305
	Percent subbasin in valley classification	Percent basin in high intrinsic potential		
14	Percent large trees in 100-m riparian buffer;	Percent basin in sedimentary geology;	656.638	689.220
	Mean annual precipitation	Area		
14b	Percent large trees in 100-m riparian buffer;	---	644.078	674.628
	Mean annual precipitation	Area		
15	Percent subbasin in high intrinsic potential;	Percent basin in conifer vegetation class;	736.767	796.897
	Mean annual precipitation;	Area;		
	Percent subbasin in valley classification;	Mean annual precipitation;		
	Number of tributaries	Percent basin in valley classification		
16	Percent large trees in 100-m riparian buffer;	Percent basin in sedimentary geology;	805.234	828.679
	Number of tributaries;	Percent basin in valley classification;		
	Percent subbasin in sedimentary geology;	Mean annual precipitation;		
	Percent subbasin in volcanic geology;	Mean annual precipitation;		
	Mean annual precipitation	Number of tributaries		

Table 4.5. Bayesian hierarchical models for juvenile coho salmon in subbasins of Oregon’s mid-coast. For each model, site-scale variables that are hierarchically connected to subbasin-scale variables and are listed next to one another in the table columns. The Bayesian Information Criterion or BIC value allows for a comparison of model effectiveness by capturing the residual variance and a penalty term. The model with the lowest BIC value is considered to be the best fitting model.

Model Number	Site-scale Variables	Subbasin-scale Variables	BIC, 2002
1	Wood count;	Percent subbasin in valley classification;	3036.45
	Network distance to spawning habitat;	Percent subbasin in valley classification;	
	Network distance to rearing habitat;	Number of tributaries;	
	Network distance to summer habitat;	Percent subbasin in high intrinsic potential;	
	Slope;	Percent subbasin in sedimentary geology;	
	Percent sand in habitat unit;	Percent subbasin in sedimentary geology;	
	Percent gravel in habitat unit;	Percent subbasin in sedimentary geology;	
	Percent bedrock in habitat unit;	Percent subbasin in volcanic geology;	
	Boulder count	Percent subbasin in volcanic geology	
2	Wood count;	Percent subbasin in conifer vegetation class;	2635.68
	Network distance to rearing habitat	Number of tributaries	
3	Slope;	Percent subbasin in valley classification;	2678.59
	Network distance to rearing habitat;	Number of tributaries;	
	Percent gravel in habitat unit	Percent large trees in 100-m riparian buffer	
4	Wood count;	Percent large trees in 100-m riparian buffer;	2802.46
	Slope;	Percent subbasin in valley classification;	
	Stream order;	Number of tributaries;	
	Network distance to rearing habitat;	Percent subbasin in high intrinsic potential;	
	Percent bedrock in habitat unit	Percent subbasin in volcanic geology	
5	Network distance to spawning habitat;	Percent subbasin in valley classification;	2790.70
	Network distance to rearing habitat;	Number of tributaries;	
	Network distance to summer habitat;	Percent subbasin in high intrinsic potential;	
	Stream order;	Number of tributaries;	
	Slope	Percent of subbasin in high intrinsic potential	

Table 4.5. Continued.

Model Number	Site-scale Variables	Subbasin-scale Variables	BIC, 2002
6	Wood count; Boulder count; Slope; Percent sand in habitat unit; Percent gravel in habitat unit	Percent large trees in 100-m riparian buffer; Percent subbasin in sedimentary geology; Percent subbasin in sedimentary geology; Percent subbasin in sedimentary geology; Percent subbasin in sedimentary geology	2814.73
7	Wood count; Network distance to rearing habitat	Percent large trees in 100-m riparian buffer; Number of tributaries	2639.28
8	Stream order; Network distance to spawning habitat; Percent gravel in habitat unit	Number of tributaries; Percent subbasin in sedimentary geology; Percent subbasin in valley classification	2671.80
9	Percent sand in habitat unit; Stream order; Network distance to spawning habitat	Percent subbasin in sedimentary geology + percent subbasin in volcanic geology; --- ---	2616.09
9b	Percent sand in habitat unit; Stream order; Network distance to spawning habitat	Percent subbasin in sedimentary geology; --- ---	2609.42
9c	Percent sand in habitat unit; Stream order; Network distance to spawning habitat	--- --- ---	2581.41
10	Slope; Network distance to spawning habitat; Stream order	Percent subbasin in valley classification; Percent subbasin in high intrinsic potential; Number of tributaries	2669.43

to control for spatial autocorrelation (Gelfand et al. 2006).

The program WinBugs 1.4 (Spiegelhalter et al. 2003) was used to fit the Bayesian models. Unlike modeling software available for frequentist statistics, WinBugs requires that each model be written and run individually because there is no automated stepwise procedure available. A small group of biologically meaningful models were written and run; sixteen models of adults in 2001 and 2002 and ten models of juveniles for 2002 (Table 4.4 and Table 4.5 respectively). Further models were written and run by refining models with the lowest BIC by reducing variables. The parameters selected for reduction were chosen because they had limited utility in estimating the mean of spawner abundance or juvenile density. The usefulness of a variable was determined by examining the parameter's estimate and posterior interval. Posterior intervals that include zero imply that the variable may not be useful.

By assuming that the response variables of juvenile density or adult spawner abundance follow normal distributions, I fit Bayesian hierarchical models with normal likelihood and either normal or non-informative priors. I am assuming that the ecological data fits a normal` distribution. For some variables I chose to use non-informative priors – a conservative choice because I am not familiar with other studies that could give guidance to the choice of prior values. As an example, I present adult spawner model number 5b (Table 4.4).

Example: Adult Spawner Model Number 5b. Let j = 1, 2,…., 10 index the 10 basins of the Oregon coast in which this model pertains. Let i = 1,….,n_j index the number of subbasins present in each basin j.

$Y_{ij} \sim N(\theta_{ij}, 1/\sigma^2_j)$

$\theta_{ij} = B_{0j} + B1_j(\text{\% large trees in riparian zone})_{ij}$ *Subbasin Level

$B_{0j} \sim \text{Normal}(0, 0.001)$

$B_{1j} \sim \text{Normal}(\mu_{1j}, 1/\sigma^2)$

$\mu_{1j} = B_2 + B_3(\text{mean annual precipitation})_j$ *Basin Level

$1/\sigma^2_j = \text{gamma}(0.01, 0.01)$

$1/\sigma^2 = \text{gamma}(0.01, 0.01)$

In this model, I am seeking to identify Y_{ij} (the abundance of adult spawners based on subbasin i in basin j) conditional on θ_{ij} with a precision of $1/\sigma^2_j$. The θ_{ij} are conditionally independent and drawn from some population of θ. In this model, θ_{ij} is a linear function of the percent large conifers in the riparian zone of the subbasin. The average slope of this relationship is a linear function of the mean annual precipitation at the basin level.

Results

Adults

Based on BIC values, three of the top four models for adults in 2001 and 2002 were the same (Table 4.6). These three models (numbers 5, 13, and 14) were selected for further assessment. In model number 5, one of the sets of parameters was removed

Table 4.6. Bayesian Information Criterion (BIC) results for adult coho salmon models from 2001 and 2002. BIC allows for a comparison of model effectiveness by capturing the residual variance and a penalty term. The model with the lowest BIC value is considered to be the best fitting model. Models 5b and 14b were created by altering the set of variables in models 5 and 14 respectively.

	Year	
Model Number	2001	2002
1	801.80	853.47
2	914.67	971.09
3	811.94	877.45
4	716.11	771.23
5	616.31	686.81
5b	603.11	637.88
6	694.49	720.09
7	726.73	785.10
8	649.65	719.13
9	703.84	757.15
10	677.20	700.06
11	734.42	700.70
12	746.98	793.54
13	611.47	694.31
14	656.64	689.22
14b	644.08	674.63
15	736.47	796.90
16	805.23	828.68

(percent subbasin in high intrinsic potential at the subbasin scale connected with percent basin in sedimentary geology at the basin scale). The resulting model (5b) had the lowest BIC for 2001 and 2002 among all models evaluated and included the subbasin variable, percent large trees in the 100-m riparian buffer, connected with mean annual precipitation at the basin scale. Model number 13 was not altered because alteration would have led to a model the same as 5b. Model 14 was modified by removing the basin scale parameter percent basin in sedimentary geology. This resulted in a model with a lower BIC than the original model, but still higher than 5b (Table 4.6).

Aside from the identification of models with low BIC, another result may be gleaned from an evaluation of the entire group of adult models. Parameters that were important in the explanation of the dependent variable are assessed by examining the 95% posterior interval for the coefficient. If this interval contains zero it suggests that the parameter is not useful. In the adult hierarchical models, meaningful parameters that describe basin level variation were uncommon. However, in the models where basin level variables meaningfully contributed to the model, the same combination of variables was visible (Table 4.7). Mean annual precipitation and the number of tributaries at the basin scale seemed to be connected with the geology and percent of conifers in the riparian zone. These relationships appeared to be important in modeling the mean adult spawning run at the subbasin scale. I also note that these sets of variables are present in the models that were identified as best using BIC values. However, in isolation in models 5, 5b, 13, 14, and 14b, the relationships were not strongly meaningful. This could reflect the lack of interaction between these variables and the variables present in the other models.

Table 4.7. Important combinations of variables from Bayesian hierarchical models of the mean of adult coho salmon at a subbasin scale.

		Median Estimate and 95% Posterior Interval	
Model Number	Parameters	2001	2002
6	intercept for mean annual precipitation (basin scale) and percent large trees in riparian buffer zone (subbasin scale)	0.31 (0.02 - 0.62)	0.44 (0.12 -0.79)
7	intercept for mean annual precipitation (basin scale) and percent sedimentary geology (subbasin scale)		0.58 (0.18 - 1.02)
8	intercept for mean annual precipitation (basin scale) and percent sedimentary geology (subbasin scale)		0.48 (0.02 - 0.92)
13	intercept for mean annual precipitation (basin scale) and percent large trees in riparian buffer zone (subbasin scale)		1.91 (0.21 - 4.47)
16	intercept for mean annual precipitation (basin scale) and percent sedimentary geology (subbasin scale)	0.37 (0.09 - 0.77)	0.56 (0.24 - 0.88)
16	coefficient for number of tribs (basin scale) and mean annual precipitation (subbasin scale)		14.67 (0.52 - 28.99)

Juveniles

A comparison of BIC values from initial modeling efforts for juvenile coho salmon identified model 9 as the best (Table 4.8). In an attempt to improve this model, parameters in the prior probability for the subbasin scale were successively dropped and replaced with non-informative priors. In model 9b, percent subbasin in volcanic

Table 4.8. Bayesian Information Criterion (BIC) results for juvenile coho salmon models from 2002. BIC allows for a comparison of model effectiveness by capturing the residual variance and a penalty term. The model with the lowest BIC value is considered to be the best fitting model. Models 9b and 9c were created by altering variables in model 9.

Model Number	BIC Results
1	3036.45
2	2635.68
3	2679.59
4	2802.46
5	2790.70
6	2814.73
7	2639.28
8	2671.80
9	2616.09
9b	2609.42
9c	2581.41
10	2669.43

geology was dropped and in model 9c percent subbasin in sedimentary geology was dropped. Subbasin-scale variables were chosen because of the simplicity of the original model, and because there was no clear indication through the assessment of the parameter coefficients that the specific subbasin variables contributed to the explanatory power of the model. The replacement of the subbasin scale variables with non-informative priors reduced the number of estimated parameters in the model, and model 9c resulted in the lowest BIC value.

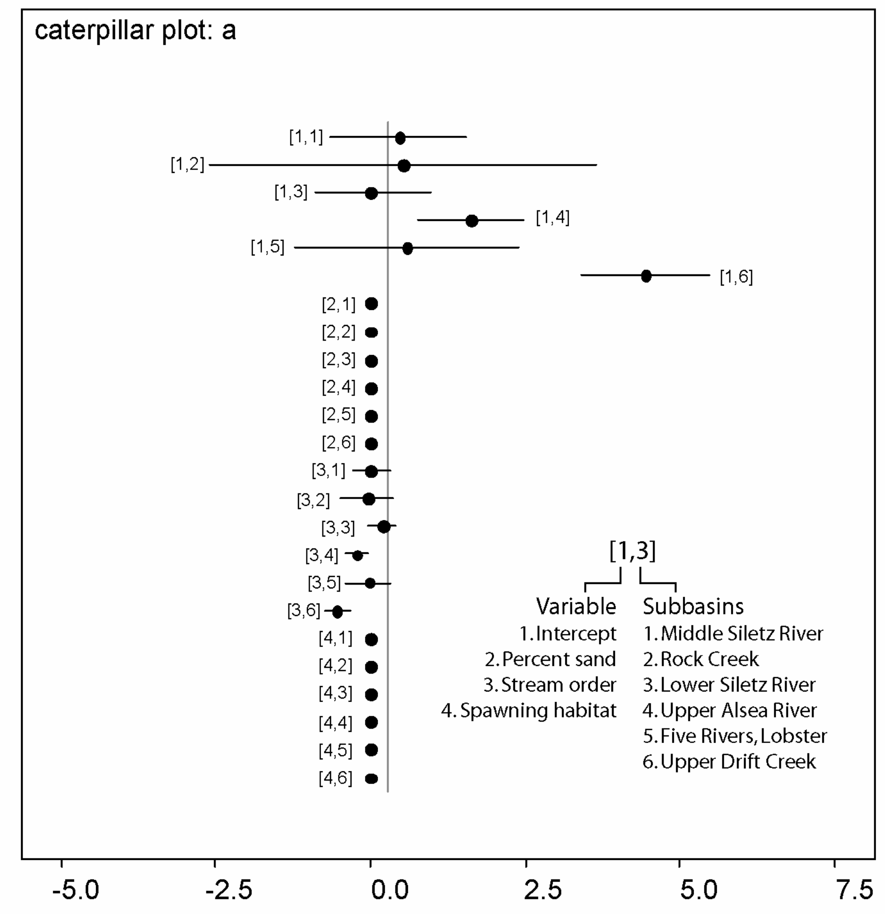
As with the adult models, I looked for meaningful parameters that did not include 0 in their posterior interval. In none of the juvenile models were subbasin level parameters identified (meaning, all 95% posterior intervals for subbasin variables contained zero). However, the presence of the subbasin level, and therefore a hierarchical approach, was still important in the organization of the information as reflected by variation of the intercept parameter between subbasins. This variation is visible in “caterpillar plots” that display the estimated values and the 95% posterior intervals for all variables in a model (Figure 4.4 from juvenile model #9c). Therefore, including the subbasin scale using non-informative priors is appropriate until a more specific relationship and variable is identified.

Discussion

The juvenile and adult life history stages of coho salmon have different habitat needs and levels of mobility that may be conducive to separate analyses. Also, because of life history differences, an exploration of different spatial scales for each stage may be a biologically meaningful approach. Hierarchical Bayesian modeling provided a method through which to explore relationships between variables at different spatial scales. This approach affirmed the usefulness of subbasin and basin scales for modeling adult coho salmon, and sites and subbasin scales for modeling juvenile coho salmon.

The first hypothesis explored in this paper focused on adult coho salmon. I hypothesized that the spatial levels of organization relevant for assessments of the abundance of adult coho salmon spawners were the subbasin and basin scales. Studies documenting the importance of subbasin scale clumping of spawning adults (Neville et al. 2006) and larger scale metapopulation level patterns analogous to the basin scale (Cooper and Mangel 1999) provide context for interpreting the results of this study.

Figure 4.4. The caterpillar plot for juvenile coho salmon model #9c displays the posterior estimate and 95% interval for each parameter in the model. These intervals may be interpreted by examining their overlap and whether they include 0. Intervals that include 0 are not considered to significantly contribute to the model result. Intervals that do not overlap display the importance of modeling including the hierarchical scale of division. This allows variability to be different with different parameters rather than needing to be shared throughout the dataset.



The hierarchical model results lend support to the idea that multiple levels of organization are reflected in the abundance of adult coho salmon. Evidence for this may be found in the recurring importance of two large-scale variables (percent large trees in 100-m riparian buffer and mean annual precipitation) in describing adult spawner abundance in several models over two years (Table 4.7) and their presence in the model with the lowest BIC (Table 4.4) in both 2001 and 2002. Riparian trees at a subbasin scale were identified as important. The large scale of a subbasin does not allow for an assessment of the spatial relationship between spawning habitats, instream wood, and source trees. However, riparian trees have been tied to in-channel wood (Beechie and Sibley 1997), which is known to accumulate gravels (Bilby and Ward 1989) necessary for spawning (Hall and Baker 1982) and the formation of pool habitats (Montgomery et al. 1995). Precipitation has long been recognized as an important physical cue for adults to migrate upstream to spawn (Allen 1959). Further, mean precipitation in a basin may also be a surrogate value describing local climate which will effect vegetation, and ultimately, the number and size of riparian trees. Therefore, the significance of riparian trees and precipitation variables in models of adult spawning abundance are consistent with the biological needs of adult coho salmon.

Developing and selecting a model with a low BIC is useful, but it is also important to consider the context for this model that is evident from assessments of all other models. As previously mentioned, mean annual precipitation (basin scale) and percent of trees in the riparian buffer (subbasin scale) appeared as important descriptors of the mean of adult spawners. Other variables that appeared to be important in other models include percent sedimentary geology (subbasin scale) paired with mean annual precipitation (basin scale) and the number of tributaries (basin scale) also paired with mean annual precipitation, this time at the subbasin scale (Table 4.7). The variable mean annual precipitation was almost always the basin scale variable in the set of important variables. This consistency at the basin scale indicates greater stability of adult abundance at the basin scale with more variation at the subbasin scale.

The Bayesian hierarchical analysis used in this research confirms that the scales of subbasin and basin work together in describing conditions conducive to adult coho occupancy. Therefore, topology of dispersal by adults may best be described by a combination of large and moderate spatial scales that are analogous to population level dispersal. This conclusion provides a framework of multiple large spatial scales for the exploration of questions regarding persistence and habitat use by adult coho salmon.

Large spatial scales of adult coho salmon may well be connected with large scale environmental processes, such as disturbance, that effect survival of individuals, and ultimately the entire population of salmon. Disturbance will make some subbasins more or less hospitable to populations of salmon over time. The adult behavior that facilitates the consistent occupancy of available habitats is the propensity of a small portion of the adult population to stray (Labelle 1992, Nickelson 1998). Straying generally describes the behavior of adults that do not return to their natal streams to spawn. Adults that stray may return to a different part of their natal basin, or to an entirely different stream system to spawn, thereby allowing for the recolonization of new or recovering habitats and the movement of genetic material among subpopulations of fish. Future analysis that directly explores large scale environmental conditions with behavioral diversity of adult coho salmon may be useful in understanding population level persistence of this species.

A foundation for further research of ecological processes and spatial scale was set in this project by identifying spatial scales that are useful for exploring the adult life history stage of coho salmon. The analysis of adult distribution included only two years of data and future work that includes more years that span a variety of environmental conditions, such as major flooding, drought, or large scale disturbances would be worthwhile. Such temporal analysis would strengthen studies over large regions and might include changes in basin-level productivity in response to large-scale disturbance events. Another hierarchical analysis of adults would benefit from the incorporation of a site-specific scale because fine-scale habitat variation has been shown to be important in the selection of spawning sites (Neville et al. 2006).

The second hypothesis explored in this paper identified site and subbasin scales for assessments of densities of juvenile coho salmon. Juvenile coho must find all the habitats necessary for them to survive for a year in freshwater before migrating to the ocean as smolts. Habitat needs for juvenile coho salmon change seasonally (Groot and Margolis 1991, Quinn and Peterson 1996). Mainstem pools are important in the summer, while off-channel and slow water habitats are significant in the winter (Nickelson et al. 1992). Therefore, local habitat conditions appear to be ecologically significant for juvenile fish and this was confirmed by the selected Bayesian model. The model with the lowest BIC incorporated local variation without specifying relationships to higher levels of spatial organization. The three variables in this model were percent sand, stream order, and the network distance to spawning habitat. The amount of fines, including sand, in a pool is important for juvenile survival. High percentages of fines decrease salmonid survival and growth in the first year by shifting the food web towards taxa that are not prey food for juvenile salmon (Suttle et al. 2004). Stream order is a useful georeferencing metric because it places the pool within the context of the stream system. For example, in Oregon’s coast range, a pool that is located in a first order stream is generally small with areas of high gradient. By contrast, a pool in a third order stream may be wider and have lower gradients than the first order stream, and is also downstream of several other smaller tributaries that may deliver food or other nutrients to the pool through drift (Vannote et al. 1980). Typically, juvenile coho will have higher densities in lower-order stream reaches than in higher order stream reaches (Rosenfeld et al. 2000). The network distance to spawning habitat is one of the juxtaposition variables that references the pool to another necessary habitat. Flitcroft (2007b) identified juxtaposition variables as possibly important when exploring differences in juvenile densities among subbasins over time, with subbasins with large distances between seasonal habitats having lower densities compared to basins with short distances. It is interesting to note that the site-level variables in the juvenile model with the lowest BIC included both substrate and network juxtaposition metrics. The importance of these variables is mirrored by the results described in Flitcroft (2007b) in which juvenile coho salmon were best modeled with a combination of instream and network variables. The identification of similar variables in a Bayesian modeling approach confirms the importance of both substrate and network juxtaposition variables for describing juvenile density. The combination of these metrics is ecologically informative because they capture the local environmental conditions that the juvenile fish are responding to.

While the inclusion of subbasin variables was not part of the lowest BIC model of the density of juvenile coho salmon, examining the caterpillar plot of the parameter estimates from this model indicates that variation present at the intercept of the model varies by subbasin. It would be useful to continue exploring variables that represent subbasin variation because I have clearly not identified the most important elements of variation at the subbasin scale. The juvenile analysis would also be enhanced by the assessment of more years of data, which would help address the responsiveness of juveniles to changes in larger scale environmental conditions over time.

The juvenile modeling results support my assumption that the juxtaposition of seasonal habitats and local habitat conditions are reflected by the topology of juvenile occupancy. Further exploration of multiple years of juvenile site and subbasin variables need to be incorporated in additional research to properly explore the interplay between ecological processes and spatial scale that juvenile coho salmon are responding to. What was surprising in this analysis was the lack of clear identification of any subbasin scale variables in determining juvenile density. Beechie et al. (1994) identified the larger scale variable of land use as an important consideration in habitat loss that reduced coho salmon smolt output in the Skagit River. Land use was not a variable that was incorporated into this study, but is clearly an important descriptor of large scale environmental conditions for coho salmon. It is also possible that the way that I structured the hierarchical models in this project did not capture the synergism among scales that is important for juvenile coho salmon. More work exploring specific variables at larger spatial scales needs to be done to better understand the interaction between spatial scales on the abundance of juvenile coho.

Conclusion

A hierarchical modeling approach provided a framework to explore the complexity of spatial scales for juvenile and adult coho salmon. The adult and juvenile life history stages of coho salmon have different levels of mobility and drives. These differences helped define the spatial scales that were used to analyze these two life history stages. Considering the context of spatial scale and stream network connectivity allowed ecologically meaningful interpretations of the results. It is evident that the interplay of spatial scales is different for adult than for juvenile coho salmon. Juvenile coho salmon appear to respond to local variation within the frame of larger subbasin variation, while adult coho salmon are connected to subbasin and basin variation and variables.

In this study, different life history stages were analyzed at different scales which were intended to reflect population level persistence strategies and the difference in mobility and habitat needs between life history stages. Management that seeks to restore, protect or enhance coho salmon populations must consider the implications of scale and life history stage. In order to maintain the capacity of coho salmon as a whole to survive, the ability of the different life history stages to remain present and vital in the population must be maintained. Considering the spatial scale and extent occupied by each life history stage is a platform for determining the needs of the fish. Juveniles need great diversity of habitats in close proximity to one another, while adults need access to a variety of spawning sites within and among basins. Therefore, management that does not consider each life history stage individually, and together, may not adequately meet the survival needs of populations of coho salmon.

Pacific salmon are adapted to survive in the dynamic stream environment of the Pacific Northwest (Reeves et al. 1995). Ecological and physiological processes may impact salmon at different spatial scales. Joint consideration of population needs and ecological processes through multiple spatial scales makes tenable the management question of how population persistence will be achieved in a continuously changing environment.

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Chapter 5

How Important are Network Considerations Anyway?

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Summary and Conclusions

Stream ecology is a relatively new science, so understandably, the theoretical underpinnings continue to evolve. The research described in this dissertation started as an investigation of the implications of stream network structure on the abundance and distribution of juvenile coho salmon (*Oncorhynchus kisutch*) and evolved into the development of variables and theory that include stream network relationships. The dissertation is primarily focused on three key goals: the development and application of a theoretical base for analyzing aquatic obligate species that incorporates the underlying structure of the stream network; exploring the importance of stream network variables using multiple spatial scales in an assessment of juvenile coho salmon density; incorporating multiple spatial scales into hierarchical Bayesian models for the adult and juvenile life history stage of coho salmon. The results of this research point to further work, and also identify new ways of interpreting and exploring patterns in the river landscape.

Chapter 2 begins with a discussion of the place of stream networks in ecological theory and the current lack of a stream network base from which to interpret and expand on theory describing the movement of aquatic obligate species. I propose and develop a dynamic network topology as a framework for study design, analysis, and interpretation. The dynamic network topology includes the idea that habitats change over time in response to disturbance events or stream flows and native aquatic species are adapted to these habitat reconfigurations. The concept of dynamic network topology moves beyond static predictions of aquatic communities (Vannote et al. 1980) and integrates the consideration of hierarchical processes (Frissell et al. 1986) into a dynamic stream network (Benda et al. 1998, Poff et al. 1997).

In Chapter 3, I explore the importance of a stream network context with an analysis of ecological processes affecting juvenile coho salmon at three spatial scales (site, patch, and subbasin). Multiple spatial scales have been identified as important when exploring distributions (Schlosser 1995) and productivity (Poff and Huryn 1998) of fishes. In the site scale analysis, a combination of both network and instream metrics are found to be important in understanding the patterns of distribution of juvenile coho salmon. Further, the network juxtaposition variables that describe the proximity between habitats that are important seasonally for juvenile coho salmon appear to differentiate between subbasins that have increasing or decreasing juvenile densities between years. The proximity between seasonal habitats has been identified as important for Chinook (*O. tshawytscha*) (Isaak and Thurow 2006) and other fishes (Jones et al. 2003). At the scale of a patch of juvenile coho salmon, it appears that larger subbasins may have a nested spatial structure in the distribution of juvenile coho salmon. This nested structure could be associated with larger quantities of habitats that might be found in larger stream networks or could reflect an overlapping distribution of smaller patches of juveniles. The subbasin scale analysis pointed to the importance of the adult spawning run size in connection to the number of stream km occupied by juvenile coho. In years of low adult run size, the stream km occupied by juveniles was lower than in years of higher run sizes. It is possible that adults that spawn lower in the stream system in years of low abundance are not occupying spawning habitats in the closest proximity to the seasonal habitats necessary for their progeny. This introduces some interesting questions about how adults distribute themselves at spawning and what effect that may have on the survival of their young.

Bayesian hierarchical methods are used in Chapter 4 to structure models that are meant to represent two spatial scales in analysis of the abundance of adult and juvenile coho salmon. Multiple spatial scales allow for the interaction between ecological processes that may occur in nature. Subbasin and basin scales are hierarchically organized to explore adult coho salmon abundance. These large spatial scales were chosen for adults based on the mobility of adults, and because adults define the distribution of coho salmon through homing and straying behavior during the spawning season. The hierarchical model that best fitted the adult data identified the variables: percent of large trees in the riparian buffer at the subbasin scale modeled with mean annual precipitation at the basin scale. These variables are ecologically important for adult coho salmon and are associated with processes of habitat creation (Bilby and Ward 1989, Benda et al. 2004). Sites and subbasins are used for juvenile coho salmon hierarchical models. These smaller spatial scales are used for juveniles to reflect their need to find seasonal habitats for a year of freshwater occupancy in their natal stream network. Juveniles may move around within their natal stream system (Kahler et al. 2001, Nielsen 1992), but they do not cross salt water in search of alternate basins and habitats. This may mean that local scales best reflect the movement and needs of juvenile coho salmon. The hierarchical model that best fitted the juvenile data identified a set of site level variables connected with non-informative subbasin priors. The site scale variables were: percent sand, stream order, and the network distance to spawning habitat. These three variables capture local instream condition and the network proximity of an important seasonal habitat.

The combination of a network perspective and multiple spatial scales of analysis are a consistent theme in Chapters 2, 3, and 4 of this dissertation. This theme was intended to create a framework that may better represent the impact of stream processes on coho salmon abundance and distribution. The results of the investigations in each chapter of this dissertation support one another and confirm the usefulness of a network perspective that incorporates multiple spatial scales. The variables selected in the best fitting hierarchical Bayesian model, in Chapter 4, for juvenile coho salmon closely resemble the conclusions of the site scale investigation in Chapter 3 that both instream and network variables are important local descriptors of coho occupancy and abundance. These interpretations confirm the premise of Chapter 2 that considerations of aquatic species and ecological processes within a stream network framework is a useful way to approach analysis. Further, the use of multiple spatial scales was useful in Chapter 3 for the interpretation of results and in Chapter 4 as the model structure itself. The combination of a stream network perspective at multiple scales resulted in novel applications of statistical method and ecological interpretation.

Throughout this dissertation, the structure of the stream as an interconnected network guided ecological interpretation, statistical approaches, and study design. The contribution of this work for ecological investigation is two-fold. First, the focus on integrating a stream network framework into considerations of aquatic life history stages at multiple spatial scales is novel and proved useful. Second, using analytic approaches that incorporate network structure is unusual and may be useful for other investigations of aquatic species. The ultimate goal for any ecological investigation is to contribute to the body of work that describes the natural world in a meaningful and thoughtful manner. It is in this vein that the work of this dissertation has been undertaken.

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